Comparative biomass structure and estimated carbon flow in food webs in the deep Gulf of Mexico

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ABSTRACT

A budget of the standing stocks and cycling of organic carbon associated with the sea floor has been generated for seven sites across a 3-km depth gradient in the NE Gulf of Mexico, based on a series of reports by co-authors on specific biotic groups or processes. The standing stocks measured at each site were bacteria, Foraminifera, metazoan meiofauna, macrofauna, invertebrate megafauna, and demersal fishes. Sediment community oxygen consumption (SCOC) by the sediment-dwelling organisms was measured at each site using a remotely deployed benthic lander, profiles of oxygen concentration in the sediment pore water of recovered cores and ship-board core incubations. The long-term incorporation and burial of organic carbon into the sediments has been estimated using profiles of a combination of stable and radiocarbon isotopes. The total stock estimates, carbon burial, and the SCOC allowed estimates of living and detrital carbon residence time within the sediments, illustrating that the total biota turns over on time scales of months on the upper continental slope but this is extended to years on the abyssal plain at 3.6 km depth. The detrital carbon turnover is many times longer, however, over the same depths. A composite carbon budget illustrates that total carbon biomass and associated fluxes declined precipitously with increasing depth. Imbalances in the carbon budgets suggest that organic detritus is exported from the upper continental slope to greater depths offshore.

The respiration of each individual "size" or functional group within the community has been estimated from allometric models, supplemented by direct measurements in the laboratory. The respiration and standing stocks were incorporated into budgets of carbon flow through and between the different size groups in hypothetical food webs. The decline in stocks and respiration with depth were more abrupt in the larger forms (fishes and megafauna), resulting in an increase in the relative predominance of smaller sizes (bacteria and meiofauna) at depth. Rates and stocks in the deep northern GoM appeared to be comparable to other continental margins where similar comparisons have been made.

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1. Introduction

The food webs on and associated with the deep-sea floor are assumed to be dependent on a slow rain of detrital particles (particulate organic carbon or POC) from the overlying water column (Agassiz, 1888; Rowe and Gardner, 1979; Lampitt, 1985; Honjo and Manganini, 1993; Lampitt et al., 1995, 2000), supplemented by the occasional fall of a large carcass (Rowe and Staresinic, 1978; Smith, 1985; Smith et al., 1998), lateral input from continental margins (Anderson et al., 1994; Rowe et al., 1994; Jahnke, 2001), geographically isolated seeps of deeply buried hydrocarbons (Paull et al., 1984; Brooks et al., 1987; MacDonald et al., 1989), or flows of sulfide-rich hydrothermal fluids (Van Dover, 2000; Tunnicliffe et al., 2003). The decline in the

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supply of organic matter (OM) is presumed to be rapid, based on the logarithmic decline of biomass (Rowe, 1983), total community oxygen consumption (SCOC) (Smith, 1978a, b; Smith and Hinga, 1983; Archer and Devol, 1992; Rowe et al., 1994; Duineveld et al., 1997; Heip et al., 2001; Seiter et al., 2005), and direct measures of POC accumulation (Biscaye and Anderson, 1994; van Weering et al., 2001) across continental margins.

The bioenergetics of deep-ocean sediment communities are seemingly simplified because the principal supplies of carbon and energy originate outside and separate from the benthic boundary layer (Smith et al., 2001). However, gaining accurate understanding of how these communities cycle OM is complicated by the combination of low biological rates and the remoteness of the habitat. The present study was no exception. However, this effort utilized a team of investigators, each concentrating on different biological groups, at the same diverse sites, thus providing a rare opportunity to consolidate all the standing stock information from all benthic biological components into a single, internally comparable analysis. The group's strategy was to select a limited number of locations where the community composition and structure was markedly different, rather than comparing sites along a single depth gradient.

2. Methods

2.1. Experimental design and sampling site selection

Designing a tractable sampling program to investigate both community function and structure required that the study be conducted in two phases. The first was a survey of the distribution of the entire biota, conducted during May and June 2000 (Fig. 1). In June 2001, four contrasting locations were selected from the preliminary results of the survey. Sites MT3 (and later MT1) and S36 were chosen because of high densities of organisms at shallow (upper continental slope in the Mississippi Canyon) and deep locations (deep continental slope in the DeSoto Canyon),

respectively, and sites S42 and MT6 were chosen because they represented sites with low densities of organisms at shallow and deep locations. The following year (2002), the study was extended south into the Mexican Exclusive Economic Zone to five sites on the Sigsbee Abyssal Plain, and of these S1 and S4 were included in this food web analysis. The sediment community oxygen consumption (SCOC) at two sites had been measured in previous studies (Hinga et al., 1979; Rowe et al., 2002) and therefore, these were repeated in this sampling (MT3 and S4).

There were three distinct steps in this comparative food web analysis. The first was to construct an inventory that represents precise and accurate estimates of the standing stocks of the size categories of the biota, in terms of organic carbon, at the seven study sites (MT1, MT3, S42, S36, MT6, S1, and S4 in Fig. 1). These data came directly from the results of others, using a broad mixture of sampling methods, sometimes involving transformations from other biomass units into organic carbon. The second step was to couple the stocks with rates of processes such as SCOC, POC fluxes, total detrital carbon inventories, and carbon burial rates, which were also measured by others. These three sets of quantitative measurements define the overall carbon cycling and provide general estimates of the turnover times of the living and detrital stocks at each site. The third step in this synthesis was to develop internally consistent carbon budgets that would illustrate how material is cycled by the individual size groups at each location. This latter, final stage was substantially more speculative because it involved (1) estimating the respiration of each size category from allometric models in the literature, (2) assumptions about the secondary production of each size category and, finally, (3) algebraic solutions to solve for unknown predator–prey relationships.

2.2. Standing stocks

The standing stocks were determined for each of the sampling sites, based on standard methods for quantitative assessments for
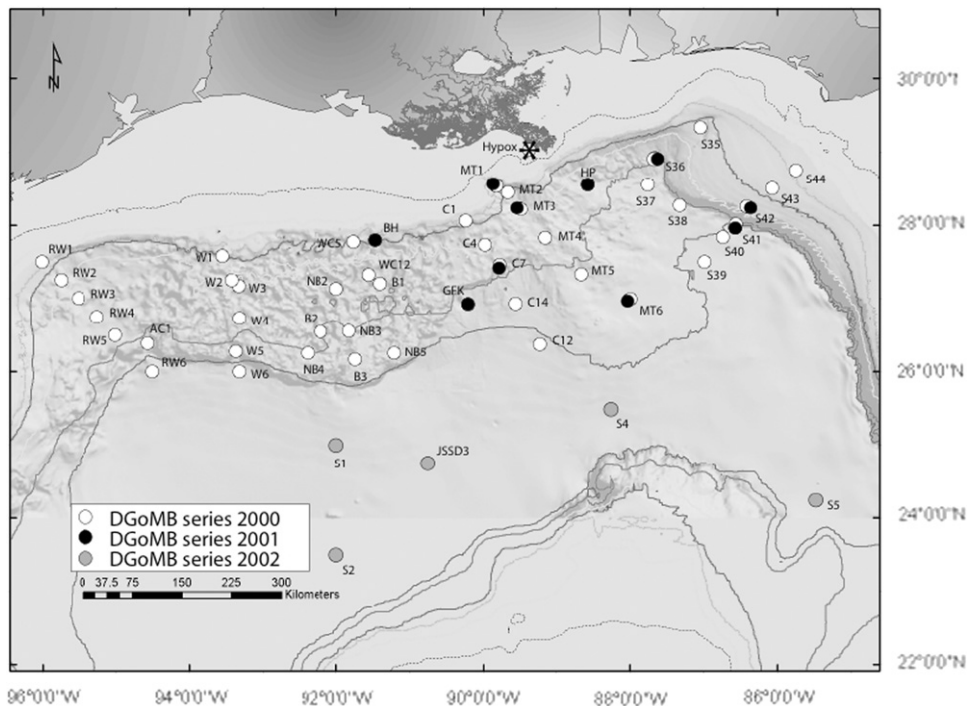

Fig. 1. Location of sampling sites, northern Gulf of Mexico. Open circles are the "experimental" sites at which rates of biological processes have been measured. Figure, from Deming and Carpenter (2008), by Shelly Carpenter.

each category within the community: bacteria, meiofauna (metazoans and Foraminifera), macrofauna, megafauna, and fishes. The chemical and physical properties of the sediments, bacterial stocks and biomass, and the metazoan meiofauna were estimated from subcores mounted within GOMEX box cores (Morse and Beazley, 2008; Deming and Carpenter, 2008; Baguley et al., 2004, 2005, 2008). The bacteria counts per wet sediment volume were based on epifluorescent staining (DAPI and Acridine Orange); the total biomass of bacteria was calculated from the sizes of the stained cells (Deming and Carpenter, 2008). The protist meiofauna, principally the Foraminifera, were assessed using ATP analyses of subcores from box cores at 10 of the sites, including six of the seven locations in this study (Bernhard et al., 2008). ATP concentrations were converted to organic carbon using established conversions (DeLaca, 1986). The metazoan meiofauna standing stocks were based on ludox density separation, followed by sieving through 45 μm sieve, of the top 3 cm of subcores mounted within the box cores at all sites (Baguley et al., 2004). The macrofauna were sampled by sieving (>300 mm) the top 15 cm of the GOMEX box cores, with five replicates per site, aboard ship. The biomass of the meiofauna and the macrofauna were estimated from measurements of animal dimensions using an ocular micrometer and assuming a specific gravity of 1.2. This "wet preserved weight" was converted to carbon equivalents following conversion factors for macrofauna (Rowe, 1983) and meiofauna (see Baguley et al., 2004). The "meiofauna" category includes both the protists and the metazoans lumped together, in this analysis. The density per m^2 of the megafauna and the fishes were estimated by determining the area of sea floor covered by the trawls (Powell et al., 2003) or multiple bottom photographs taken at each survey site (Ziegler, 2002). The biomasses were determined from wet displacement volumes of fresh material measured aboard ship, converted to carbon units (Rowe, 1983). The five continental slope sites were visited in 2000, 2001 and 2002, and this allowed an assessment of variation between years and samples. The photography has been helpful in the qualitative characterization of each habitat (Ziegler, 2002).

All stocks were converted to units of mg C m^{-2} to a depth of 15 cm to put the stock values into units that can be compared to respiration rates, POC fluxes and burial of organic carbon in the sediments. The stock sizes were the most important values in developing a carbon budget because they were measured directly by standard, well-established methods.

2.3. Carbon budget

Total SCOC has been estimated using a benthic lander to deploy incubation chambers on the sea floor, from profiles of the concentration of oxygen in the pore water on recovered cores, or by incubating sediment cores aboard ship (see Rowe et al., 2008). The sum of all respiration estimates for each size group living within the surficial sediments (bacteria, meiofauna and macrofauna) should theoretically equal the mean SCOC rate at each site studied. Carbon burial within the sediments was estimated from the inventory of carbon in the top 15 cm of sediment (Morse and Beazley, 2008) and a combination of long-term burial and bioturbational mixing estimated from natural and bomb-produced radionuclide profiles (Yeager et al., 2004; Santschi and Rowe, 2008). The total input of organic carbon detritus to the community at each site should equal the SCOC, the detrital carbon burial rate and the export of living material such as reproductive products, migration or predation (Fig. 2). That is, at each site at steady state, the input of POC is balanced by the loss of OC to remineralization (SCOC), loss to burial and loss to export. This can
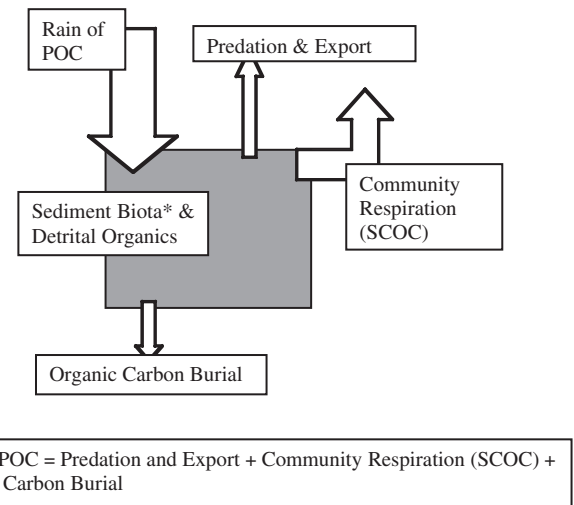

Fig. 2. Model of carbon distribution and cycling in surface sediments. *Sediment biota includes bacteria, meiofauna (metazoa+Foraminifera) and macrofauna.

be represented by the equation

$$\mathrm{d}[OC]/\mathrm{d}t = 0 = \text{POC Input} - \text{SCOC} - \text{Burial} - \text{Export} \qquad (1)$$

where rates are expressed (in this study) in units of mg C m^{-2} d^{-1}.

The input is the rain of sedimenting particulate matter (POC) to the benthic boundary layer (Pace et al., 1987), but can also include an input from carcasses (Smith et al., 1998), *Sargassum* sp. (Snelgrove et al., 1996), and mass movements of sediment downslope (Santschi and Rowe, 2008), whose precise values remain unknown. The composition of the sediment OM is not well known and remains a persistent long-term question in biogeochemistry. We presumed that the "rain" of POC is a complex assemblage of detrital material derived from the water column (Biggs et al., 2008). It is presumed to be composed of biodegradable substrates (Ittekkot et al., 1984; Khripounoff and Rowe, 1985) derived from phytoplankton cells, cellular debris and fecal pellets (Premuzic et al., 1982; Wakeham and Lee, 1993; Deming and Baross, 1993), often in aggregations of flocculated cells (Richardson and Jackson, 2007).

Two approaches were utilized for the estimates of the POC input to the sea floor. One was to assume that the input was equal to the sum of the SCOC and burial (Jahnke, 2001). The second was to consult the estimate from Biggs et al. (2008), in which POC arrival at the sea floor was estimated from surface chlorophyll concentrations and a model of the first-order decay of POC in its descent through the water column (Pace et al., 1987). The differences between these two rates have contributed to our interpretations of the trophic conditions at each of the various habitats.

2.4. Food web structure and carbon budget

At all sites, it was presumed that the bacteria feed only on organic detritus, the meiofauna feed on bacteria and organic detritus (Kemp, 1990); the macrofauna feed on the latter three components; the megafauna feed on the latter four components; but the fishes feed only on the megafauna and the macrofauna. Although the relative proportions of the food sources to each feeding stock are unknown, it was presumed that each stock would prefer to feed on the largest size available because this would be the most energetically efficient pathway (Roberts and Moore, 1997; Jorgensen et al., 2002) in a starkly resource-limited environment (Post, 2002a, b; Belgrano et al., 2005). The secondary

production of each stock at steady state was partitioned proportionately into the consumers in higher levels of the food web.

The general system-level carbon budget equation above can be expanded into a set of coupled equations each of which represent a component or "trophospecies" of the food web at steady state, where

$$\begin{aligned} d(\text{fishes})/dt = {} & \text{feeding}_{\text{(on carcasses, megafauna and macrofauna)}} - \text{respiration} \\ & - \text{feces} - \text{reproduction} - \text{loss to predation}_{\text{(by bigger fishes)}} \\ & - \text{loss to fisheries} \end{aligned} \quad (2)$$

$$\begin{aligned} d(\text{megafauna})/dt \\ = {} & \text{feeding}_{\text{(on carcasses, macrofauna, meiofauna, bacteria and sedimentary detrital OM)}} \\ & - \text{respiration} - \text{feces} - \text{reproduction} \\ & - \text{loss to predation}_{\text{(by fishes)}} - \text{loss to fisheries} \end{aligned} \quad (3)$$

$$\begin{aligned} d(\text{macrofauna})/dt = {} & \text{feeding}_{\text{(on meiofauna, sediment detrital OM and bacteria)}} \\ & - \text{respiration} - \text{feces} - \text{reproduction} \\ & - \text{loss to predation}_{\text{(by megafauna and fishe)}} \end{aligned} \quad (4)$$

$$\begin{aligned} d(\text{meiofauna})/dt \\ = {} & \text{feeding}_{\text{(on sediment detrital OM, smaller protists and larval stages, and bacteria)}} \\ & - \text{respiration} - \text{feces and stercomata} - \text{reproduction} \\ & - \text{loss to predation}_{\text{(by the macrofauna and megafauna)}} \end{aligned} \quad (5)$$

$$\begin{aligned} d(\text{bacteria})/dt = {} & \text{feeding}_{\text{(on detrital OM in the sediments)}} - \text{respiration} \\ & - \text{reproduction} - \text{loss to predation}_{\text{(by megafauna, macrofauna and meiofauna)}} \end{aligned} \quad (6)$$

$$\begin{aligned} d(\text{sedimentOM})/dt = {} & \text{POC particle rain} + \text{carcasses} + \text{hydrocarbon seeps} \\ & + \text{feces}_{\text{(from all metazoans)}} + \text{mass sediment input downslope} \\ & + \text{Sargassum and other larger plants} - \text{consumption by bacteria} \\ & - \text{consumption by deposit feeding}_{\text{(by the megafauna, macrofauna, meiofauna)}} \\ & - \text{long-term burial} - \text{erosional export processes} \end{aligned} \quad (7)$$

The respiration rate for each size category or "trophospecies" in the equations has been estimated from literature values (Smith and Hessler, 1974; Smith, 1978b, 1983; Smith and Laver, 1981; Childress et al., 1990; Hannah et al., 1994; Piepenburg et al., 1995; Heip et al., 2001; Rowe et al., 2003; Baguley et al., 2008), based on animal size and ambient temperature (Mahaut et al., 1995), and measured by incubation of trawl-caught organisms in aquaria aboard ship or in the laboratory. Growth efficiency (growth/assimilated carbon × 100) was assumed to be 10% throughout.

The general strategy was to create the most parsimonious predator–prey relationships possible, given the stock sizes, respiration and production, to achieve steady state. The most productive prey dominated as source terms for the predators (Jorgensen et al., 2002). The governing principle has been to transfer all the production from a prey to the next consumer (Jorgensen et al., 2002), but when (if) that production of the prey was greater than the demand of the next level, then the excess was split among other potential consumers at the next level. If the production was too low to supply the demand of the next level, then other sources lower in the web, such as detritus and bacteria, were included, as available. In no case did a "smaller" category consume a "larger" group.

3. Results

3.1. Standing stocks

Standing stocks in each category at all the sites (Fig. 1) have been plotted as a function of depth (Fig. 3) to provide a "global" comparison of how the stocks were related in general over the entire sampling area. Bacteria dominated the total biomass; its linear decline with depth was statistically significant (Deming and Carpenter, 2008). Metazoan meiofauna [thus not including the Foraminiferans] and macrofauna had stock sizes that were much lower and both declined exponentially as a function of depth (Baguley et al., 2008; Yeager et al., 2004; Morse and Beazley, 2008). The trawl-caught megafauna and fish stocks occurred in even lower concentrations but the decline of the megafauna with depth was not significant.

In general, the macrofauna biomass was greater than that of the meiofauna at depths less than about 2 km, whereas the metazoan meiofauna had higher biomass below that (Fig. 3). This difference is reflected in both the intercepts and the slopes of the two regression lines. Foraminifera were quantified at a limited number of sites and are not included in Fig. 3. They were included in the meiofauna fraction at six of the seven sites discussed below. At those locations the Foraminifera had an average biomass of $51\,\text{mg C m}^{-2}$ (Std. Dev. = 47, $n = 10$), and this constituted an average of 52% (Std. Dev. = 16.4, $n = 8$) of the total meiofauna, in terms of organic carbon, at those locations. While the metazoan meiofauna displayed significant decline relative to depth (Fig. 3), no such patterns emerged with the Foraminifera. The megafauna and the fishes had about the same biomasses, but they were about an order of magnitude lower than the smaller meio- and macrofauna.

The mean standing stocks of each size category (fish, megafauna, macrofauna, meiofauna (protists and metazoans), and bacteria) at each of the chosen process sites (MT1, MT3, MT6, S36, S42, S1 and S4, Fig. 1) are presented in Table 1. The sediment dwellers are displayed in Fig. 4, exclusive of the bacteria. The variation in stocks along the rows allows a comparison of the carbon inventory of each size group at each site, as organism size category increased, whereas the variation down the columns provides a comparison of differences in a particular size category at the different experimental sites, from shallow to deep water. There were about two orders of magnitude more detrital OM than living biomass at all the sites. There was universally more OM, both living and detrital, at the shallow sites compared to the deep ones. At all sites, regardless of depth, most of the living OM was found in the smaller size groups (Figs. 3 and 4). This illustrates that the larger organisms were of much lower relative biomass in deep water. The organic detritus had a range of 7.6E5 down to $2.2\text{E5}\,\text{mg C m}^{-2}$, while the bacteria maximum was 2.6E3 down to a minimum of $1.0\text{E3}\,\text{mg C m}^{-2}$. The small, sediment-dwelling animals declined by a factor of 10, whereas all the larger forms decreased by a factor of 100 over the same depth interval (3 km). The lowest values in detritus and total living matter were not at the greatest depths (S1 and S4, depth > 3400 m), as might have been expected, but at an intermediate depth site (MT6, depth = 2750 m) on the Mississippi Fan.

Of the total organic carbon, the highest concentration was the detritus (Morse and Beazley, 2008), followed by the bacteria (Deming and Carpenter, 2008), at both the shallow and the deep sites. The "dead" carbon was several orders of magnitude higher than the bacterial carbon. The animal stocks were orders of magnitude lower than the detritus and bacteria components, and the ratio between the bacteria plus detritus to the total metazoan stock [(bacteria+detrital carbon)/(meiofauna+macrofauna+megafauna+fishes)] was much larger at the deepest sites (a ratio
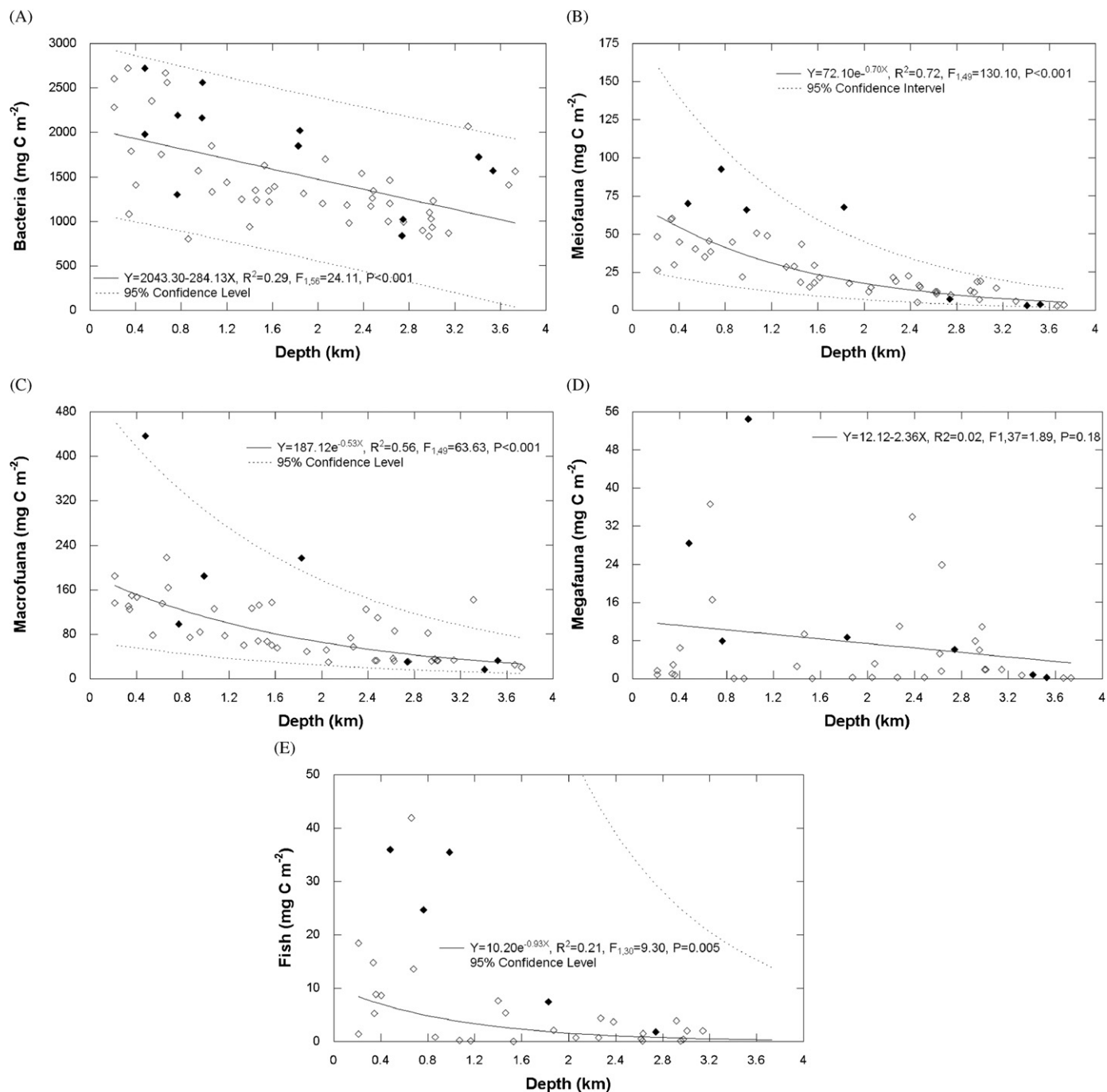
Fig. 3. Standing stocks of each biotic variable, as indicated, in $mg\,C\,m^{-2}$. The sediment biota were sampled to a depth of 15 cm (bacteria, metazoan meiofauna and megafauna).

comparing the mass of the potential 'food' in the mud to the mass of the organisms potentially feeding on whole sediment).

3.2. Sediment community carbon budget

Table 2 lists the rate information for SCOC (Rowe et al., 2008) along with the total living stock sizes (Table 1). The last three columns and rows allow comparison of organic carbon reminer-alization rates (SCOC) with the total stocks, either by site or across the depth gradient. The sum of the burial and the community respiration rates can be assumed to be more or less equal to net organic carbon flux to the sea floor at that site (Jahnke, 2001). In

general, net accumulation (Yeager et al., 2004; Santschi and Rowe, 2008) was small relative to respiration. The SCOC was coupled tightly with depth, as follows:
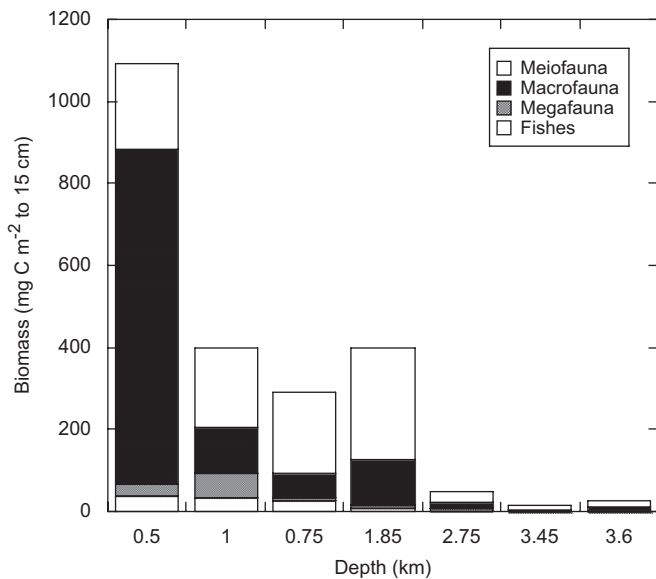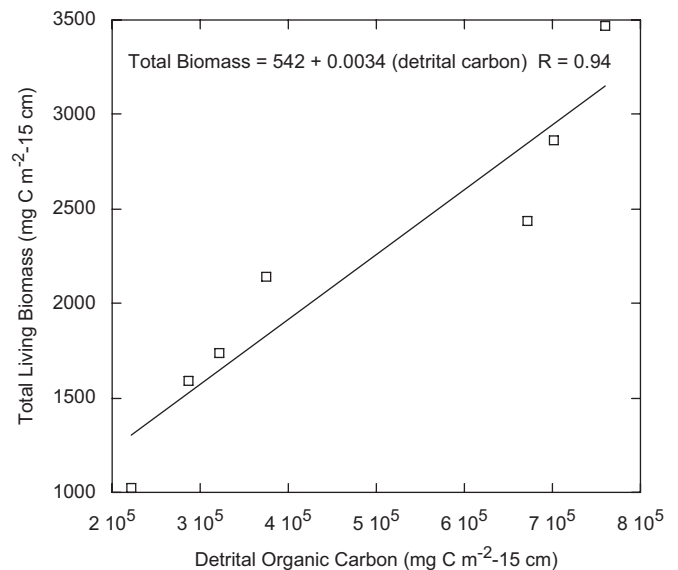
$$Log\ SCOC = 2.31 - 0.48(\text{depth in km})(r = 0.93) \qquad (8)$$

where SCOC has units of $mg\,C\,m^{-2}\,d^{-1}$ (from Rowe et al., 2008).

The rate at which the total carbon stock turns over has been calculated by dividing the stock at each site by the SCOC (Table 2). The total living biota turns over on the order of months at the upper- to middle continental slope sites but this increases to at least a year on the abyssal plain. The detrital carbon turns over much more slowly, but the general trend was the same as that for the biota. At the shallower sites, the turnover time was on the

Table 1
Distribution of organic matter (mg C m^{-2}, down to a depth of 15 cm in the sediment) in the detrital and living fractions at the seven study sites (Fig. 1)

Depth (km)	Site	Sed. Org. C[a]	Bacteria[b]	Meiofauna[c]	Macrofauna[d]	Megafauna[e]	Fishes[f]	Total
0.5	MT1	7.6E5	2585 (390:3,3)	208	816 (90,13)	30.6	35.9	3468
1.0	MT3	7.02E5	2465 (160:4,4)	194	110 (14,10)	59.5	35.4	2864
0.75	S42	3.75E5	1855 (490:3,3)	197	60 (6.6,9)	7.9	24.7	2144
1.85	S36	6.72E5	2035 (32:5,3)	272	110 (13,12)	9.43	7.4	2433
2.75	MT6	2.22E5	975 (80:3,3)	27	15 (2.4,10)	6.67	1.8	1025
3.4	S4	3.21E5	1720 (210:3)	10.5	5 (0.7,4)	0.75	0	1736
3.6	S1	2.87E5	1570 (210:3)	13.8	10 (2.3,2)	0.19	0.4	1594

Values in parentheses are σ_n, where available, followed by the number of replicate cores.
[a] Morse and Beazley (2008).
[b] Deming and Carpenter (2008).
[c] Baguley et al. (2008); Bernhard et al. (2008).
[d] Wei et al. (in preparation).
[e] Powell et al. (2003).
[f] The bacteria data from MT1 through MT6 are the means from 2000 to 2001; S4 and S1 were taken in 2002; the parentheses enclose the relative standard error for the biomass estimates, assuming the standard error for the cells per square meter in Deming and Carpenter apply as well to the biomass estimates. This is followed by the numbers of box cores from which the counts were based for each of the years, as presented in Deming and Carpenter.

Fig. 4. Distribution of biomass in units of organic carbon at each "process" site. Bacteria (Table 1) are not included.

Fig. 5. Biomass of the entire biota down to depths of 15 cm, as a function of the total detrital organic carbon within the same sediment layer, at six of the "process" sites in Fig. 1.

Table 2
Relationship between depth, total detrital organic carbon, total living organic carbon, sediment community oxygen consumption (SCOC, mg C m^{-2} d^{-1}, with standard deviations, from Rowe et al., 2008) and carbon turnover time in days for biota (living carbon) and years for OC (detrital organic carbon), where 'time' equals the stock divided by the rate

Depth (km)	Site	Sed. Org. C	Total living	SCOC	Biota ($t = d$)	[OC] ($t = y$)
0.5	MT1	7.60E5	3468	36.5, 15.1	95	57
1.0	MT3	7.02E5	2864	36.3, 13	79	53
0.75	S42	3.75E5	2144	32.4, 7.1	66	32
1.85	S36	6.72E5	2433	29.1	84	63
2.75	MT6	2.22E5	1025	15.7	65	39
3.45	S4	3.21E5	1736	3.9[a]	445	226
3.6	S1	2.87E5	1594	3.9[a]	409	202

The stocks are mg C m^{-2} down to 15 cm depth in the sediment.
[a] Mean for the two deep sites.

order of tens of years, whereas on the abyssal plain the turn over approached 200 years. The total living biota (bacteria, meio- and macrofauna) was strongly related ($r = 0.94$) to the total detrital organic carbon inventory in the sediment (Fig. 5).

3.3. Food web structure and carbon flow

Respiration rates calculated for each size category at each site (Table 3) illustrate that total respiration declined with depth, in general, as indicated by the regression above from Rowe et al. (2008). The sediment biota also followed this same pattern (Fig. 6). The three deep sites were substantially lower than the four shallow sites. The bacterial respiration was the highest, with the exception of the canyon head site (MT1), whose metazoan faunal biomass was dominated by a dense population of a single, newly described species of amphipod, *Ampelisca mississippiana* Soliman and Wicksten 2007. Approximately one-half of the total SCOC was attributed to this macrofaunal species (Soliman and Rowe, 2008) (Fig. 6). Of the other locations (Table 3, Fig. 6), the bacteria accounted for ca. 76% of the respiration at the mid-slope sites and more than 90% of the remineralization at the three deepest locations. The megafauna and fishes, on the other hand, made trivially small contributions to the total respiration (Table 3, Fig. 6).

The standing stock and rate data have been assembled into four different illustrations of the food webs at the seven target

Table 3
Estimated respiration rate (mg C m^{-2} d^{-1}) for each size group, based on allometric relationships and temperature

Site	Depth (km)	Bacteria[a]	Meiofauna[b]	Macrofauna[c]	Megafauna[d]	Fishes[e]
MT1	0.5	12.7	8.4	15.4	0.37	0.18
MT3	1.0	27.5	7.5	1.35	0.12	0.30
S42	0.75	19.2	11.6	1.62	0.023	0.21
S36	1.85	13.5	15	0.64	0.011	0.030
MT6	2.75	13.4	1.8	0.54	.017	0.007
S4	3.45	3.0	0.87	0.06	0.0012	0.0021
S1	3.60	2.1	1.53	0.24	0.00046	8.6E−05

[a] Calculated as SCOC—Meiofauna and Macrofauna respiration. SCOC from Rowe et al. (2008).
[b] From Baguley et al. (2008), adjusted upward to include Foraminifera (Bernhard et al., 2008).
[c,d] Calculated, based on mass and temperature, from the equations of Mahaut et al. (1995).
[e] Calculated, based on mass and temperature, from the equations of Clarke and Johnston (1999).
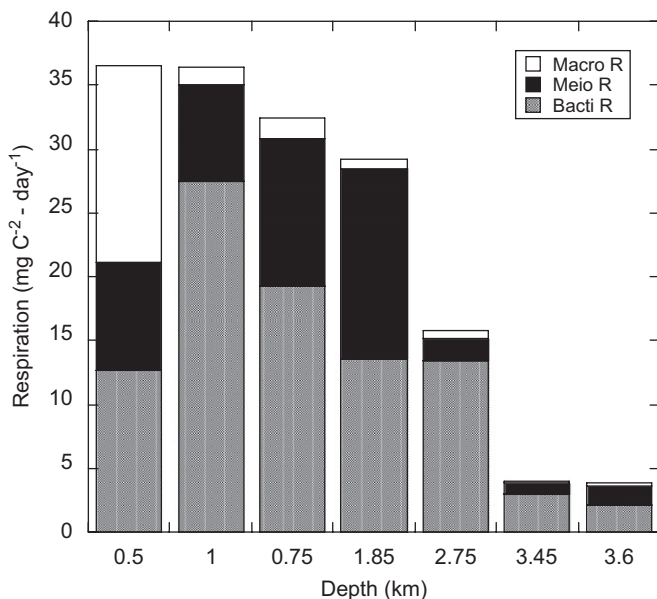

Fig. 6. Distribution of estimated respiration among size groups at each "process" site: does not include megafauna and fishes.

habitats (Fig. 7). MT1 (the near-shore canyon head location at 450–500 m depth) and MT6 (at 2750 m depth on the Mississippi sediment fan) are presented individually because of their unique properties. The three upper- to mid-continental slope sites (S42, MT3 and S36 at 740–1850 m depth) have been lumped together, as have the two abyssal plain sites (S1 and S4 at 3650 and 3400 m depth). The rationale for consolidating these food webs is that the faunas are grouped into the same "faunal zones" based on similarities in macrofaunal species composition (Wei and Rowe, 2006; Wei et al., in preparation). The boxes represent each stock, as labeled. The arrows into the "organic carbon" box represent fluxes of particulate carbon (POC) into the seafloor, whereas the single arrows out of each stock represent transformation of OM to carbon dioxide (respiration). The arrows between living boxes represent predator–prey transfers. All the stocks have units of mg C m^{-2}, whereas the arrows have units of mg C m^{-2} d^{-1}, as in all the tables. Each stock is represented by one of the equations above, with the stocks on the left and the fluxes on the right. The

statistical variation in each flux is unknown, but it would be proportional to that given for the replicates in stock sizes in Table 1 or to the spread in the values depicted in the regressions of Fig. 3A–E, at any given depth.

Steady state has been assumed and therefore the sum of the fluxes into each stock must equal the sum of the fluxes out of each stock. Because food that is not assimilated simply returns as feces directly to the detrital carbon compartment (as indicated in the equations above), the un-assimilated fecal material was ignored in the four budgets. That is, the arrows represent the assimilated carbon, not the total flux into the trophospecies. Organic particulate matter remobilized as dissolved OM was assumed to be consumed by free-living bacteria, but there was no differentiation in these budgets between particulate and dissolved organics. Growth efficiency was assumed to be 10%. Fluxes between stocks have been rounded off to one or two significant digits. The fluxes between the stocks, mostly predator–prey relationships, have been based on the presumed secondary production (growth) and respiration, constrained by and adjusted to attain steady state. When no value is entered on a figure, the partitioning from prey to predator could have multiple solutions and there was no valid rationale for arbitrarily providing a value for the flow.

3.4. The food web in the Mississippi Canyon head (MT1)

In the head of the Mississippi Canyon (MT1–Fig. 7) a single species of amphipod (A. mississippiana Soliman and Wicksten 2006) reached high densities consistently over a 3-year period, which allowed its secondary production to be estimated independently (Soliman and Rowe, 2008). A unique feature of MT1 was that considerable carbon was cycled through the macrofauna, based on the secondary production estimates and total SCOC (Rowe et al., 2008). The α (within habitat) diversity of the macrofauna was low at this site, because of the dominance by the amphipod (Wei and Rowe, 2006). The relative role of bacteria and meiofauna in the total remineralization (SCOC) was seemingly reduced, a consequence of the macrofaunal dominance. On the other hand, the production of the amphipods provided a source of food for larger fishes and invertebrates (Franz and Tanacredi, 1992), which were relatively abundant and diverse. Two sedentary megafaunal invertebrates had high densities and biomass (the anemone Actinauge longicornis and the bivalve Amygdalum politum). We assume that they consume the near-bottom suspended material. Eight species of megafaunal crustaceans were sampled, but their specific food resources were difficult to ascertain. Of 136 trawl-caught specimens of fishes, there were 17 different species. The abundant macrourids (rattails) Bathygadus macrops, Caelorinchus caelorhinchus, and C. caribbaeus, along with the gadids (hake) Laemonema goodebeanorum and Urophycis cirrata were the most prominent fishes in this assemblage (Powell et al., 2003). They are considered "bathydemersal" and we would presume they feed on the abundant amphipods or the megafauna. The POC input estimated from the surface-water pigment concentration (77 mg C m^{-2} d^{-1}, Biggs et al., 2008) was two times the amount required to support the calculated demand (total respiration, production and export), resulting in a positive imbalance in the carbon budget.

3.5. The food web at mid-slope depths

In the set of sites on the middle slope (S42, MT3 and S36, at 750–1850 m depth, Fig. 7) all had high diversity and comparatively high biomass in all size categories. While the mean biomass of the macrofauna was lower than the Mississippi Canyon head, the diversities were higher (Wei et al., in preparation). Total SCOC
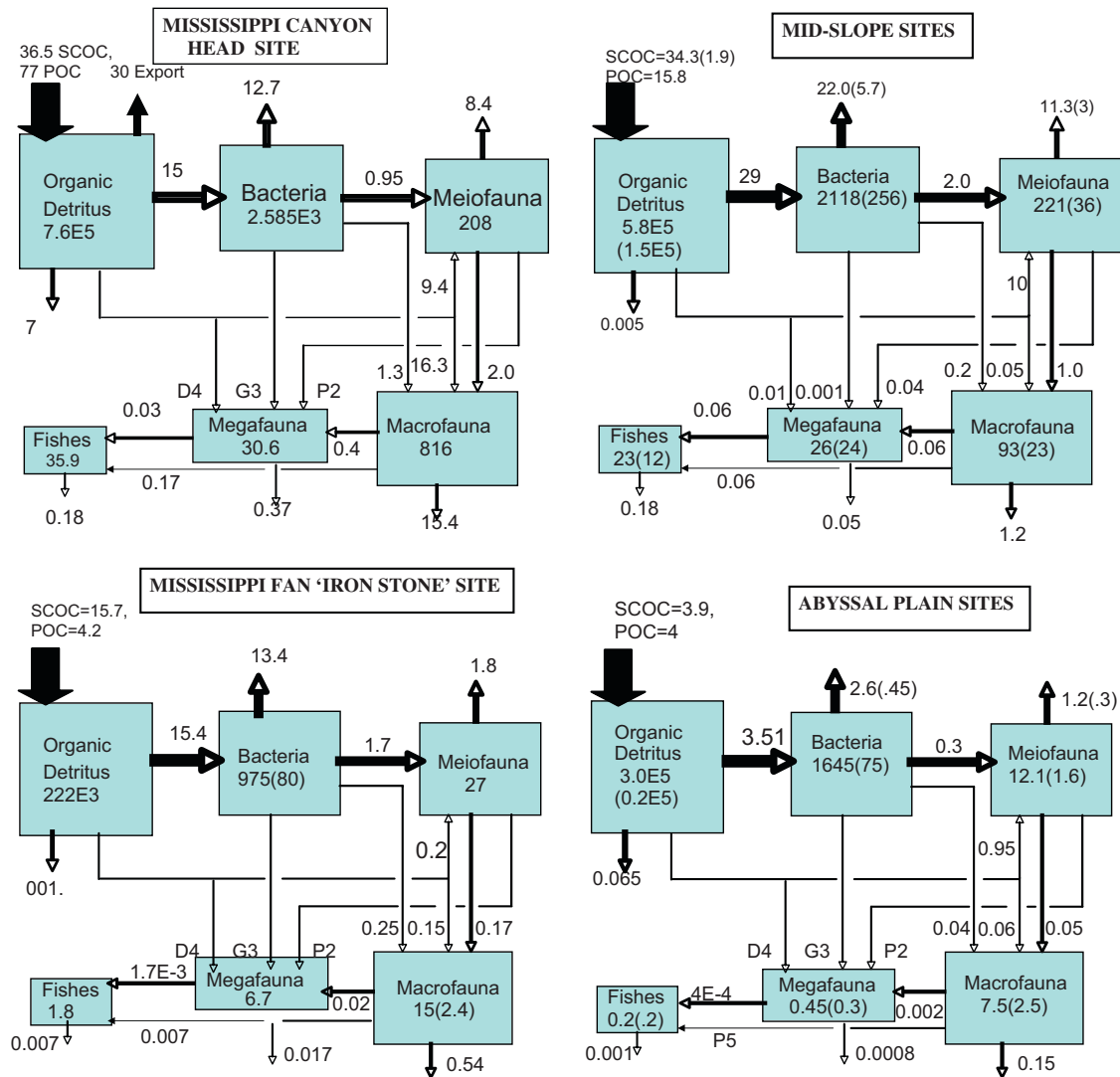
Fig. 7. Four food webs representing MT1, the mean of S42, MT3 and S36 (mid slope), MT6 (the "ironstone" site), and the mean of the abyssal plain sites (S1 and S4). Arrows into the "detritus" box are organic carbon input required to balance total sediment community oxygen consumption (SCOC), units of $mg\,C\,m^{-2}\,d^{-1}$. Parenthetical values are POC influx estimated from surface pigments (see text). Arrows out of each "living" box are respiration, in $mg\,C\,m^{-2}\,d^{-1}$. Parenthetical values on the stocks for the mid-slope and abyssal plain are Std. Dev. of the mean values.

was no different, statistically, from the canyon head, however, at these sites, the demand for and cycling of organics was not partitioned as equally between the macrofauna, meiofauna and bacteria. The largest fraction was cycled through the bacteria, which remineralized most of the carbon. The net carbon demand (SCOC = ca. 34 $mg\,C\,m^{-2}\,d^{-1}$, Figs. 6 and 7) by the biota was greater than the estimated POC input, suggesting that an additional source of carbon and energy was needed for steady state. An average of 22 megafauna species (range of 15–27) was encountered at these three sites and their mean biomass was 25.6 $mg\,C\,m^{-2}$ (7.9–59.4 $mg\,C\,m^{-2}$). The megafauna was dominated by the giant isopod *Bathynomus giganteus*, the red crab *Chaceon quinquedens* and the holothuroid echinoderm (sea cucumber) *Mesothuria lactea*. The single abundant species that occurred at all three sites was the red crab. The predominant fishes were the macrourids (rattails) *Nezumia cyrano*, *N. aequalis*, *Coryphaenides mexicanus*, and *Coryphaenoides zanophorus*; but the ophidiid (cusp eel) *Dicrolene introniger* was the only species that was sampled at all three locations. The halosaurid *Aldrovandia affinis* was encountered only at the deep site in DeSoto Canyon (S36). Prey items of these species are known to be spread among

small crustaceans, polychaete annelid worms and bivalve mollusks, based on stomach contents (FishBase, Froese and Pauly, 2000).

3.6. The food web at the Mississippi Fan "iron stone" site

The species found at the single site studied on the Mississippi Fan (MT6, Fig. 7), directly down slope from the canyon, had little faunal affinity to the other sites (Wei and Rowe, 2006) and thus has been considered here separately (Figs. 6 and 7). The SCOC (ca. 16 $mg\,C\,m^{-2}\,d^{-1}$) was less than half of the mid-slope mean. This, however, was approximately four times the POC input model estimate, suggesting another source of OM was required to balance the carbon budget at steady state. The biomass (Table 1) of the bacteria was the lowest of all the sites, but the meiofauna and the macrofauna, while low, were still above the abyssal sites further offshore. The megafauna biomass was relatively high (6.7 $mg\,C\,m^{-2}$) and diverse, with 23 species. Of these there were seven species of decapod crustaceans and 10 species of echinoderms. The echini were represented by ophiuroids (brittle stars)

and asteroids (sea stars), and a dominant purple elasipod holothuroid (sea cucumber) that defies identification so far. The gut of the large, widely distributed sea star *Dytaster insignis* was full of pelagic *Sargassum* detritus. There was virtually no overlap in species composition between the mid-slope megafauna (MT3, S42 and S36) and this site (MT6) on the Mississippi Fan. This site had only one species of bottom-dwelling fish, the macrourid (rattail) *Coryphaenoides rudis*. The trawl sample in the 2000 survey also contained "iron stone" (132 l, weighing ca. 115 kg, more than any other trawl sample), as well as the fauna described above. The bottom photographs exposed a very smooth bottom in general, with some distinct tracks and trails (*lebenspuren*) and lumpy areas of cobble to pebble-sized material which resembled the iron stone in the trawl. The texture of the sediment in our photographs was similar to the iron stone photographed by Pequegnat (1983) in this area.

3.7. The abyssal plain food web

At the abyssal plain sites (S1 and S4, Figs. 6 and 7) the bacteria and the meiofauna combined were functionally dominant, utilizing 96% of the available organic input (4 mg C m^{-2}). The higher forms (macrofauna, megafauna and fishes) occurred in very reduced numbers (Table 1) and consumed only 4% of the input. The POC rain predicted by Biggs et al. (2008) and the SCOC (Fig. 7) were in general agreement, and about an order of magnitude lower than that on the mid to upper slope. Diversity and biomass of the macrofauna and megafauna were substantially reduced, and no bottom-dwelling fish was sampled, as the reader will note from Fig. 3. The bacterial densities and biomass were higher on the abyssal plain than on the lower slope (Fig. 3), but it must be noted that the abyssal plain was sampled in 2002, whereas the bulk of the other data are from 2000 to 2001 (Deming and Carpenter, 2008).

4. Discussion

The first issue to reiterate is that there were three levels of confidence that can be placed on the components of the food web carbon budgets. The sediment-dwelling stock data at each location were generated by established techniques and thus are reasonably accurate, as are the confidence intervals (Fig. 3). The megafauna and fish stock data, however, are more equivocal because they were based on trawls, which are notoriously difficult to quantify. The bottom photography did not adequately "ground truth" the trawl data because the megafauna and fish were so sparse. Some of the trawls were repeated in consecutive years, but this does not qualify as legitimate replication because variation could occur on yearly time scales (Ruhl, 2007). The total community respiration (SCOC, in Rowe et al., 2008) was reasonably accurate, we believe, because the chambers used have been included in comprehensive inter-calibrations (Tengberg et al., 1995, 2005), and these values have been reinforced by the laboratory incubations of cores and profiles of oxygen concentration in the pore water (Rowe et al., 2008). The respiration rates of the size groups (Table 3, Fig. 6) were based on allometric models (Mahaut et al., 1995) but these have not been validated. The respiration measurements conducted on a few species of megafauna that were alive when recovered were only from the shallow sites (MT1, S42 or MT3). Thus the respiration rates (Table 3 and Figs. 6 and 7) for the "size" categories (trophospecies), although seemingly reasonable (Gillooly et al., 2001), must be acknowledged to be speculative model-based estimates.

The bacteria rates are of particular concern. Our bacteria respiration was estimated by subtracting the sum of the meiofauna and macrofauna rates from the SCOC or "whole community" respiration. This algebraic approach has been practiced by others previously (Rowe and Deming, 1985; Piepenburg et al., 1995; Heip et al., 2001; Rowe et al., 2003), but it relies on assumptions that have not been validated. At all deep locations (the exception being MT1, Figs. 6 and 7) the bacteria in our budgets dominated the total SCOC, which has become a widely accepted presumption for deep-ocean food webs (Richardson and Young, 1987; Alongi, 1990; Rowe et al., 1991, 2003; Heip et al., 2001). However, the direct uptake of radio-labelled organic substrates and tritiated thymidine incorporation in incubations of re-pressurized samples aboard ship produced respiration and growth rates (Deming and Carpenter, 2008) that were substantially lower than our indirect algebraic estimates. For example, the overall mean of the integrated secondary production estimated in these incubations was 33 μg C m^{-2} d^{-1} ($\sigma = 26$) for the six deep sites (no rates are available for MT1). The mean of the mid-slope sites (S42, MT3 and S36) was 8.6 μg C m^{-1} d^{-1} ($\sigma = 4.5$), whereas that of the abyssal plain (S4 and S1) was 60 μg C m^{-2} d^{-1} ($\sigma = 15$). These "growth" rates would equal respiration rates of approximately 86 and 600 μg C m^{-2} d^{-1}, respectively, given a growth efficiency of 10%. Note that these units are in micrograms, as opposed to milligrams used in Table 3 and Figs. 6 and 7. These respiration and production rates are ca. 20 times lower than our mid-slope values and about five times lower than our abyssal plain rates (Figs. 6 and 7). If both the SCOC rates in Rowe et al. (2008) and the values generated by Deming and Carpenter (2008) are accepted, then the overall role of the bacteria in these deep-sea sediments compared to the animals would be very low. Deming and Carpenter have suggested that a disproportionate fraction of bacteria in these abyssal sediments, as in other semi-enclosed basins, may be inactive due to their recent delivery to depth from shallower sites via lateral advection. Rowe and Deming (1985) suggested that the labels used in such measurements are only a fraction of the total qualitative and quantitative substrates available to the bacteria naturally in the sediments, and thus the total utilization would be expected to be substantially larger than the label alone. This nonetheless is an enigmatic disparity which must be confronted in future investigations (Kemp, 1990).

The second assumption was that the "growth efficiencies" were 10%. This value was used because it has been applied widely in other benthic food web models (Christensen and Pauly, 1993; Rowe, 1996, 1998; Jarre-Teichmann et al., 1997; Rowe et al., 2003). It is important because growth directly affects each level of the food web. We believe that growth efficiency could likely be lower at the deep, depauperate end of the "food" gradient on the abyssal plain (S1 and S4, Fig. 7) where food limitation is extreme, but perhaps higher than 10% in the canyon head (MT1, Fig. 7), based on the production to biomass ratios of *A. mississippiana* (Soliman and Rowe, 2008).

The degree to which these budgets are sensitive to alternative growth efficiencies was tested by changing the rate for all the stocks together and by altering each one separately. The results of reducing the efficiency to 5% reduces the transfer of carbon from stock to stock and thus each consumer is forced to rely more on the original source—detrital organics—for steady state to be maintained. This increases the total carbon demand by the assemblage and thus the input POC must be increased to maintain steady state. This reduction in efficiency might be reasonable, given the remote nature of the habitats. However, this widens the disparity between the POC flux model and a budget's total carbon demand. If the efficiencies are increased, then the opposite adjustment is necessary: less POC input is needed to maintain steady state. Altering individual stock growth efficiency had a slightly different effect. For example, if the bacterial growth

efficiency alone were elevated to 50% (which might be reasonable in highly enriched environments), then more bacterial carbon would be available to higher stocks (trophospecies), thus reducing the higher-level consumers' dependence directly on carbon in the detritus.

That these models (Figs. 2 and 7) are oversimplifications goes without saying. Given these equivocations, however, what can be learned from the budgets? The composite carbon budgets clearly demonstrate that the upper slope (MT1, MT3, S42 and S36) receives about 10 times more OM than the abyssal plain (S1 and S4), based on higher SCOC and total biomass. The lower slope "iron stone" site (MT6) was about midway between the two in both depth and SCOC, as would be expected from work on other continental margins (Smith, 1978,a, b; Archer and Devol, 1992; Anderson et al., 1994; Rowe et al., 1994; Duineveld et al., 1997; van Weering et al., 2001). The SCOC of the upper slope set (MT1, MT3, S42 and S36) was 10 times less than numerous measurements on the adjacent northern Gulf of Mexico continental shelf (Rowe et al., 2002), as would be expected, because the depth ranges of the studies differed from one to two orders of magnitude (10–200 m on the shelf versus 450–1850 m on the slope). While this was new for the Gulf of Mexico, it was not unexpected, based on numerous studies around the world (Smith, 1978a, b; van Weering et al., 2001; Witte and Pfannkuche, 2000). A puzzlement, however, was that the canyon head trough (MT1) was more similar in SCOC to the mid-slope locations (MT3, S42 and S36) than to the adjacent continental shelf. The proximity of MT1 to the direct *debouchement* of the mud-laden Mississippi River plume (Bianchi et al., 2006) suggested to us, *a priori*, that this location would have substantially higher SCOC than those located further offshore.

The POC input to the sea floor predicted from the surface-water pigment model (Table 2) was more than twice the measured SCOC in the Mississippi Canyon trough (MT1). This imbalance suggests that this habitat exports material to deeper water. The mean input of POC and SCOC at the mid-slope sites (Fig. 7: MT3 in the Mississippi Canyon, S42 on the Florida slope and S36 in the De Soto Canyon) and on the Mississippi Fan in the "ironstone" field (MT6), on the other hand, did not balance either, but in the opposite direction. The estimate of POC input from the pigment model (Biggs et al., 2008) did not supply enough material to meet the carbon demand in terms of SCOC, suggesting an additional source would be necessary to balance a steady-state budget. This missing source, we infer, is lateral offshore export (Walsh et al., 1981; Anderson et al., 1994; Jahnke, 2001; Bianchi et al., 2006; Santschi and Rowe, 2008) and downslope movement of detrital material from the upper slope or shelf, including the heads of the canyons. The upper- to mid-slope depth range has been assumed to be a "depocenter" which receives export from the shelf (Walsh et al., 1981; Rowe et al., 1994; van Weering et al., 2001). Such material is probably supplemented by detrital plant material such as *Sargassum* spp. and *Thalassia testudinum*, as these were often observed in the trawl samples, the bottom photographs and animal guts.

The Mississippi Fan at the "ironstone" site (MT6) was also peculiar because radiocarbon-dated sediments were inexplicably old near the surface, leading Santschi and Rowe (2008) to suggest that the material was not recent pelagic detritus but had been transported to MT6 in a mass wasting process such as a slump from somewhere up on the slope. Other evidence supports this. The high quantities of ironstone at this site could be formed through the oxidation of reduced iron species that originally occurred buried within upper slope or even shelf sediments. We would infer that this previously buried material was transported to deep water, and, in the process of re-oxidation, formed the reddish stone veneer which is now widespread throughout this

area (Pequegnat et al., 1972). This oxidation could have been a chemical reaction alone, when the reduced iron ended up exposed to plentiful oxygen in surficial sediments exposed to the bottom water of the lower slope environment. It could have contributed to the bioenergetics of the food web, since iron-oxidizing bacteria, if present, could use the reduced iron as an energy source. The oxygen utilized by the bacteria would be incorporated into the total SCOC, we presume, but probably would have had only a small contribution to the total SCOC, based on similar comparisons on the continental shelf (Rowe et al., 2002).

A remaining issue is the relationship between carbon cycling and faunal community structure and composition. The Mississippi Canyon head (MT1, Fig. 7) shared faunal affinities with all the other shallow locations along the entire northern upper continental slope. Other sites within the same assemblage had higher macrofauna α (within habitat) diversity because they were not dominated by a single species (*A. mississippiana*). This dominant species appeared to be thriving on the extraordinarily soft substrate, filtering digestible matter out of heavy concentrations of suspended particulate matter derived from the plume of the Mississippi River. We suspect that the fluvial clay and silt are transported down into the canyon head as hyperpycnal flows along the sea floor (Bianchi et al., 2006). The consistency in the population density over 4 years (Soliman and Rowe, 2008) implies that the peculiar conditions in the Mississippi Canyon head are persistent. Similar "blankets" of amphipods have been observed in shallow eutrophic habitats such as Boston Harbor (Gallagher and Keay, 1998). The imbalance in our carbon budget at this site leads us to concur with Bianchi et al. (2006) that this location exports material to deeper water.

Pequegnat et al. (1990) divided the megafauna on the Florida margin into three separate depth-related zones, based on similarities in species composition, but we have no evidence that differences in species composition were important at our oversimplified, reductionist level of analysis. Candidates for functionally dominant keystone species (Paine, 1980, 1995) would be the ubiquitous red crab *C. quinquedens* and the conspicuous giant isopod *B. giganteus*. The site on the Florida margin, S42 at 750 m, may sit within a faunal transition zone, as suggested in the literature (Menzies et al., 1973). The peculiar "ironstone", lower slope (2750 m) site (MT6, Fig. 1), first discovered by Pequegnat et al. (1972), was chosen as an "experimental" location because the standing stocks were low, not because of the rock-laden sediments. At this site, the echinoderms replaced the crustaceans as dominants. A mid-slope "echinoderm boundary" has been observed elsewhere, but never adequately explained (Rowe and Menzies, 1969; Pequegnat et al., 1990). The α (within habitat) diversity and total density of metazoan organisms were all low at the deep end of the depth range (Wei and Rowe, 2006), possibly because the biota becomes more harshly resource limited (Rex, 1983; Rex et al., 1997; Levin et al., 2001). It is tempting to infer that the faunal boundaries observed are a function of the decline gradient in food supply and that the ubiquitous "echinoderm boundary", therefore, lies somewhere between an input of 30 and 15 $mg\,C\,m^{-2}\,d^{-1}$.

The relative distribution of biomass among the size groups suggests that, when the input of organics is limitingly low, the large organisms are eliminated and functional importance shifts to smaller forms (Thiel, 1975, 1979; Polloni et al., 1979; Haedrich and Rowe, 1977; Thistle, 2001; Baguley et al., 2005), following well-established principles for detritus-based food webs (Ulanowicz, 1986; Jorgensen et al., 2002; Dinmore and Jennings, 2004). On the abyssal plain, the megafauna and the fishes had virtually disappeared. Resource partitioning estimated from the biomass distribution among these trophospecies (Grant and Schwinghamer, 1987; Rowe et al., 1991, 2003; Heip et al., 2001;

Piepenburg et al., 1995) suggests that the importance of the smaller heterotrophs (meiofauna and bacteria) in OM cycling increases with depth as resources become limiting. This is in contrast to high biomass communities in shallow water and at high latitudes in which the microbiota is often of relatively meager importance in both biomass (Christensen and Pauly, 1993; Arntz et al., 1994; Jarre-Teichmann et al., 1997) and SCOC (Rowe et al., 1994, 2002 (NEWPs)). Our single exception was the Mississippi canyon head (MT1) at which OM appeared to be cycled directly through all trophospecies, with the bacteria, meiofauna (Foraminifera and metazoans) and macrofauna components partaking more or less equivalently of the available detritus (Figs. 6 and 7), implying that they compete for the same resources (Post, 2002a, b).

5. Conclusions

- Both community biomass and SCOC decreased by a factor of 10 over the depth gradient of the sites studied (3 km), but the highest values were about an order of magnitude lower than the adjacent continental shelf.
- The total biota turns over on time scales of months on the upper continental slope but this is extended to years on the abyssal plain at 3.6 km depth. The detrital carbon turnover is many times longer, however, over the same depth interval.
- The relative importance of the size groups to total biomass and carbon cycling shifted from larger to smaller categories as resources become prohibitively limiting with increasing depth.
- A comparison of the carbon budgets across the depth gradient suggested that the Mississippi Canyon head on the upper continental slope exports organic detritus to deeper habitats.
- With the exception of the canyon head, the carbon demand at sites down the continental slope was greater than the model-based POC input estimated from surface-water pigments, suggesting that the basin margin supplemented the communities organic resources.
- Validation of our models will require direct observations, experimental manipulations (Snelgrove et al., 1996; Powell et al., 2002; Smith and Baco, 2003; Ruhl, 2007) and isotope analyses (Post, 2002b; Schuller et al., 2004) that parallel those in terrestrial and shallow-water food webs (Winemiller and Layman, 2005).

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