ABSTRACT

PURINTON, BRETT LEON. ^{14}C As a Tracer of Labile Organic Matter in Antarctic Benthic Food Webs (Under the direction of Dr. Dave DeMaster & Dr. Carrie Thomas)

^{14}C measurements were made on surface plankton, surface sediment, benthic invertebrate gut contents and body tissue samples to assess the effectiveness of this radioisotope as a tracer of labile organic carbon in Antarctic benthic food webs. Samples were collected on five cruises to the West Antarctic Peninsula shelf between November, 1999 and April, 2001 as part of the FOODBANCS Project (Food for Benthos on the Antarctic Continental Shelf). The ^{14}C contents of the deposit feeder body tissues (-127 ± 13 per mil) were substantially enriched relative to the surface sediment (-234 ± 13 per mil) (Tukeys HSD, $p=0.05$) and statistically similar to the organic matter collected in plankton tows (-135 ± 10 per mil). Selective ingestion was the primary feeding strategy used by echiuran worms and certain holothurians (i.e., *Peniagone* sp.) for incorporating labile organic carbon into their tissues as demonstrated by the large difference between surface sediment and gut contents ^{14}C activities (105 ± 13 per mil). Digestive and/or assimilatory selection was the primary feeding strategy used by irregular urchins and several other holothurians (*Protelpidia* sp., *Bathyplores* sp., and the head-down conveyor belt feeder, *Molpadia* sp.) for incorporating labile organic carbon into their tissues as demonstrated by large differences (41.9 ± 6.9 per mil) between their fore gut contents and body tissue ^{14}C activities. Despite large fluctuations in carbon export from the euphotic zone, benthic feeding strategies remained constant over the 15-month sampling period. Selective assimilatory processes also were evident in ^{13}C and ^{15}N data, but the ^{14}C measurements were a better tool for tracking labile organic carbon during ingestive and assimilatory processes.

**^{14}C AS A TRACER OF LABILE ORGANIC MATTER IN ANTARCTIC
BENTHIC FOOD WEBS**

By

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1. Introduction:

Over the past century, the Earth's atmospheric carbon dioxide (CO₂) content has increased from 280 to 379 ppm as a result of human activity. This atmospheric CO₂ increase, however, represents only 38% of the total CO₂ released from fossil fuel burning and deforestation (Sundquist, 1993). Over the next hundred years the average global warming associated with increased anthropogenic greenhouse gases (of which CO₂ is the predominant contributor) is believed to be on the order of 2-4°C (IPCC, 2001), with the largest effects (as much as 10° C) occurring in high latitudes (McKnight, 1999; IPCC, 2001). One of the largest sinks for anthropogenic CO₂ is the oceans, and therefore, understanding the marine carbon cycle is essential for predicting the climatic impacts of this important greenhouse gas.

Carbon reaches the ocean primarily by air-sea gas exchange as well as by riverine transport, where it is supplied in dissolved and particulate phases and in organic and inorganic forms. One process that maintains relatively low carbon dioxide levels in the atmosphere is the marine biological pump, which takes dissolved inorganic carbon from surface waters and transforms it to particulate calcium carbonate or organic matter. The particulate carbon settles through the water column, where much of the calcium carbonate is lost via dissolution in the deep ocean and most of the organic matter is recycled via grazing or microbial processes. Some of this particulate carbon, however, reaches the seabed. If the carbon is buried in the seabed, it is essentially removed from the atmosphere-ocean system.

The flux of organic carbon to the seabed is of critical importance to the benthic community because it is the major source of food and energy. Burial of this material in

the sediment column is affected by a number of factors including bacterial regeneration, bioturbation intensity, and sedimentation rate (Hedges & Keil, 1995). One factor controlling bioturbation intensity is consumption by deposit feeders (Jumars & Self, 1986). These benthic fauna can make up >50% by weight of the benthic food web (Hessler & Jumars, 1974; Gage & Tyler, 1991) and can ingest more than 50% of the depositional flux of organic matter on the continental margin (Miller et al., 2000).

Continental margin sediments are the primary oceanic deposit where marine particulate organic matter accumulates (Hedges & Keil, 1995). There are numerous inputs of this material to shelf and slope environments including particulate flux from the photic zone, riverine particulates and re-suspended sedimentary matter (lateral advection). The nutritional value of detritus determines its potential utilization by deposit feeding fauna (Tenore et al., 1984). Fresh organic matter has been shown to be rapidly ingested and degraded by benthic fauna and bacteria (Poremba, 1994). Fresh phytodetritus is directly available for consumption and utilization by megafauna, whereas older more refractory material is only indirectly available to most of the benthos, primarily through microbial degradation (Findlay & Tenore, 1982; Kristensen & Holmer, 2001). Ahrens et al. (2001) examined the assimilation of fresh phytoplankton by a benthic polychaete and found that fresh plankton was absorbed with a 55-95% efficiency compared to bulk sedimentary organic matter, which was absorbed at 5-18% efficiency. The incorporation of the fresh phytodetritus into body tissues is nearly six times more efficient than the incorporation of aged material (Kristensen and Mikkelsen, 2003). This fresh material is enriched in ^{14}C relative to bulk sedimentary organic matter, and therefore, provides a connection between age and food quality.

Stable isotopes of carbon and nitrogen have been widely used in the past to track organic matter moving through food webs (Tieszen et al., 1979, 1993; Rau et al., 1991). These tracers, however, are greatly affected by metabolic activities both during the production of organic matter (Francois et al., 1993; Laws et al., 1997; Popp et al., 1999; Rau et al., 1991), as well as, during degradation and recycling by fauna and bacteria (Tieszen et al., 1993). Because $\Delta^{14}\text{C}$ is isotopically corrected for variations in ^{13}C (Stuiver & Polach, 1977), these metabolic effects are essentially removed, therefore making $\Delta^{14}\text{C}$ a more dependable tracer of food quality.

1.1. Background and Hypotheses

^{14}C is naturally produced in the atmosphere when a neutron hits a ^{14}N nucleus resulting in proton emission. Stratospheric bomb testing in the 1950's and 1960's resulted in a large increase (+700 per mil) of radioactive carbon (^{14}C) in the atmosphere (Broecker and Walton, 1959; Nydel and Lovseth, 1983). This ^{14}C entered terrestrial and marine food webs as it was taken up by land plants and plankton through photosynthesis.

The ^{14}C activities of inorganic and organic materials in the ocean can result from a mixture of ^{14}C -depleted (older carbon) and ^{14}C -enriched (recently exchanged with the atmosphere) carbon sources. The relative contributions of both vary widely throughout the world's oceans. Near the West Antarctic Peninsula the Antarctic Ocean Circumpolar Current flows west to east causing upwelling of subsurface water. The upwelled water can be hundreds of years old, meaning that it is depleted in ^{14}C relative to current atmospheric concentrations. The mixing of upwelled and surface water results in lower surface ocean ^{14}C activities, which is known as the reservoir effect. The rates of

upwelling in the Antarctic are so great that they overwhelm the rates of air/sea gas exchange resulting in biota in the surface ocean with a negative $\Delta^{14}\text{C}$ activity (-145 per mil, or an age of 300 years) relative to the modern standard (Gordon & Harkness, 1992; Berkman & Forman, 1996).

^{14}C has been used as a tracer of freshly produced organic matter from the euphotic zone into deep-water food webs. Pearcy and Stuiver in 1983 measured ^{14}C in benthic fish and large invertebrates from the Oregon continental margin (~2800m water depth), but their data provided only limited evidence supporting the theory that surface production sustains benthic communities in deep water habitats. More recently, however, ^{14}C measurements made by Williams et al. (1987) demonstrated a direct connection between surface organic carbon production and abyssal-pelagic fish tissue. DeMaster et al. (2002) also used ^{14}C data to show a similar link between surface organic carbon production and deposit feeder tissue on the North Carolina continental slope.

Deposit feeders optimize the ingestion and assimilation of organic matter (Taghon, 1982; Taghon et al, 1978, Hudson et al., 2003) using optimal foraging behaviors, which include two strategies: 1) particle selection in which an animal preferentially selects food-rich material (Taghon et al., 1978; Fauchald and Jumars, 1979; Billet et al., 1988; Lopez and Levinton, 1987; Self and Jumars, 1988; Levin et al., 1997; Ferner and Jumars, 1999) and 2) assimilatory selection in which an animal may feed on bulk sedimentary material but primarily digests and incorporates the labile organic matter (Mayer et al., 1997; Penry and Jumars, 1990; Jumars 2000).

One of the main factors affecting the supply of freshly produced organic matter to the sea bed is seasonal variations in primary production. The WAP is subject to extreme

seasonal variations in ice cover and the high rates of primary production during the summer can be one to two orders of magnitude greater than the primary production in the winter (Holm-Hansen, 1985; Clarke, 1988; Knox, 1994; Wefer, 1989). In Marguerite Bay (68°S), near the southern reaches of the Antarctic Peninsula, some species of benthic invertebrates respond to this oscillating food supply as they reduce their metabolic activities and stop feeding during much of the austral winter (Fraser et al., 2002). Near Palmer Station (64°S), further north on the Antarctic Peninsula, numerous benthic fauna have been shown to feed year round, based on ^{234}Th activities in gut samples (McClintic, 2002).

In this study we use radiocarbon to track the recently produced organic material from phytoplankton as it is transported from the euphotic zone to the seafloor of the West Antarctic Peninsula (WAP). We also use this tracer to resolve feeding strategies in benthic deposit feeders (Pearcy & Stuiver, 1983; Williams et al., 1987, 1992; DeMaster et al., 2002). Sampling of deposit feeding invertebrates, surface sediments, and surface plankton over five FOODBANCS cruises (FOOD for Benthos on the Antarctic Continental Shelf) between November, 1999 and February, 2001 enabled us to track the production and fate of freshly produced organic matter over several seasons and assess the feeding strategies of deposit feeders.

Two goals were emphasized during this research project. The first was to use ^{14}C to assess food quality and food source for deposit feeders on the WAP. The second goal was to use ^{14}C measurements in benthic substrates and tissues to track recently produced organic carbon during the ingestion and digestion/assimilation processes of benthic deposit feeders. With these goals in mind two hypotheses were formulated and tested.

The first: recently produced, plankton-derived organic matter is the predominant source of assimilated organic carbon for benthic deposit feeders on the WAP. The second: recently produced planktonic organic matter (as tracked by ^{14}C measurements) is acquired through species-specific feeding strategies involving particle selection and selective digestion/assimilation.

2. Materials and Methods:

2.1. Sample Collection

Sample collection was completed on five separate research cruises denoted as FOODBANCS (FB) I - V. Sample collection began in November of 1999 and ended in February of 2001 (Table 1). The *R/V Laurence M. Gould* was utilized for cruises I, II, IV and V, and the *R/V Nathaniel B. Palmer* was used for cruise III. Samples were collected at three sites off the coast of the West Antarctic Peninsula near Palmer Station at a water depth of 550 to 600 meters. The three stations were chosen to establish a cross-shelf transect within the Palmer Station LTER region (Figure 1). Site B was located near the Palmer Station LTER mooring and was the location of two sediment traps (150 & 170m above the sea bed) deployed between cruises.

2.1.1. Collection of Deposit Feeders

Deposit feeding fauna were collected at all three stations and on all five cruises. This was accomplished using a 9 meter Otter trawl. Six primary organisms were targeted for collection and analysis to evaluate different feeding strategies. Four surface deposit feeders including three holothuroids: *Bathyplores sp.*, *Peniagone sp.*, *Protelpidia sp.*, and

an echiuran worm as well as two subsurface deposit feeders including an irregular urchin (*Amphineustes sp.*) and the head-down deposit feeding holothuroid, *Molpadia sp* were collected over the five FOODBANCS cruises. All of the specimens sampled were adults and had no obvious damage as a result of collection.

The animals were dissected and frozen within 12-24 hours of collection. Samples of body tissue were removed from the body wall of each individual, making certain to exclude all gut and reproductive tissues. Samples of gut contents were collected from the fore, mid and hind guts of the *Molpadia sp.*, *Bathyplores sp.* and *Protelpidia sp.*, avoiding contamination from gut tissue. Whole gut contents were collected in the *Amphineustes sp.*, *Peniagone sp.* and the echiuran worm due to the small amount of gut sediment present in those species. For *Peniagone sp.*, whole gut samples from 4-5 individuals had to be combined to obtain sufficient material for analysis. Due to the small diameter and fragile nature of the echiuran gut the entire gut including the gut lining was collected and analyzed.

2.1.2. Collection of Surface Plankton

Surface plankton was collected using a Tucker trawl which had an opening of 1 x 1.5m and an 80µm mesh net. Samples of surface plankton were collected at each site on each cruise over a period of 30 minutes. Ice algae were collected by melting blocks of sea ice and then concentrating the algae by settling and centrifugation. Following collection, the plankton were frozen and then shipped back to North Carolina State University for processing.

2.1.3. Collection of Surface Sediment

Surface sediment was collected using a Mega-corer. Each core was subsampled in ½ cm intervals for the first 2cm and every 1cm after that down to 20-35cm. These samples were transferred to 65ml glass Wheaton vials and dried at 65°C for 24 to 48 hours or until dry. During cruise FB-V, a distinct layer of phytodetritus occurred on the surface of the seabed. This surface floc layer was judged to be the top 1-2cm, consisting of softly packed brown sediment. A color change from brown to olive grey was evident between the floc layer and the bulk sediment.

2.2. Laboratory Analyses

To limit carbon contamination from laboratory materials and other samples, all glassware was combusted in a muffle furnace at 510°C for 6 hours prior to use. All other lab equipment was cleaned using methanol and rinsed with DI water.

Tissue and gut samples were maintained frozen until processed at NCSU. The frozen samples were placed in glass beakers and dried in a 65°C oven for 48 hours. Following drying, the samples were ground using a glass stirring rod or a mortar and pestle in order to achieve homogeneity. The samples were placed in 16mL Teflon capped glass scintillation vials for long-term storage.

2.2.1. Isotopic Analyses

After drying, samples were pretreated to remove inorganic carbon. Approximately 0.2-0.3g of sample were placed in a 16ml glass vial and 750µL of 1 N HCl were added. The acidified samples were placed in a fume hood for 12 hours to allow

sufficient time for inorganic carbon dissolution. Subsequently, they were moved back into the 65°C oven to dry for 24 hours. After acidification, samples were combusted using a Thermo Finnigan 1112 EA CN analyzer. This unit combusts the sample and uses a gas chromatographic column and thermal conductivity detector (TCD) to measure the organic carbon and nitrogen contents of the sample (precision wt. % carbon +/- 0.22%, wt. % nitrogen +/- 0.07%). The resulting CO₂ was then cryogenically isolated in a glass ampule using liquid nitrogen and processed for isotopic analyses (Blair & Carter; 1992). ¹⁴C analyses were performed at the Woods Hole Oceanographic Institute using an accelerator mass spectrometer ($\Delta^{14}\text{C}$ precision of Oxalic Acid Standard (n=4), +/- 2.4 per mil). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses were performed using a Finnigan MAT 252 equipped with a Carlo Erba CNS 1500 analyzer at the University of North Carolina (precision +/- 0.2 per mil). Daily calibration of the instrument was performed using acetanilide as a working standard to bracket the sample size range of the FOODBANCS samples. Interlaboratory comparison of the carbon and nitrogen isotopic measurements were made in order to determine the accuracy of the instrumentation.

2.3. Statistical Analysis

Analysis of variance (ANOVA) was conducted on all data. If significant variation was evident as a result of the ANOVA, then Tukeys Studentized Range (HSD) Tests were performed to compare the means of differing populations. All statistical results are reported with a 95% confidence interval.

3. Results:

Radiocarbon and stable isotopic compositions were determined on a total of 150 samples (see Appendix). Samples of surface plankton and surface sediment from site B were analyzed from every cruise. Deposit feeder tissues and gut content samples were collected and analyzed from every cruise in order to examine seasonal variations in feeding strategies.

Due to the limited data set and numerous variables (species, site and season) differences in ^{14}C activities among the three study sites were assumed to be negligible in order to evaluate the temporal variation. Although variation between sites might be important, seasonal changes in carbon export from the euphotic zone were presumed to be more significant. The temporal differences associated with gut passage time (~24hrs; Hudson et al., 2004; Miller et al., 2000) and tissue turnover (months to years; Gage & Tyler, 1991) make gut contents (fore gut contents from *Batyplotes sp.*, *Molpadiid sp.*, and *Protelpidia sp.*; whole gut contents from echiuran worm (including gut lining) the optimal samples for assessing seasonal variations of ingested material. Differences in the ^{14}C activities of fore gut and whole gut contents among cruises were found to be insignificant (ANOVA, $p=0.5870$), so data were grouped for greater statistical power.

Figure 2 shows the average $\Delta^{14}\text{C}$ activities of surface plankton, body tissue, surface sediment and sediment trap material. Average body tissue, surface plankton and sediment trap $\Delta^{14}\text{C}$ activities remained constant and statistically similar ($p<0.05$) during the FOODBANCS study. Average activities of -125.6 ± 12.8 per mil, -135.0 ± 10.1 per mil and -152.6 ± 9.1 per mil were calculated respectively.

The average $\Delta^{14}\text{C}$ content of surface sediment was calculated using data from the first four cruises, excluding FB-V data because of the interannual depositional event (no such layer was detected during the summer of 2000). The average $\Delta^{14}\text{C}$ content for surface sediment over the first four cruises was -233 ± 13 per mil. FB-V surface sediment had a distinctly enriched $\Delta^{14}\text{C}$ value (-177 ± 16 per mil) as a result of an interannual event depositing several centimeters of phytodetritus. The organic carbon content of this layer was twice that measured on all other cruises (Figure 3).

Gut contents (fore gut contents from *Batyploetes* sp., *Molpadiid*, sp., and *Protelpidia* sp.; whole gut contents from echiuran worm (including gut lining) was collected and analyzed to assess the feeding strategies of the benthic fauna. Figure 4 shows average $\Delta^{14}\text{C}$ activities of gut contents for the six species investigated. As a result of the Tukeys HSD procedure two distinct groupings of individuals resulted; the *Peniagone* sp. and the echiuran worm were highly particle selective ($p < 0.05$) (large difference between fore gut contents ^{14}C and surface sediment ^{14}C activities), whereas the *Molpadiid* sp., *Amphineustes* sp., *Protelpidia* sp., and *Bathyploetes* sp. were less particle selective.

To assess internal changes in the freshly produced organic carbon $\Delta^{14}\text{C}$ activities were contrasted in the fore gut and hind gut samples ($n=10$) of *Protelpidia* sp., *Molpadiid* sp. and *Bathyploetes* sp. Down-gut organic carbon was significantly ($p < 0.03$) depleted in ^{14}C relative to the sediment in the fore gut. An average decrease in $\Delta^{14}\text{C}$ activity of 15 ± 6 per mil was observed in all 3 species.

The stable isotopes of carbon and nitrogen were measured to provide independent assessments of organic carbon source and food quality (Fry, 1984, 1988; Rau et al.,

1991). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data from WAP samples showed some selective preference for the heavier isotopes of both carbon and nitrogen in body tissue samples (Figure 5). The isotopic measurements of surface sediment resembled that of fore gut sediment (-25 per mil $\delta^{13}\text{C}$, 4 per mil $\delta^{15}\text{N}$). Body tissue $\delta^{13}\text{C}$ values ranged from -10 to -27 per mil, whereas the $\delta^{15}\text{N}$ values ranged from 4 to 16 per mil. Surface plankton had a narrow range in $\delta^{15}\text{N}$ (1-6 per mil) but varied widely in $\delta^{13}\text{C}$ (-37 to -15 per mil). Ice algae, which are typically enriched in ^{13}C (Wada et al., 1987; Hobson et al., 1995), had a value of -19.9 +/- 0.5 per mil $\delta^{13}\text{C}$ and 3.0 +/- 0.4 per mil $\delta^{15}\text{N}$.

4. Discussion:

4.1. Goal 1: Use ^{14}C to assess food quality and food source for deposit feeders on the WAP.

H1: Recently produced, plankton-derived organic matter is the predominant source of assimilated organic carbon for benthic deposit feeders on the WAP.

Numerous studies have investigated the export of organic carbon from the euphotic zone near the WAP (summarized in Karl et al., 1996). Large seasonal fluctuations have been measured in export near the Antarctic coast due to sea ice cover and diminished light levels (Holm-Hansen, 1985; Clark, 1988; Knox, 1994) with large blooms generally following the ice melt in the spring (R. Smith et al., 1995, 1996). These studies, however, are limited with respect to delivery rates of organic carbon to the sea floor.

Particle traps placed 150 and 170m above the ocean bottom near the Palmer Station LTER mooring site revealed minimal seasonal change in carbon delivery near the sea bed during the first three deployments (Figure 6) (Smith et al., In Prep.). These traps, which collected material between cruises, provide an estimate of the organic carbon delivery to the benthos. The traps that were deployed between FB-IV and FB-V showed a large increase in organic carbon delivery relative to previous fluxes, which corresponds with the phytodetritus layer observed during FB-V. This interannual event could be a source of organic carbon loading to the sediment, possibly adding to the food bank for the benthos (McClintic, 2002; Mincks, In Press). This interannual deposition of high organic content material to the sediment trap during FB-V did not result in a large increase in the ^{14}C content measured in that sediment trap (Figure 7).

Deposit feeders ingest a diverse range of materials from the surface sediment. The bulk sediment ^{14}C activity originates from numerous carbon inputs. A fraction of this material is fresh, recently deposited detritus from the surface ocean; however a large part is older, more refractory organic matter (Wakeham et al. 1997). This combination of sources results in an average $\Delta^{14}\text{C}$ activity of -233 ± 13 per mil for the upper half centimeter of the seabed, which is significantly different from the average plankton ^{14}C activity (-135 ± 10 per mil) (Tukey HSD, $p > 0.05$). The 80 per mil difference between plankton and bulk surface sediment emphasizes the addition of older more refractory organic carbon in the seabed probably as a result of the resuspension and lateral advection of previously deposited sediment and mixing due to bioturbation with older sediments as well as the preferential remineralization of fresh material.

The production of ^{14}C enriched organic matter in Antarctic continental shelf surface waters relative to that observed in surface sediments allows for the tracking of recently produced planktonic material from the euphotic zone through benthic faunal communities. The surface plankton ^{14}C activity is statistically similar (Tukey HSD, $p>0.05$) to that of deposit feeder body tissue (Figure 2), which demonstrates the relationship between recent organic matter production at the surface and assimilation by deposit feeders on the seafloor. With the consistent delivery of ^{14}C enriched organic carbon to the seafloor as demonstrated by the particle traps and the similar ^{14}C activities of surface plankton and benthic deposit feeder body tissues, we conclude that the predominant food source to these benthic fauna is recently produced planktonic organic matter. The recycling of older more refractory organic matter by bacteria has been suggested as a possible food source to benthic fauna in the deep sea (Frindlay & Tenore, 1982; Kristensen & Holmer, 2001). If this were the case near the WAP, benthic fauna would show a decreased body tissue ^{14}C relative to surface planktonic organic matter instead of a statistically similar ^{14}C activity.

4.2. Goal 2: Use ^{14}C measurements in benthic substrates and tissues to track recently produced organic carbon during the ingestion and digestion/assimilation processes of benthic deposit feeders.

H2: Recently produced planktonic organic carbon (as tracked by ^{14}C measurements) is acquired through species-specific feeding strategies involving particle selection and selective digestion/assimilation.

The ability of the various deposit feeders to maintain a ^{14}C enriched body tissue resembling that of surface plankton is believed to be the result of two primary behaviors; selective ingestion and selective digestion and/or assimilation. An index of selective particle ingestion can be determined by subtracting the $\Delta^{14}\text{C}$ activity of the surface organic sediment from the $\Delta^{14}\text{C}$ activity of the organic matter in the gut contents of the deposit feeder. This difference reflects the animal's ability to preferentially ingest the relatively fresh food sources (presumably the more labile organic carbon) relative to the organic material in the bulk surface sediment (Figure 4). In contrast, an index of selective digestion/assimilation can be determined by subtracting the ^{14}C content of the organic material in the gut contents from the ^{14}C content of the deposit feeder's body tissue (Figure 8). This difference represents the animal's ability to preferentially digest and assimilate the more recently produced planktonic organic material from the bulk ingested sediment, assuming steady state input to the fore gut.

Of the six species studied, only the echiuran and *Peniagone sp.* ingested material with a ^{14}C content even close (within ~ 10 per mil) to that of their body tissue. The other four organisms showed a range of selectivity, exhibiting a mean ^{14}C difference between gut contents and body tissue of 42 ± 22 per mil. The highest indices of selective particle ingestion were exhibited by the echiuran worm and the holothurian *Peniagone sp.*, both of which are surface deposit feeders. There appears to be little difference in the particle selection indices for the mobile surface deposit feeder (*Peniagone sp.*) as compared to the surface deposit feeder with limited mobility (echiuran worm).

Particle selection has been hypothesized as a means to reduce inter-species competition for labile organic carbon (Bock & Miller, 1999; Uthicke & Karez, 1999).

Miller et al. (2000) hypothesized that mobility in deep-sea deposit feeders may help control competition; however this is not obvious in the data from the WAP. The six organisms studied covered a range of feeding depths and mobilities. As mentioned above, the echiuran worm and the *Peniagone sp.* were the most selective and yet one is highly mobile (*Peniagone sp.*), and the other has only limited mobility. The other four organisms include: surface (*Bathyplores sp.* & *Protelpidia sp.*) and sub-surface deposit feeders (*Amphineustes sp.* & *Molpadia sp.*) as well as mobile (*Bathyplores sp.*, *Protelpidia sp.*, *Amphineustes sp.*) and limited mobile species (*Molpadia sp.*). Although both sub-surface deposit feeders (*Amphineustes sp.* & *Molpadia sp.*) were in the group exhibiting limited selective ingestion, there were two surface deposit feeders (*Bathyplores sp.* & *Protelpidia sp.*) with comparable ^{14}C data showing equally limited ingestive selection. Therefore, species that are subsurface deposit feeders do not necessarily exhibit reduced selective particle ingestion abilities relative to some surface deposit feeders.

Gut morphology also has been shown to be related to selective particle ingestion. Hudson et al. (2003) observed that *Bathyplores natans*, common in the NE Atlantic deep sea, exhibited ingestive selection for labile material and it has a relatively small and narrow gut. This trend is consistent with our ^{14}C data concerning deposit feeders on the West Antarctic Shelf because the echiuran worm and the holothurian *Peniagone sp.*, having the narrowest guts and smallest gut contents, were the most particle selective deposit feeders of the 6 species studied.

The comparison of gut contents to surface sediment ^{14}C does have potential complications. There are a number of factors that could affect the ^{14}C activity of the gut

contents including preferential particle retention (Tabhon et al., 1978) and enzyme addition through digestive secretions (Massin, 1980). The preferential retention of labile particles in the gut is generally attributed to more complex gut structures, whereas a simple plug flow reactor has been described for most holothuroid species (Penry, 1989) and is probably applicable to the echiuran worm as well. The addition of digestive chemicals primarily takes place in the fore gut and these compounds should have a ^{14}C activity similar to that of the body tissues. Massin (1980) attributed an enrichment of fore gut organic carbon contents in benthic invertebrates to digestive secretions and found that a 4-8% enrichment was present. If similar processes occur in the species studied in this project, digestive secretions could account for a 2-5 per mil ^{14}C enrichment based on an isotope mass balance calculation. Although this would change the calculated amount of particle selection, it would not change the overall conclusions that the echiuran worm and the *Peniagone sp.* are the most particle selective deposit feeders.

The strong particle selection exhibited by the echiuran worm and *Peniagone sp.* is also supported by ^{234}Th data from these animals. ^{234}Th is a naturally occurring, particle reactive radioisotope with a 24.1 day half life. This radionuclide is scavenged from the water column by settling particles, which makes it a good tracer of recently deposited material on a hundred-day time scale. The higher the ^{234}Th in the gut contents, the greater the particle selectivity of the species (Miller et al., 2000). The concentration of this tracer is unaffected by the addition of digestive compounds to the gut, and therefore, supports the findings presented here. Figure 9 presents the gut contents ^{234}Th data from the same animals in which ^{14}C measurements were made (McClintic, 2002). The increased ^{234}Th concentration in the echiuran and the *Peniagone sp.* gut contents (relative

to bulk surface sediments and other benthos) supports the conclusion that these organisms were the most particle selective ingestors. ^{234}Th has been positively correlated to phytodetritus (chl-a, phaeopigment) (Demopoulos, 2003), however, this tracer does not have a direct link to labile organic carbon in the way that ^{14}C does.

The use of whole gut measurements in the echiuran worm (including gut lining), *Peniagone sp.* and *Amphineustes sp.* may have biased to some extent the results concerning organic carbon selection and assimilation. By collecting the whole gut contents, not only was the most recently ingested material included in the sample, but also the material that was about to be defecated. The latter material is presumably depleted in ^{14}C due to the preferential breakdown of fresh material during gut passage. Consequently, the calculated ^{14}C enrichments from particle selection based on whole gut analyses may have been underestimated (relative to measurements based solely on fore gut contents). The use of whole-gut ^{14}C data in the calculation of assimilatory effects maximizes the differences between body tissue and gut contents (relative to comparisons of body tissue and fore gut contents). A potentially larger problem, however, is the inclusion of the gut lining in the echiuran samples. This tissue is likely to be highly enriched in ^{14}C , similar to the body tissue. The incorporation of this tissue could contribute to the enriched ^{14}C activities measured in the echiuran samples. However, it is unlikely that the inclusion of gut lining accounts for all of the enhanced particle selection measured in the echiuran samples because ^{234}Th activities support the conclusion that *Peniagone sp.* and the echiuran are the most highly particle selective deposit feeders.

Feeding structures including tentacles (Holothuroidea) (Moore & Roberts, 1994), ciliated proboscis (Echiuroidae) (Ruppert & Barnes, 1994) and specialized tube feet in

the case of the irregular urchin (Echinoidea) (Jangoux & Lawrence, 1982) have been linked to selective ingestion of labile food particles. All of the organisms studied during this project, excluding the echiuran worm, rely on the secretion of a sticky substance at the end of their tentacles or tube feet to collect sediment (Moore & Roberts, 1994; Jangoux & Lawrence, 1982). Grain size, surface texture, specific gravity and organic coatings have all been linked to particle selection of high food quality material in deposit feeders (Taghon, 1988). Many of these characteristics contribute to the stickiness of the particle, and therefore, result in preferential collection by benthic fauna (Taghon et al., 1990; Guieb et al., 2004). In this way, deposit feeders may be indirectly collecting the more recently produced organic material (and thereby the more recently produced and labile carbon).

Although tentacle shape was not directly studied during this research project, this characteristic has often been associated with particle selection. The structure of the tentacle as either digitate or peltate is hypothesized to control the degree of particle selection by an individual organism. Peltate tentacles with their fine branching are believed to be more selective ‘sweepers’ of particles, whereas digitate tentacles are thought to be less selective ‘grabbers’ or ‘rakers’ of surface particles (Moore & Roberts, 1994). Our ^{14}C data, however, do not support this association concerning tentacle shape and food selection. The *Molpadia sp.* with its digitate tentacles showed a similar selective ability (a 64 per mil difference between fore gut contents and surface sediment) compared to *Bathyplores sp.* (69 per mil) and the *Protelpidia sp.* (63 per mil), which have fine peltate tentacles. The specialized proboscis occurring in the family *Echiuridae* appears to be highly selective for the freshest material, as exemplified by the elevated ^{14}C

activity in the echinuran gut contents. This enhanced selectivity may be the result of this deposit feeder's ability to collect recently deposited sediment from the very top (or floc layer) of the sediment column.

The ^{14}C activities of inter-species body tissues are similar; therefore, those species that are poor particle selectors must make up the difference through selective digestion and/or assimilation. The relative decrease in selective ingestion observed in the 4 Antarctic deposit feeders (*Molpadia sp.*, *Protelpidia sp.*, *Bathyplores sp.*, *Amphineustes sp.*) is complemented by a contrasting increase in selective digestion and/or assimilation (Figure 8). The mechanisms behind this selective digestion/assimilation could be multifaceted including mechanical such as gut architecture and/or biochemical such as enzymatic reactions (Plante et al., 1989, 1996; Mayer et al., 1995, 1997; Thomas and Blair, 2002; Jumars, 2000a,b). Our conclusion is that independent of the species and feeding strategy, deposit feeders on the WAP primarily utilize recently produced planktonic organic matter originating in the surface ocean.

Changes in the composition of organic compounds such as proteins, carbohydrates and lipids in benthic invertebrates during ingestion and digestion have been studied, mostly through feeding experiments (Kofoed, 1975; Yingst, 1976; Kemp, 1986; Grémare, 1990; Olivier et al., 1996; Thomas & Blair, 2002). Down-gut digestive processes resulted in a significant decrease in ^{14}C activity between the fore gut and hind gut contents. This down-gut decrease in the ^{14}C content of the gut material (and by inference the lability of the organic matter) was evident in all 10 individuals (*Molpadia sp.*, *Protelpidia sp.*, *Bathyplores sp.*) examined over the course of this study. This perceived preferential degradation of ^{14}C enriched material could be caused in part by the

secretion of digestive enzymes (^{14}C enriched similar to body tissue) in the fore gut and absorption of this reactive material in the mid and hind guts. As was discussed earlier, the addition of digestive compounds in the fore gut could result in as much as a 2-5 per mil enrichment in ^{14}C activity, and the down-gut trend for the 3 Antarctic deposit feeders is approximately 15 per mil, indicating a likely decrease in the proportion of freshly produced planktonic organic matter downgut. Future studies of these processes may consider separation of dissolved and particulate material when analyzing the ^{14}C activity of gut contents.

The relative contributions of both selective ingestion and selective digestion/assimilation appear to remain constant seasonally. Calculated ^{14}C differences between fore gut contents and surface sediment (representing selective ingestion) and between body tissue and fore gut contents (representing selective assimilation; Figure 10: a, b), exhibit a limited seasonal change across the 6 species examined on the WAP. Although the absolute values of the ^{14}C enrichments from particle selection and digestive/assimilatory processes vary somewhat with season, the relative enrichment between species remains essentially constant over time. The flocc layer observed during FB-V resulted in a reduction in the calculated amount of selective ingestion exhibited by many of the species studied. This reduction in particle selection may result from the deposit feeders' response to the unusually high abundance of relatively fresh organic matter in the phytodetritus layer.

4.3. Stable Isotopic Analysis

The isotopic abundances in an animals tissue is largely the result of the animals' diet (Cherrier et al., 1999; Fry & Sherr, 1984). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ have been widely used to

track food source in food webs (Fry & Sherr, 1984; Wada et al., 1987). However, these isotopes are affected by metabolic as well as environmental factors (Popp et al., 1999; Rau et al., 1991), which can result in wide ranging values. Analyses of stable isotopes were performed in order to examine food sources, selective ingestion, selective assimilation and trophic relationships (Fischer, 1991; Rau et al., 1991; Frazer, 1996; Popp et al., 1999; Villinski et al., 2000; Williams et al., 1992) (Figure 5).

In the stable isotope data set the fore gut contents and the surface sediment occupy the same area in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, whereas they were quite different when contrasting their ^{14}C activities. The source materials for the recently produced organic carbon (surface plankton and ice algae) have a wide range of $\delta^{13}\text{C}$ values, and similar $\delta^{15}\text{N}$ values compared to both surface sediment and fore gut contents. Because of this result, it is unclear in stable isotope space if deposit feeders selectively feed or if they feed on bulk organic carbon. The enrichment observed in ^{14}C activity with respect to differences between gut contents and surface sediment provides a clearer view of this selective process. The wide variations in ^{13}C could be due to temperature effects and/or dissolved CO_2 concentration during production (Popp et al., 1999; Rau et al., 1991). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ have been shown to be affected by the timing, duration, and conditions of a bloom event. As nutrients become more depleted, $\delta^{13}\text{C}$ values tend to rise (Farquhar et al., 1982; Rau et al. 1992, 1996). Closed system process occurring under sea ice could affect the isotope values of plankton (Rau et al., 1992). Gibson et al. (1999) showed that as CO_2 is depleted under the ice, due to limited mixing with the atmosphere, $\delta^{13}\text{C}$ varied. The changing environment encountered in an upwelling zone can have large scale effects on the measured $^{13}\text{C}/^{12}\text{C}$ ratio of particulate organic carbon (Rau et al., 2001). These

processes might explain some of the variation measured during the five FOODBANCS cruises

Body tissue is enriched in both ^{13}C and ^{15}N with respect to fore gut contents and surface sediments. However, because of the large range in source material $\delta^{13}\text{C}$ values, it is difficult to attribute this shift to the assimilation of freshly produced planktonic organic material. Commonly the shift in stable isotopes between plankton and deposit feeder body tissue is attributed to trophic level effects, which have been estimated to be about 1‰ for ^{13}C and 3-4‰ for ^{15}N per trophic level (Fry and Sher, 1984; Minagawa and Wada, 1984) due to the selective retention of the heavy isotope during metabolic breakdown within the body. These effects are taken into account when the ^{14}C contents are expressed using the $\Delta^{14}\text{C}$ format, because all of the data are normalized to a common $^{13}\text{C}/^{12}\text{C}$ ratio.

5. Conclusions:

Benthic megafauna near the WAP rely on two processes to optimize the incorporation of recently deposited planktonic material throughout the year. A combination of selective ingestion (particle selection) and selective digestion and/or assimilation results in a seasonally constant body tissue ^{14}C . These two processes appear to be unaffected by seasonal changes in carbon export out of the euphotic zone.

Selective ingestion is a species specific characteristic that has limited correlation to mobility or feeding location. The surface deposit feeding, echiuran worm and the holothurian *Peniagone sp.* primarily rely on selective ingestion for incorporation of labile carbon into their body tissue. The other four species studied, which included both surface

deposit feeders and sub-surface deposit feeders, exhibited a limited extent of particle selection. The three holothurians (*Molpadia sp.*, *Protelpidia sp.*, *Bathyplores sp.*) and the irregular urchin (*Ampineustes sp.*) primarily rely on selective digestion/assimilation for incorporation of labile carbon into their body tissue.

Over the six species of deposit feeders examined in this study the combination of selective ingestion and selective digestion/assimilation resulted in body tissue ^{14}C that was statistically similar to that of recently produced surface plankton. This leads us to conclude that independent of surface production, deposit feeders on the WAP are capable of surviving on predominantly recently produced organic matter. ^{14}C is a good tracer of labile organic matter in benthic food webs. The tracer indicates that benthic invertebrates are highly selective for the recently produced (and presumably labile) organic matter as they ingest and assimilate organic matter on the Antarctic shelf.

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Table 1: FOODBANCS field collections. Five cruises covering the austral summer of 1999 through the austral summer of 2001.

Cruise Number	Start Date	End Date
FB - I	11/23/1999	12/7/1999
FB - II	3/9/2000	3/17/2000
FB - III	6/6/2000	6/17/2000
FB - IV	10/24/2000	11/14/2000
FB - V	2/20/2001	3/9/2001

Figure 1: Field stations for FOODBANCS project, site A (64° 12.4' S; 64° 47.3' W), site B (64° 48.0' S; 65° 21.0' W), and site C (65° 12.4' S; 65° 22.5' W). Site B is near the Palmer Station LTER mooring site.

Figure 2: Average organic ^{14}C values from surface plankton and body tissue from all five FOODBANCS cruises. Surface sediment is averaged over the first four cruises, excluding FB-V due to the interannual floc layer observed during that cruise. (*) Body tissue $\Delta^{14}\text{C}$ is statistically similar to that of surface plankton and sediment trap $\Delta^{14}\text{C}$ (Tukeys HSD, $p < 0.05$).

Figure 3: Weight percent organic carbon in surface sediments (0 - 0.5cm) from FB-I - FB-V. Measurements are single analyses (± 0.016 instrument error) made at site B. FB-V is believed to be an interannual depositional event, possibly contributing to the food bank of organic carbon in the sediment.

Figure 4: Average $\Delta^{14}\text{C}$ activity of gut contents (fore gut contents from *Batyplores sp.*, *Molpadiid sp.*, and *Protelpidia sp.*; whole gut contents from echiuran worm (including gut lining), *Peniagone sp.*, and *Amphineustes sp.*) and surface sediment averaged over all 5 FOODBANCS cruises. Large differences between surface sediment and gut contents are suggestive of particle selection. All organisms investigated showed enriched gut contents with respect to bulk surface sediment. (*) The echiuran worm and the holothuroid *Peniagone sp.* gut contents are statistically more enriched in $\Delta^{14}\text{C}$ (Tukeys HSD, $p < 0.05$) than the other 4 deposit feeders.

Figure 5: $\delta^{13}\text{C}$ content versus $\delta^{15}\text{N}$ content for FOODBANCS samples. The wide range in isotopic values measured in the planktonic organic source material (e.g., $\delta^{13}\text{C}$ content of plankton and ice algae; -37 to -15 per mil), as well as the metabolic processes affecting these isotopes limit the effectiveness of these measurements for tracking recently produced organic matter in this environment.

Figure 6: Organic carbon flux rates calculated from sediment traps located at site B, 150 and 170m above the seabed. Flux rates in these traps over the first three deployments remained similar ($p < 0.05$). The trap collected during FB-V received a relatively large organic carbon flux, which was consistent with the occurrence of a phytodetritus layer on the ocean floor (Smith et al., In Prep.).

Figure 7: Between cruise trap data in comparison to seasonal plankton ^{14}C values. Particle traps integrate over a period of three months. The large depositional event during FB-V did not result in a large increase in sediment trap $\Delta^{14}\text{C}$. Error bars indicate the standard deviation between multiple samples of plankton from the same site and the deviation between the top and bottom trap during the second trap deployment.

Figure 8: Assimilatory selection is defined as the difference in the $\Delta^{14}\text{C}$ activity of the gut contents (fore gut contents from *Bathyplores* sp., *Molpadiid* sp., and *Protelpidia* sp.; whole gut contents from echiuran worm (including gut lining), *Peniagone* sp., and *Amphineustes* sp.) and the body tissue. (*) The echiuran worm and the holothuroid *Peniagone* sp. exhibited the most highly enriched gut contents resulting in the smallest difference between the gut $\Delta^{14}\text{C}$ and the body tissue $\Delta^{14}\text{C}$ (Tukeys HSD, $p < 0.05$). The organisms that had limited selective ingestion show greater internal enrichment as a result of digestive and/or assimilatory processes.

Figure 9: Plot of gut contents (fore gut contents from *Batyplores* sp., *Molpadiid* sp., and *Protelpidia* sp.; whole gut contents from echiuran worm (including gut lining), *Peniagone* sp., and *Amphineustes* sp.) ^{234}Th . The increased values measured in the echiuran and the *Peniagone* sp. are the result of particle selection (McClintic, 2002).

Figure 10: A) Seasonal plot of selective ingestion determined by subtracting the surface sediment $\Delta^{14}\text{C}$ content from the gut contents (fore gut contents from *Bathyplores* sp., *Molpadiid* sp., and *Protelpidia* sp.; whole gut contents from echiuran worm (including gut lining), *Peniagone* sp., and *Amphineustes* sp.) $\Delta^{14}\text{C}$. Seasonal trends in surface production of organic matter appear to have little effect on this index of selective ingestion. The floc layer observed during FB-V results in the decreased differences measured during that cruise. B) Seasonal plot of selective digestion/assimilation determined by subtracting the gut material $\Delta^{14}\text{C}$ from the body tissue $\Delta^{14}\text{C}$. The higher the calculated value the greater the selective process. Although the absolute values of the $\Delta^{14}\text{C}$ enrichments from particle selection and digestive/assimilatory processes vary somewhat with season, the positions of the data relative to the other species remains essentially constant over time. The data shown in this figure come from single species analyses per season, with the analytical error in the $\Delta^{14}\text{C}$ measurement (± 2.4 per mil) approximately equal to the size of the symbol.

APPENDIX A
 $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C/N, and $\Delta^{14}\text{C}$ FOODBANCS Data

Gut Contents Samples				
FOODBANCS Sample	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Atomic C/N	Corrected $\Delta^{14}\text{C}$
FBV-B Echi #2 WG W/ Lining, CRS799	-25.2	9.27	6.22	-118.55
FBV-C Scoto 2/3 FG, CRS775	-26.44	4.31	8.30	-155.43
FBV-B, Molp. #1 FG, CRS754	-26.02	5.27		
FBV-B, Molp#1 FG, CRS754	-25.74	5.16	7.18	-180.37
FBV-B, Molp. #1 HG, CRS754	-25.24	4.11		
FBV-B, Molp#1 HG, CRS754	-25.23	3.65	6.66	-196.67
FBV-B Scoto2 FG CRS754	-25.95	4.17		-172.18
FBV-B Scoto2 MG CRS754	-26.66	1.67	8.54	
FBV-B Scoto2 HG, CRS754	-26			-173.26
FBV-A Echiuran FG, CRS734	-25.49		10.26	-127.91
FBV-A Molp #2 FG, CRS734	-24.89	6.32	8.70	-163.77
FBV-A Peni Ind. 1-4 WG, CRS734	-23.73	5.52	6.32	-128.29
FBV Bathyplores FG	-27.12			
FBV-C Peniagone WG, CRS776	-25		7.03	-128.69
FBV-C Urchin WG, CRS778	-25		8.27	-174.17
FBV-C Urchin Chitin, CRS778			6.28	
FBV-C Benthuria HG, CRS776	-25		8.27	-155.43
FBV-C Benthuria FG, CRS776	-27.12		9.14	-157.73
FBIV-B Green Echi#1 WG, CRS706	-25.59	9.65	6.73	-132.10
FBIV-A Benthuria #2 WG, CRS689	-25.31		9.65	-160.19
FBIV-A Peni. 1-5, CRS689	-25.16	6.69	5.83	
FBIV-B Molp#2 FG, CRS661	-25.55	4.59	7.82	
FBIV-B Molp#2 MG, CRS661	-25.19	4.48	6.87	
FBIV-B Molp#2 HG, CRS661	-24.99	4.85	7.14	
FBIV-C Urchin#1WG, CRS649	-26.43	3.59	9.00	-176.60
FBIV-C Molp#2 FG, CRS638	-26.27	6.38	7.68	-176.69
FBIV-C Molp#2 MG, CRS638	-25.75	7.07	6.28	
FBIV-C Molp#2 HG, CRS638	-25.32	4.22	7.16	
FBIV-C Scoto#1 FG, CRS638	-25.5	5.4	7.33	-188.03
FBIV-C Scoto#1 MG, CRS638	-26.78	3.57	9.81	-175.50
FBIV-C Scoto#1 HG, CRS638	-25.94	3.52	7.77	-179.88
FBIV-C Scoto#2 FG, CRS638	-26.68	3.85	9.39	-197.67
FBIV-C Scoto#2 MG, CRS638	-26.43	4.04	9.39	
FBIV-C Scoto#2 HG, CRS638	-25.36	4.32	7.37	
FBIII-A Peni. FG, CRS634	-25.44		8.64	-155.82
FBIII-B Bathyplores FG, CRS 614	-26.68	5.81		-181.57
FBIII-B Bathyplores MG, CRS614	-26.57	6.4		-158.08
FBIII-B Bathyplores HG, CRS614	-25.53	4.64		-212.38
FBIII-B Holo K. FG, CRS614	-25.37			-361.67
FBIII-B G. Echi #1 WG w/ lining, CRS614	-24.53	10.44	6.29	-117.75
FBIII-B G. Echi #2 WG w/ lining, CRS607	-24.82	9.91	7.18	-112.68
FBIII-B G. Echi #1 WG w/ lining, CRS607			7.16	-139.32
FBIII-B Scoto FG, CRS607	-26.29		8.34	-191.38

FBIII-B Scoto HG, CRS 607	-25.78		7.64	-237.31
FBIII B. Urchin #1 WG, CRS607			7.22	-173.22
FBIII-B Molp. #1 FG, CRS607	-25.57	6.45	8.67	-157.11
FBIII-C Molpadiid FG, CRS582	-26		7.29	-213.69
FBIII-C Molpadiid HG, CRS582	-26.02		8.32	-239.38
FBIII-C Scoto. #2 FG, CRS582	-26.42	4.47	9.77	-171.92
FBIII-C Scoto. #2 FG, CRS582	-26.66		10.10	-156.52
FBIII-C Scoto. #2 FG, CRS582	-26.61		9.65	-172.72
FBIII-C Scoto. #2 FG, CRS582	-26.66		9.90	-186.54
FBIII-C Peniagone WG, CRS582	-26.38		6.39	-133.13
FBI-A G. Stichopid #1 FG, CRS551	-25.58	4.42	10.35	-151.85
FBI-A Scoto #2 MG, CRS538	-26.85		9.61	-181.07
FBI-A Echi #1, WG CRS538	-24.86	7.15	7.09	-119.04
FBI-A B. Urchin #1 WG, CRS538	-23.78	5.91	7.17	-161.19
FBI-B Scoto #1 HG, CRS529	-32.9	3.74	7.10	
FBI-B Scoto #1 MG, CRS529	-25.93	3.64	0.09	
FBI-B Scoto #1 FG, CRS529	-29.51	3.27	0.09	
FBI-C Echi #2 Gut, CRS499	-24.85	4.11	6.94	-127.19
FBI-C Peni. 1-3 WG, CRS499	-25.44	4.2	5.62	-111.69
FBI-C Molp #2 WG, CRS499	-25.84	3.83	7.22	-215.76
FBI-C Molp #3 WG, CRS499	-26.05	5.24	8.36	-174.51
FBI-C Scoto #1 FG, CRS490	-25.2	4.81	7.70	-174.20
FBI-C Scoto #1 MG, CRS490	-26.77	4.24	8.52	-165.66
FBI-C Scoto #1 HG, CRS490	-25.93	3.89	6.63	-192.00
FBI-A Molp. #1, FG CRS466	-19.55	5.5	10.84	-172.85
FBI-A Molp. #1, MG CRS466	-19.56	4.83	8.55	
FBI-A Molp. #1, HG CRS466	-32.1	3.52	7.71	
FBI-A Urchin #1 FG, CRS466	-25.44	4.11	8.80	-165.99
FBI-A Urchin #1 MG, CRS466	-24.29	4.51	7.32	
FBI-A Urchin #1 HG, CRS466	-24.22	3.85	7.82	
FBI-A Solengaster Holo FG, CRS466	-24.78	4.98	8.15	-141.60
FBI-B Scoto #2 FG, CRS434	-20.59		10.05	-129.08
FBI-B Echi #2 WG, CRS434	-24.88	6.66	10.14	-116.75
FBI-B Echi #1 Gut, CRS434	-27.88	5.42	10.00	-129.57
FBI-C Scoto #1, FG CRS404	-28.58	3.79	8.32	-156.61
FBI-C Scoto #1, MG CRS404	-27.25	3.9	10.18	-165.76
FBI-C Scoto #1, HG CRS404	-26.75	3.96	7.37	-162.68
FBI-C Holo, FG CRS404	-25.83		8.53	-191.11

Body Tissue Samples				
FOODBANCS Sample	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Atomic C/N	Corrected $\Delta^{14}\text{C}$
FBV-A Peni 1-4, CRS734	-24.75	7.31		
FBV-B G. Echi. #2, CRS799	-19.22		3.75	-150.95
FBV-C Scoto 2/3, CRS775	-22.84	7.84	4.46	-126.31
FBV-B Molpadiid, CRS754	-20.36	11.07	3.99	-131.28
FBV-B Scoto2, CRS754	-23.91	7.18	4.18	-130.08
FBV-C BL Urchin, CRS776	-24.77		5.46	-126.89
FBV-B Anemonae, CRS754	-26.73		6.01	-109.66
FBV Bathyplotes	-23.34			
FBV-A Echiuran, CRS734	-22.3		4.49	-119.82
FBV-C Peniagone, CRS776	-25.66		4.93	-124.11
FBV-C Benthuria, CRS776	-23.34		4.66	-113.92
FBV-A Molp #2, CRS734	-18.3	10.9	4.04	-139.92
FBIV-B Green Echi#1, CRS706	-20.17	15.26	3.77	-135.24
FBIV-A Benthuria #1, CRS689	-18.66	9.15	3.84	-115.47
FBIV-A Peni 1-5, CRS689	-26.28	16.23		
FBIV-A Benthuria #2, CRS689	-19.36	9.97	3.94	-128.09
FBIV-C Urchin#1, CRS649	-11.16	12.38	11.93	-141.81
FBIV-C Molp#2, CRS638	-20.69	13.58	5.11	-132.36
FBIV-C Scoto#1, CRS638	-24.87	12.7	3.69	-114.97
FBIV-C Scoto#1, CRS638	-24.86		3.84	-131.47
FBIV-C Scoto#1, CRS638	-24.96		3.93	-121.23
FBIV-C Scoto#2, CRS638	-22.54	12.88	4.34	-117.06
FBIII-A Peni., CRS634	-25.43	7.33	4.22	-105.43
FBIII-B Holo K, CRS614	-23.05		4.26	-115.37
FBIII-C Molpadiid, CRS582	-21.95		4.37	-120.77
FBIII-C Peniagone, CRS582	-23.31		5.88	-135.61
FBIII-C Scoto #2, CRS582	-21.51	8.89	4.13	-114.47
FBIII-B Scoto, CRS607	-25.1		5.09	-112.97
FBIII-B Molp #1, CRS607	-19.4		4.12	-147.87
FBIII-B G. Echi. #2 Body, CRS607	-21	3.67	3.68	-119.54
FBIII-B G. Echi. #1 Body, CRS607	-21		3.98	-119.54
FBIII-B B. Urchin, CRS607			29.82	-142.80
FBIII-B Bathyplotes, CRS614	-22.92	11.1		-114.46
FBIII-B G. Echi #1, CRS614	-19.91		4.08	-110.00
FBII-A G. Stichopid #1, CRS551	-19.55	8.76	3.98	-126.50
FBII-A B. Echi. #1, CRS538	-20.72	10.12	4.29	-111.89
FBII-A B. Urchin #1, CRS538	-10.07	9.23	11.90	-142.01
FBII-A Scoto #1, CRS538	-24.69		4.50	-145.58
FBII-C Echi #2, CRS499	-21.84	9.05	3.95	-109.65
FBII-C Echi #2, CRS499				-117.75
FBII-C Peni. 1-3, CRS499	-26.2	6.64	4.82	-104.73
FBII-C Molp #2, CRS499	-21.56	10.17	5.28	-129.88
FBII-C Molp #3, CRS499	-22.36	9.91	4.66	-147.27
FBII-C Scoto #1, CRS490	-27.19	10.1	4.47	-122.76
FBI-A Molp #1, CRS466	-20.96	10.14	4.55	-127.34

FBI-A Urchin #1, CRS466	-14.18	9.75	12.26	-136.57
FBI-A Solengaster Holo, CRS466	-24.64	9.94	5.12	-112.87
FBI-B Scoto #2 Body, CRS434	-26.4		4.17	-155.82
FBI-B Echi #2, CRS434	-19.15		3.72	-121.32
FBI-B Echi #1, CRS434	-18.57		3.67	-121.32
FBI-C Scoto #1, CRS404	-24.05		4.46	-118.64
FBI-C Holo., CRS404	-21.79	8.94	4.22	-95.28

Plankton and Trap Samples				
FOODBANCS Sample	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Atomic C/N	Corrected $\Delta^{14}\text{C}$
FBV - A CRS730	-15.15	5.98	6.58	-124.52
FBV PLK CRS 746	-18.45	4.2	6.05	-142.10
FBV, Bottom Trap	-28.52	0.92	8.83	-141.12
FBIV-B Ice Algae CRS636	-19.96		6.40	-145.72
FBIV - B CRS636 Ice Algae	-17.62	3.03	5.87	
FBIV-B PLK, CRS 670 (TT)	-32.73		6.26	
FBIV-C Krill , CRS654	-26.72		4.79	-135.40
FBIV - C CRS654 Plankton	-31.91	1.32	5.23	-125.31
FBIV Bottom Trap				-151.75
FBIII-B PLK, CRS608 (TT)	-29.24		15.21	-147.11
FBIII Top Trap			8.05	-157.41
FBIII Bottom Trap			8.02	-165.46
FBII-B PLK, CRS 526 (HN)	-29.54		7.73	-36.38
FBII-B PLK, CRS 526 (HN)	-30.71	0.23		-70.54
FBII-B CRS527	-30.33	4.29	6.48	-123.42
FBII-A CRS548	-34.34	2.7	6.06	-128.69
FBII-A CRS601	-27.08		0.24	
FBII Top Trap			7.39	
FBII Bottom Trap			6.83	-147.67
FBII Coastal Macroalgae	-20.48		27.45	-116.45
FBI Ice Algae CRS455	-19.39	2.76	9.86	-126.69
FBI CRS414 Ice Algae	-20.33	3.29	9.57	
FBI - C CRS414	-35.99	1.93	5.30	-139.91
FBI-C PLK, CRS 450 (HN)	-34.72		6.20	-146.37
Macro Algae 3-16-00 Loggard Isl.	-22.24	3.46	1.57	-127.99
Macro Algae 3-19-00 Breaker Isl.	-33.09	1.13	14.00	-127.69

Sediment Samples				
FOODBANCS Sample	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Atomic C/N	Corrected $\Delta^{14}\text{C}$
FBV Phytodetritus, CRS749	-26.94		8.57	-188.10
FBV-A Phytodetritus, CRS741	-25		8.27	-165.07
FBIII-B CRS619 0-0.5cm	-25.3	3.46	7.70	-250.84
FBIII-B CRS619 0-0.5cm	-25.02		8.71	-252.24
FBIII-B CRS619 0-0.5cm	-23.02		9.01	-231.76
FBIV - B CRS664 0 - 0.5cm	-25.47	4.23	7.98	-223.71
FBI CRS440 MC2 0 - 0.5cm	-25.56	6.48	8.16	-223.62
FBII - B CRS518 0 - 0.5cm	-25.29	4.35	7.98	-234.05

APPENDIX B

Acid pre-treatment test to determine ideal timing and concentration of HCl for inorganic carbon dissolution