



Structure of a northwest Atlantic Shelf macrofaunal assemblage with respect to seasonal variation in sediment nutritional quality

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ABSTRACT

We examined temporal variation in the relationship between benthic macrofaunal assemblage structure and sediment nutritional quality using core samples taken seasonally from a 232-m deep site in Wilkinson Basin, Gulf of Maine, from October 2003 through August 2004. The benthic assemblage was dominated by deposit-feeding polychaetes of the families Cirratulidae, Paraonidae, and Cossuridae. Assemblage composition and abundance remained relatively constant over the course of the study, despite seasonal changes in sediment nutritional quality. Constant seawater temperatures and/or relatively long species generation times may account for this pattern. Sediment depth-frequency distributions of cirratulid and paraonid polychaetes varied temporally and exhibited subsurface abundance peaks; depth-frequency distributions of cossurid polychaetes, in contrast, were temporally stable. Subsurface peaks of plant pigment concentrations matched those of the cirratulid and cossurid polychaetes, suggesting that these groups transport and cache recently deposited phytodetritus below the sediment surface. This subsurface caching may ameliorate the effects of a seasonally variable food supply, damping any seasonal response of the fauna.

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1. Introduction

Most benthic communities below the photic zone feed on detritus from phytoplankton settling to the sea floor. The supply of this primary production varies seasonally in temperate waters (Billett et al., 1983; Lampitt, 1985; Beaulieu, 2002), with variable degradation on the way to the bottom (Rice et al., 1986). Direct and indirect responses to phytodetrital inputs by a variety of benthic organisms, from bacteria to fishes, have been reported (reviewed by Gooday and Turley, 1990 and Gooday, 2002). These responses, including colonization, ingestion, aggregation around phytodetrital patches, growth, and reproduction, may occur on time scales from hours to months. Response of benthic macrofaunal populations to seasonal pulses of organic matter has been difficult to demonstrate, however, as relatively long macrofaunal lifespans and great spatial variation in macrofaunal abundance hinder the ability to detect population responses to seasonal inputs of food (Gooday, 2002). Nevertheless, some researchers (Drazen et al., 1998; Moodley et al., 1998; Galéron et al., 2001) have found seasonal change in macrofaunal density related to phytodetrital deposition.

Despite seasonal variation in supply of phytodetritus to the sediment surface, subsurface organic-matter concentrations may remain relatively constant where low temperatures inhibit microbial activity (Mincks et al., 2005). This constant subsurface food stock may compensate for any temporal variation in surficial food supply, and may explain the lack of subsurface macrofaunal response to seasonal inputs of organic matter.

The Gulf of Maine typically experiences two phytoplankton blooms yearly, one in the spring and one in the fall (Yentsch et al., 1995), with the spring bloom being much more pronounced than the fall bloom (O'Reilly and Zetlin, 1998). Winter blooms also occur occasionally (Durbin et al., 2003). These blooms are important sources of organic matter for organisms living below the photic zone in the Gulf of Maine (Charette et al., 2001). Variation in bloom timing and intensity will affect food supply to the bottom, which in turn may affect benthic macrofaunal assemblage structure. Alternatively, a relatively stable subsurface food stock may result in a stable assemblage. We examine these two hypotheses by investigating seasonal patterns in sediment nutritional quality and macrofaunal assemblage structure in a deep basin of the Gulf of Maine.

2. Materials and methods

2.1. Site description and sample collection

The study was conducted at a 232-m deep site in Wilkinson Basin (43° 00' N, 69° 54' W), one of several deep basins in the Gulf of Maine.

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The sediment at this site consists of silty clay, and bottom temperatures are relatively constant year-round at approximately 6 °C (Hopkins and Garfield, 1978). Six replicate core samples (9.5 cm diameter) were taken seasonally with either an Oktopus Minimuc or an Ocean Instruments MC-400 multicorer. Samples were taken on 23 October 2003 and 27 February, 19 April, 7 June, and 10 August 2004.

2.2. Sediment nutritional quality

Two cores from each sampling date were analyzed for sediment nutritional quality. The top 22 cm of the cores were sectioned horizontally (0.5-cm sections from 0–2 cm, 1-cm sections from 2–10 cm,

and 2-cm sections from 10–22 cm), and the sections combined for analysis.

Measures of nutritional quality included plant pigments (chlorophyll *a*, fucoxanthin—a pigment characteristic of diatoms, and pheopigment—a breakdown product of chlorophyll *a*), organic C, N, and enzymatically hydrolyzable amino acids (EHAA). Pigments were measured using the reverse-phase, high-pressure liquid chromatography method of Wright et al. (1991) on a Hitachi System 7200 HPLC. Organic C and total N were measured using a Perkin Elmer 2400 Series II CHNO/S analyzer after HCl fuming to remove calcium carbonate (Mayer et al., 1995). EHAA analyses were performed by incubating sediment with commercially available proteolytic enzymes, followed by fluorimetric measurement of the total

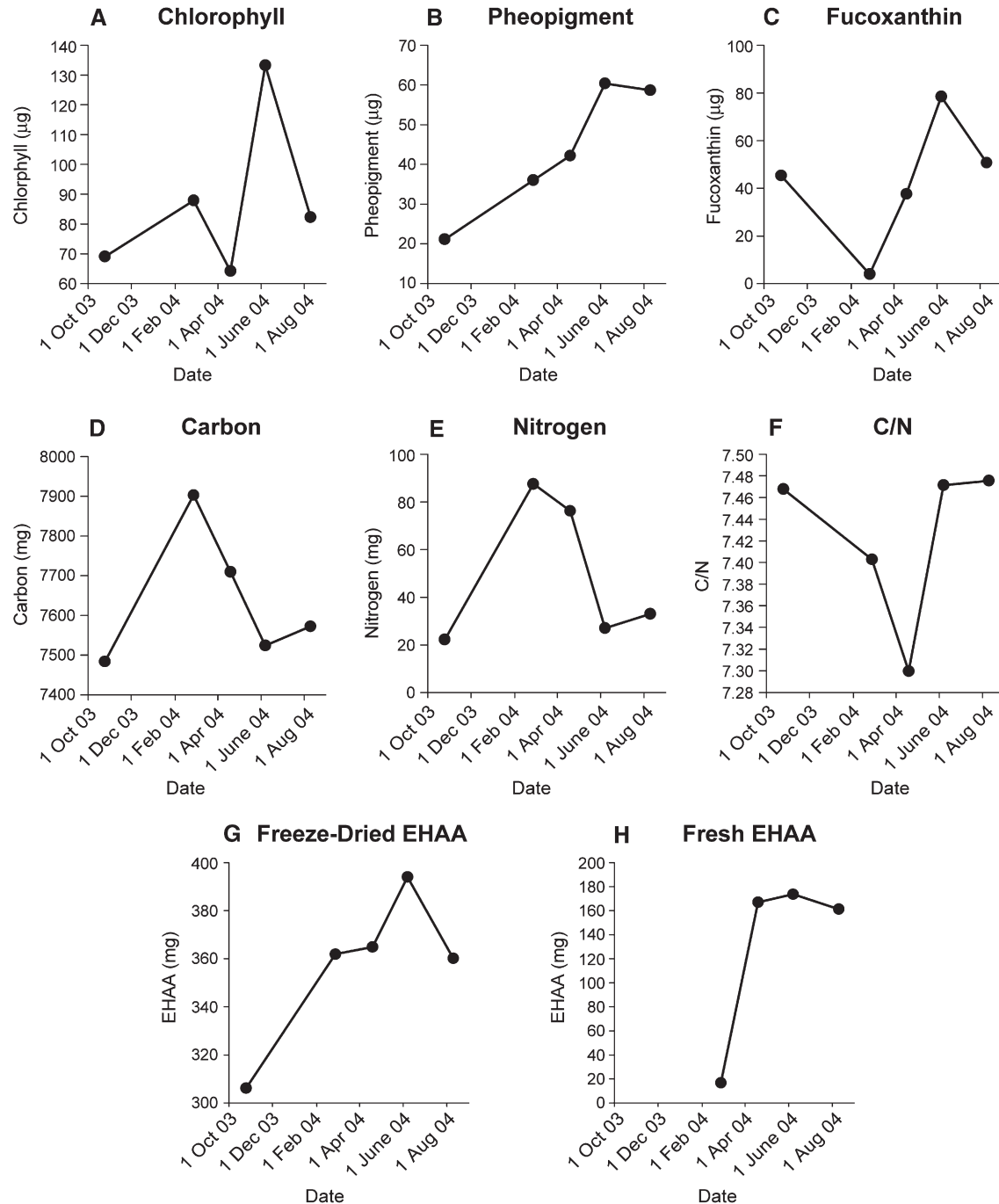


Fig. 1. Measures of sediment nutritional quality over time. All measures are inventories for the top 345 g of sediment. A. chlorophyll *a*, B. fucoxanthin, C. pheopigment, D. carbon, E. nitrogen, F. C/N, G. freeze-dried EHAA, H. fresh EHAA.

Table 1
Comparisons of sediment depth distributions over season

Variable	W	p
<i>Animals</i>		
Total fauna	1.43	0.004
Cirratulidae	1.22	0.009
Paraonidae	1.31	0.014
Cossuridae	1.07	0.104
<i>Measures of nutritional quality</i>		
Chlorophyll a	1.06	0.139
Fucoxanthin	1.17	0.014
Pheopigment	1.42	0.006
C	0.94	0.220
N	0.89	0.260
C/N	1.59	0.003
Fresh EHAA	1.04	0.147
Freeze-dried EHAA	1.38	0.021

W represents Solow et al.'s (2000) modification of the Kolmogorov–Smirnov statistic.

released amino acids (Mayer et al., 1995). This method was employed on both fresh (unfrozen, analyzed within a few hours of collection) and freeze-dried sediment, except for October 3 when only freeze-dried sediment was analyzed. Sediment porosity was measured by weighing

sediment before and after air-drying. Given water's density of 1 g ml^{-1} , pore volume in milliliters is numerically equal to the gram weight difference between the two measurements.

2.3. Macrofaunal analysis

Macrofaunal assemblages were examined using two different cores collected from the same deployment of the multicorer that yielded the cores for nutritional analysis. These two cores were sectioned as described above, fixed for at least 5 days in 10% formalin buffered with sodium tetraborate, and then transferred to 70% ethanol until sorting. Prior to sorting, samples were rinsed in tap water and sieved on a 250- μm mesh screen. All animals were removed, and polychaetes were identified to family according to Fauchald (1977). Molluscs and echinoderms were identified to class; crustaceans were identified to subclass or order according to Brusca and Brusca (1990). Although analysis to lowest identifiable taxonomic unit is preferable, it is not always feasible because of the time and effort involved. Analysis at higher taxonomic levels results in little loss of information for macrobenthos (Warwick, 1988; Pagliosa, 2005; Quijón and Snelgrove, 2006) because the functional diversity of macrobenthos is still poorly resolved below these high taxonomic levels. Although some

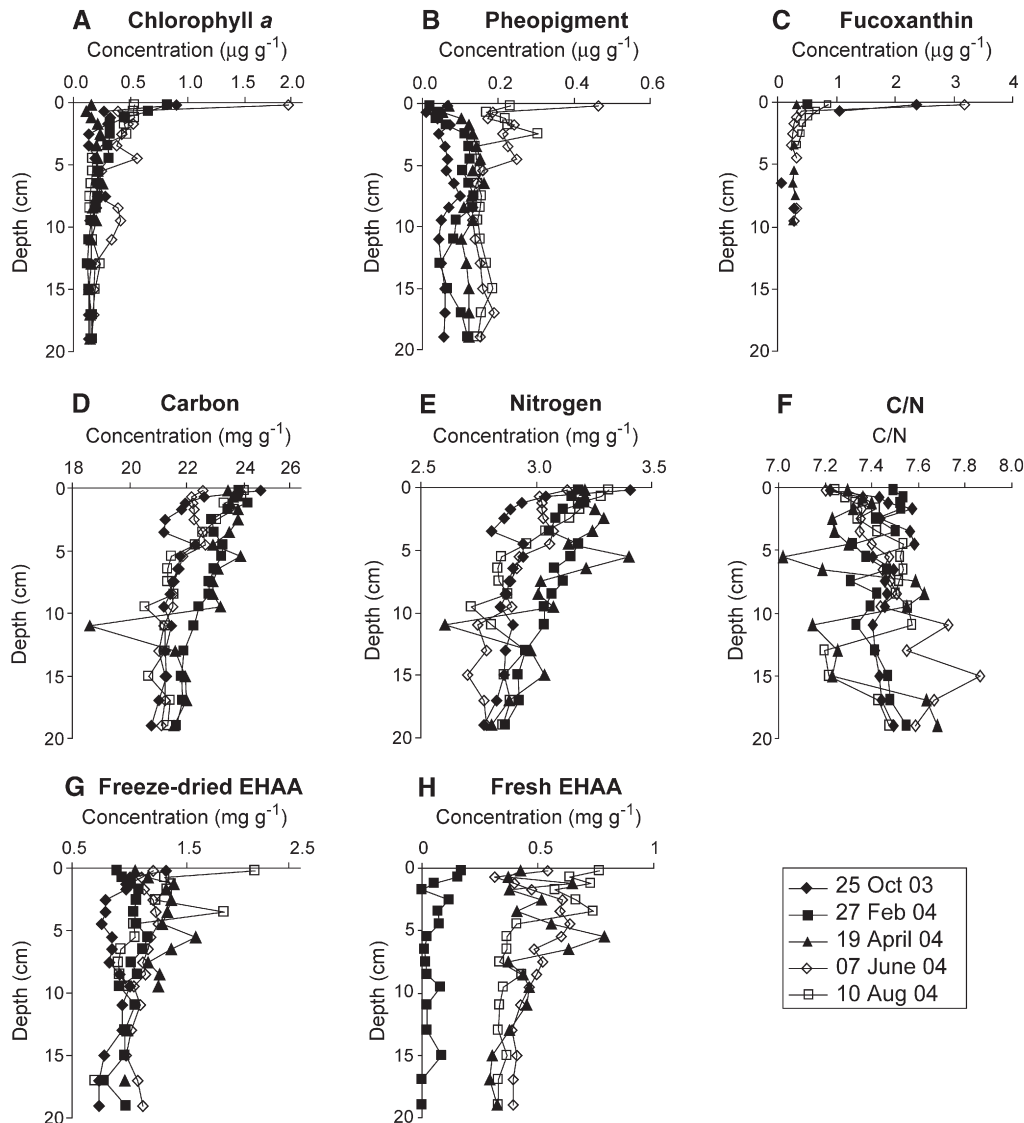


Fig. 2. Depth distributions of sediment nutritional quality measures. A. chlorophyll a B. fucoxanthin, C. pheopigment, D. carbon, E. nitrogen, F. C/N, G. freeze-dried EHAA, H. fresh EHAA.

Table 2
Mean abundances (number per 1275 cc core) of organisms collected at Wilkinson Basin

Phylum	Class	Order	Family	Feeding guild	25 Oct 2003		27 Feb 2004		19 Apr 2004		7 Jun 2004		10 Aug 2004		
					Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Cnidaria	Hydrozoa			Predator	0	0	0	0	0	0	0.5	0.5	0	0	
Nemertea				Predator	0.5	0.5	1.5	0.5	2	1	6.5	0.5	4.5	0.5	
Annelida	Polychaeta	Orbiniida	Paraonidae	Deposit feeder	5	2	14	6	40	29	34	18	16	4	
			Cossurida	Cossuridae	Crack feeder	3.5	2.5	24	4	20	5	24.5	4.5	19	1
		Spionida	Spionidae	Surface deposit feeder	1	1	0	0	0	0	7	2	3.5	0.5	
			Poecilochaetidae	Subsurface deposit feeder	0	0	0	0	7	7	0.5	0.5	3	3	
		Cirratulidae	Cirratulidae	Crack feeder	35.5	0.5	49	28	126.5	91.5	57	4	36.5	2.5	
			Capitellida	Capitellidae	Subsurface deposit feeder	2.5	0.5	2	0	0.5	0.5	6	1	2.5	1.5
		Opheliida	Opheliidae	Deposit feeder	3	1	12.5	5.5	9	2	10	3	6	4	
		Phyllodocida	Polynoidae	Polynoidae	Predator	0	0	1	1	0	0	0.5	0.5	0	0
				Hesionidae	Predator	2.5	1.5	3.5	0.5	1.5	0.5	9	4	7	5
			Pilargidae	Predator	0	0	0.5	0.5	0	0	0	0	0	0	
			Syllidae	Predator	2	1	6	5	6.5	2.5	4	1	12	2	
			Nereidae	Predator	0	0	10	8	5.5	3.5	11.5	2.5	4	2	
			Glyceridae	Predator	0	0	0	0	1	1	2.5	0.5	0	0	
			Sphaerodoridae	Surface deposit feeder	0	0	0	0	0	0	0	0	1	1	
			Eunicida	Lumbrineridae	Predator	0.5	0.5	0.5	0.5	1.5	1.5	2.5	0.5	1	0
				Dorvilleidae	Predator	0	0	1	1	1	1	0.5	0.5	1.5	1.5
			Flabelligerida	Flabelligeridae	Deposit feeder	0	0	0	0	0.5	0.5	0	0	0	0
		Terebellida	Ampharetidae	Surface deposit feeder	0.5	0.5	0	0	4.5	1.5	0	0	1	1	
			Terebellidae	Crack feeder	0	0	0	0	0	0	0	0	0.5	0.5	
				Unidentified polychaete			1.5	0.5	4	1	3	2	6.5	1.5	0
Echiura				Deposit feeder	0	0	0	0	0	0	0.5	0.5	0	0	
Sipunculida				Deposit feeder	0	0	0	0	0	0	2	2	0.5	0.5	
Arthropoda	Ostracoda			Browser	0	0	1	1	4.5	3.5	0.5	0.5	2	1	
		Copepoda		Browser	4.5	0.5	4	3	11	9	6.5	2.5	13.5	1.5	
	Malacostraca	Isopoda		Deposit feeder	0	0	0	0	0.5	0.5	0	0	0	0	
		Amphipoda		Detritivore	0	0	0	0	1.5	1.5	0.5	0.5	1	0	
Mollusca	Aplacophora			Deposit feeder	0.5	0.5	0.5	0.5	1.5	1.5	0	0	0.5	0.5	
	Gastropoda			Many	0.5	0.5	1	0	1.5	1.5	1.5	1.5	3.5	1.5	
	Bivalvia			Surface deposit feeder	6	1	9	4	15.5	9.5	15.5	8.5	9	0	
	Scaphopoda			Deposit feeder	4	2	4	1	3	2	4.5	0.5	6.5	0.5	
Echinodermata	Ophiuroidea			Omnivore	2	2	1	1	1.5	1.5	4.5	3.5	26.5	1.5	
Hemichordata	Enteropneusta			Deposit feeder	0	0	0	0	0	0	0	0	0.5	0.5	
Chordata	Ascidiacea			Suspension feeder	0	0	0	0	0	0	6	6	0	0	

nematodes and agglutinating foraminiferans were retained on the 250- μ m mesh, they were not included in this study.

2.4. Statistical analysis

Because some of the cores sampled were less than 22 cm deep, statistical analysis of biota was restricted to a depth of 18 cm, the length of the shortest core. Because of an error in sectioning, only one core from August 10 was included in analyses of depth distributions. As inventories of pigments and other nutritional measures depend partly on sediment porosity, inventories were calculated for the top 345 g of sediment of each core. This mass depth was calculated by converting linear depth intervals to mass depth intervals via the porosity measurements, calculating a cumulative mass depth curve, linearly interpolating the 345 g mass depth, and summing chemical inventories from the sediment–water interface to that point. This mass depth encompassed approximately the top 10 cm of sediment and included most of the animals found in the cores. For analyses involving both nutritional and biotic measures, the biotic measures were recalculated for the top 345 g of sediment.

For all statistical tests, the significance level was set at $\alpha=0.05$ except in the case of multiple comparisons. Significance levels were adjusted for multiple comparisons using the false discovery rate method of Benjamin and Hochberg (1995) as described by Verhoeven et al. (2005).

2.4.1. Seasonal change in macrofaunal assemblage

Seasonal change in basic assemblage structure measures (total animal abundance, abundance of major taxonomic groups, taxonomic richness, Shannon–Weaver diversity (Shannon and Weaver, 1963), and Pielou's evenness (Pielou, 1975)) were analyzed using ANOVA. To ensure that ANOVA assumptions were met, homogeneity of variance among sampling dates was examined using Bartlett's test (Sokal and Rohlf, 1981), and normality of residuals was tested using the Shapiro–Wilk test (Shapiro and Wilk, 1965) and a normal probability plot. Variables failing to meet the assumptions of ANOVA were analyzed nonparametrically using the Kruskal–Wallis test (Sokal and Rohlf, 1981).

Group-averaged hierarchical clustering and non-metric multidimensional scaling (MDS) on square-root transformed abundances and Bray–Curtis similarities among samples (Clarke and Warwick, 2001) assessed change in taxonomic composition over time. PRIMER ANOSIM and SIMPROF tests (Clarke and Warwick, 2001) established levels of significance among dates. The PRIMER BVSTEP routine (Clarke and Warwick, 2001) determined which taxa drove patterns identified in the whole-assemblage MDS. This analysis finds the subset or subsets of taxa that yield an MDS pattern similar to that of the entire assemblage. Clustering by taxon was also performed to determine which taxonomic groups had similar patterns of occurrence among samples. This

Table 3

Subsets of taxa that yielded the same MDS pattern (Spearman's $\rho \geq 0.95$) as the MDS including all taxa

Phylum	Class	Order	Family	Subset				
				1	2	3	4	
Cnidaria	Hydrozoa							
Nemertea				X	X	X		
Annelida	Polychaeta	Orbiniida	Paraonidae	X	X	X		
		Cossurida	Cossuridae	X	X	X		
		Spionida	Spionidae	X	X			
			Poecilochaetidae			X		
			Cirratulidae	X	X	X		
		Capitellida	Capitellidae		X	X	X	
		Opheliida	Opheliidae			X		
		Phyllodocida	Polynoidae					
			Hesionidae		X			
			Pilargidae		X			
			Syllidae		X			
			Nereidae	X	X	X		
			Glyceridae		X			
			Sphaerodoridae			X		
			Lumbrineridae				X	
			Dorvilleidae			X		
			Flabelligerida	Flabelligeridae			X	
Terebellida	Ampharetidae	X						
	Terebellidae	X	X	X	X			
	Unidentified		X		X			
Polychaete								
Echiura				X				
Sipunculida				X				
Arthropoda	Ostracoda			X	X			
	Copepoda			X	X	X		
	Malacostraca	Isopoda			X	X		
		Amphipoda			X	X		
	Mollusca	Aplacophora			X			
Gastropoda				X	X			
Bivalvia					X			
Scaphopoda				X	X			
Echinodermata	Ophiuroidea			X	X			
Hemichordata	Enteropneusta			X				
Chordata	Ascidiacea			X	X			

approach has the disadvantage of making two samples appear more similar if they both lack many of the same species. Therefore, any taxon contributing $<3\%$ of the individuals to any sample was excluded from this cluster analysis (Legendre and Legendre, 1983).

In addition to analyzing changes in assemblage structure by taxon, we investigated change in feeding guild diversity over time. Feeding guilds were assigned as specifically as possible based on the work of Fauchald and Jumars (1979), Brusca and Brusca (1990), Ruppert and Barnes (1994), and Rouse and Pleijel (2001). For example, some taxa were classified as deposit feeders rather than surface or subsurface deposit feeders because their feeding biology is currently unresolved. Here we introduce a new feeding guild, crack feeders, based on the work of Dorgan et al. (2005). Crack feeders burrow by crack propagation, and may feed along the surfaces of the crack as well as the sediment–water interface when the path of the crack intersects it. In a sense they are surface deposit feeders, but the surface that they often feed upon is the interior wall of a fracture, and it is important to recognize that they can acquire food particles at depths well below the sediment–water interface (Jumars et al., 2007) and that many such animals were misclassified as surface deposit feeders by Fauchald and Jumars (1979). Relationships among feeding groups were analyzed using MDS and ANOSIM.

2.4.2. Relating assemblage structure to measures of sediment nutritional quality

To determine which measures of sediment nutritional quality best correlated with taxonomic composition, a principal components analysis (PCA) by date was performed on the nutritional quality measures. EHA measurements on unfrozen samples were not used in this analysis because we lack data from the first sampling. Results of this

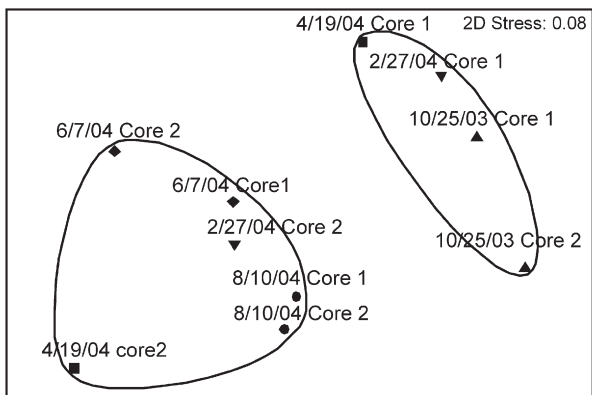


Fig. 3. Multidimensional scaling plot of square-root transformed animal abundances based on Bray–Curtis similarities. Rings indicate 65% similarity from cluster analysis.

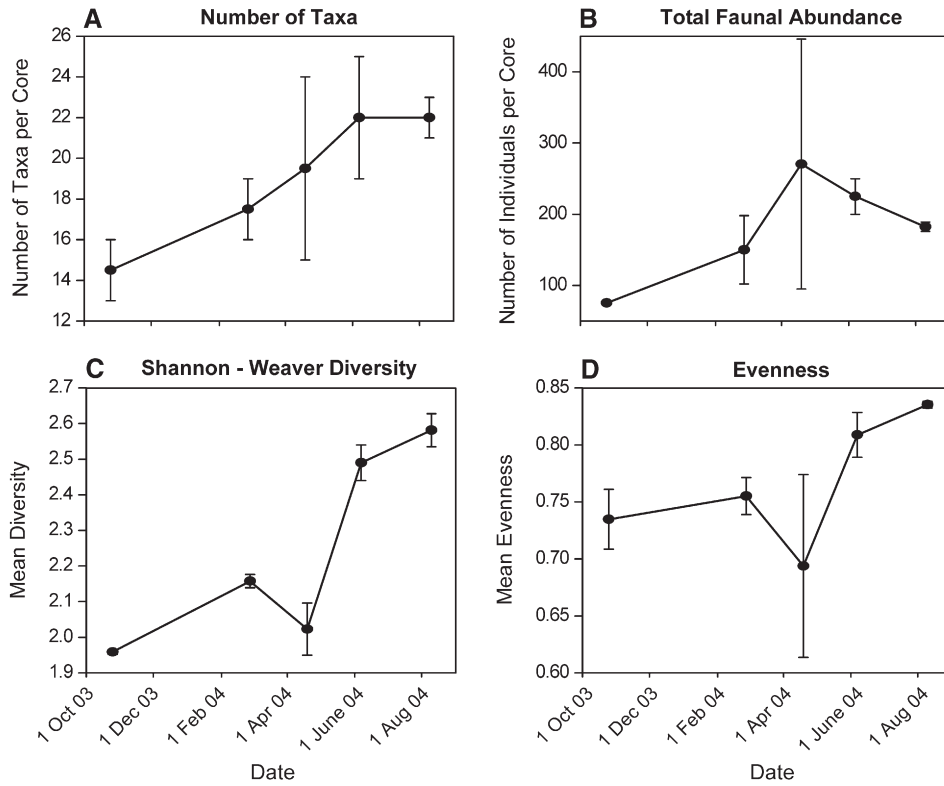


Fig. 4. Measures (mean ± standard error) of the benthic assemblage structure over time. A. Taxonomic richness, B. Total faunal abundance, C. Shannon–Weaver diversity, D. Pielou’s evenness.

PCA were then compared to an MDS performed on the mean abundances of the animals by date using the BEST-BIOENV routine in PRIMER. If two nutritional variables were correlated either positively or negatively with each other at $R^2 > 0.95$, one of those variables was excluded from the analysis because they supplied essentially redundant information. Spearman correlations (PROC CORR, SAS Institute Inc., 1985) were used to determine which sediment nutritional quality factors were correlated with total animal abundance and the diversity measures described above.

2.4.3. Depth distributions

Changes in depth distribution of macrofauna and nutritional quality over time were analyzed using the W' of Solow et al. (2000), a modification of the multiple-sample Smirnov test (Conover, 1980).

This method was also used to compare depth distributions of animals and measures of sediment nutritional quality.

3. Results

3.1. Sediment nutritional quality

Measures of nutritional quality differed in their temporal patterns, reflecting the spring and fall blooms. Chlorophyll *a* inventory peaked in June whereas pheopigment peaked in June and August (Fig. 1A, B). Fucoxanthin also peaked in June (Fig. 1C), but was almost completely absent in February, consistent with low bulk productivity and high silicate concentrations in the water column during this time of the year (Townsend and Thomas, 2001; Thomas et al., 2003). A smaller

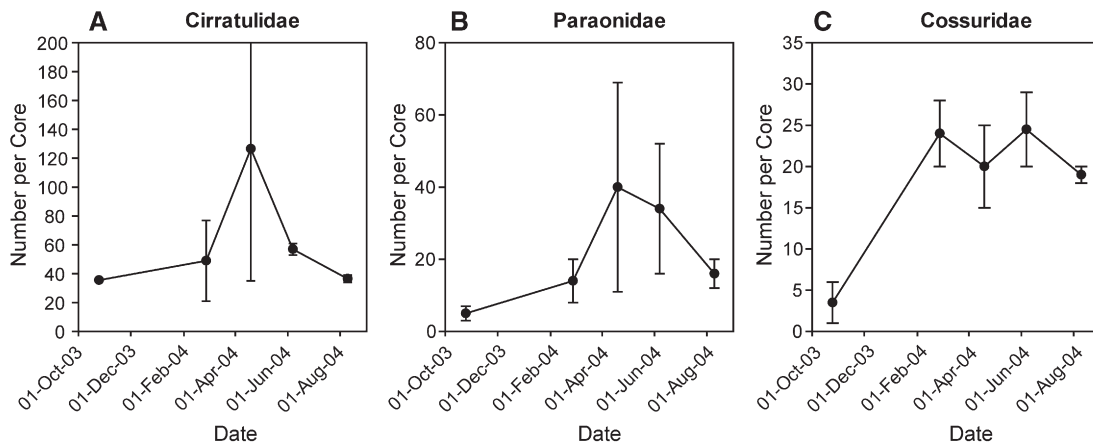


Fig. 5. Abundances (mean ± standard error) of major taxonomic groups over time. A. Cirratulidae, B. Paraonidae, C. Cossuridae. Abundances are number per 9.5 cm diameter core to a depth of 18 cm. Note differing scales for each group.

fucoxanthin peak was observed in October, indicating the fall bloom. Carbon, nitrogen, and C/N showed relatively little variation over the study (Fig. 1D–F), with the lowest seasonal values being 95%, 94%, and 98% of the highest seasonal values, respectively. Unfrozen EHAA increased dramatically from February to April and remained high through August; freeze-dried EHAA showed a peak in June (Fig. 1G–H).

Depth distributions of fucoxanthin, pheopigment, C/N, and freeze-dried EHAA varied temporally (Table 1, Fig. 2). All three pigments exhibited their highest peaks at the surface in June. Chlorophyll showed smaller peaks at 3–5 and 10 cm depths in June as well.

3.2. Macrofaunal assemblage

Thirty-five taxa were identified from the core samples (Table 2). Composition of the benthic assemblage remained relatively constant over time (ANOSIM, $p=0.06$). The multidimensional scaling plot and cluster analysis (Fig. 3) show greater differences within dates than among dates, except for 10 August 2004, when there was little difference between cores. This date drives the nearly significant ANOSIM result. Subsets of 13–18 of the 35 taxa identified yielded a multidimensional scaling pattern similar to that of the full set of taxa (BVSTEP, Spearman's $\rho \geq 0.95$, Table 3), with 11 taxa appearing in at least 3 of 4 subsets.

Total number of taxa did not vary significantly over time (Fig. 4A, ANOVA $F_{[4, 5]}=1.46, p=0.34$). Total macrofaunal abundance ranged from 10,571 to 63,714 individuals m^{-2} , but did not vary significantly over time (Fig. 4B, Kruskal–Wallis test, $X^2_{[4]}=5.67, p=0.23$). Three polychaete families, Cirratulidae, Paraonidae, and Cossuridae, accounted for 55% of all animals found. No other taxon identified made up more than 7% of the total number of animals found. Because of their relative abundance, the three dominant taxa were analyzed individually. Of these taxa, only Cossurid abundance varied over time (Fig. 5, ANOVA $F_{[4, 5]}=5.35, p=0.05$). Shannon–Weaver diversity differed over time, with the first three sampling dates being less diverse than the last two dates (Fig. 4C, ANOVA $F_{[4, 5]}=37.62, p=0.0006$). Pielou's evenness did not vary significantly over time (Fig. 4D, ANOVA $F_{[4, 5]}=2.08, p=0.22$) but trended in the same direction as the Shannon–Weaver diversity.

Clustering by taxon (excluding all taxa that did not constitute at least 3% of the total abundance of any one core) shows similar patterns

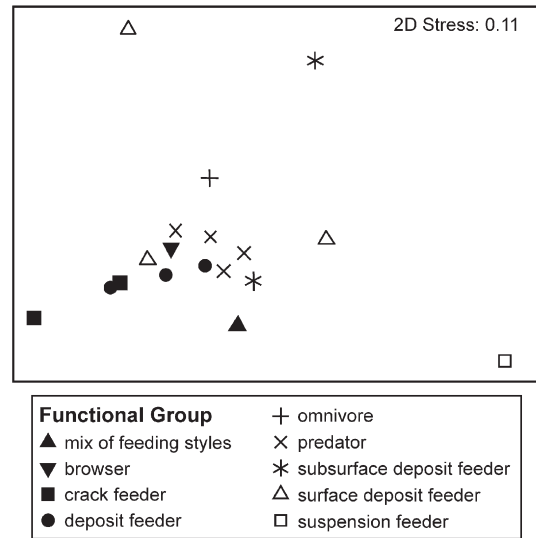


Fig. 7. Multidimensional scaling of taxa contributing at least 3% of the individuals to any one sample, showing relationships among feeding guilds.

of occurrence for scaphopods and hesionid polychaetes, cossurid and paraonid polychaetes, and bivalves and opheliid polychaetes (Fig. 6). When analyzing by feeding guild (Fig. 7), predators grouped together, suggesting that all predator species experienced similar abundance fluctuations over time. General deposit feeders also grouped together, indicating that members of this functional group also experienced similar population fluctuations over time.

Sediment depth distribution of the entire assemblage changed over time (Fig. 8A, Table 1). When the dominant infaunal families were analyzed individually, the depth distributions of cirratulid and paraonid worms differed temporally, but the distribution of cossurid worms did not (Table 1). Cirratulid worms had relatively narrow depth distributions, mostly between 2 and 5 cm (Fig. 8B). Paraonid and cossurid worms were found throughout the cores except for the top 0.5 cm (Fig. 8C–D).

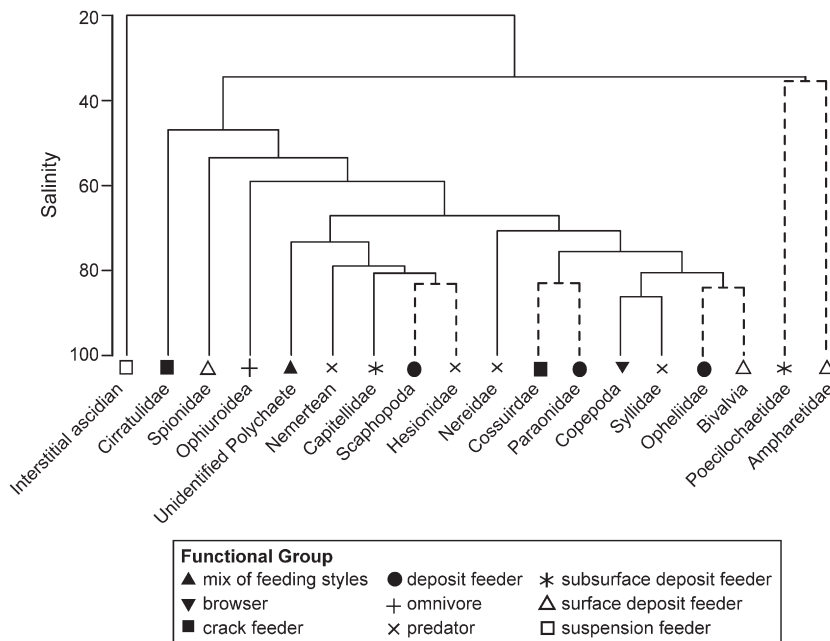


Fig. 6. Cluster analysis by taxonomic group. Only taxa contributing at least 3% of the individuals to any one sample are included. Group average method was used to link samples. Dotted lines indicate non-significant splits using a SIMPROF test.

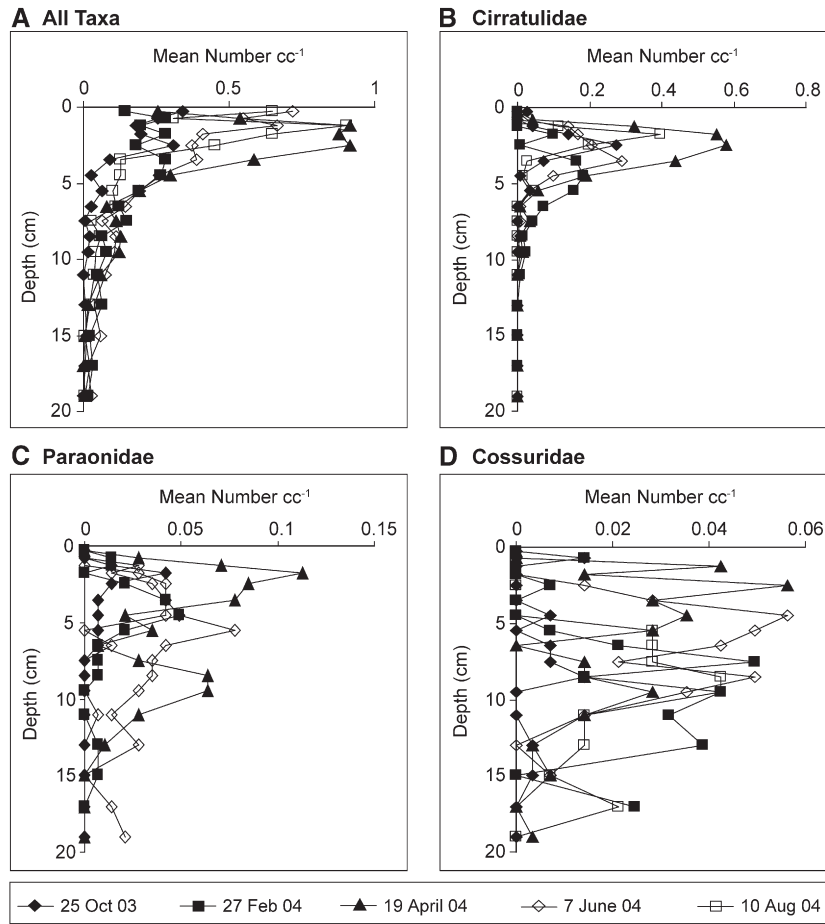


Fig. 8. Mean sediment depth distribution of A. entire assemblage B. Cirratulidae C. Paraonidae D. Cossuridae. Note differing scales for each group. Error bars omitted for clarity of presentation.

3.3. Relationship between sediment nutritional quality and macrofaunal assemblage

Nitrogen and carbon inventories varied by small amounts that were highly correlated with one another, and both were negatively correlated with mean core porosity. Therefore, of C, N, and C/N, only C was included in the PCA of nutritional quality variables, which was then compared to the benthic assemblage MDS. No subset of nutritional variables significantly explained the variation in benthic assemblage structure (BIOENV maximum $p=0.62$, $p=0.53$). Of the three major taxa, only Cossuridae showed significant correlations with nutritional variables, with abundance being positively correlated with freeze-dried EHAA inventories ($p=1$, $p<0.0001$). None of the biotic diversity measures was significantly correlated with the nutritional quality measures.

Depth distributions of pigments, C, N, and EHAA were similar to animal depth distributions on some dates (Table 4). Fucoxanthin depth distributions more closely matched those of the animal assemblage on all five sampling dates, due to peaks near the sediment–water interface for each.

4. Discussion

4.1. Sediment nutritional quality

Nutritional quality of our sediment samples varied seasonally, reflecting the spring and fall phytoplankton blooms usually experienced in the Gulf of Maine (Yentsch et al., 1995). Based on a settling rate of 75–110 m d⁻¹ (Pfannkuche, 1993), phytodetritus resulting from

Table 4
Relationship between depth distribution of all animals and indicators of sediment nutritional quality

Date	Measure of sediment nutritional quality															
	Chlorophyll		Fucoxanthin		Pheopigment		C		N		C/N		Fresh EHAA		Freeze-dried EHAA	
	W'	p	W'	p	W	p	W'	p	W'	p	W'	p	W'	p	W'	p
25 Oct 2003	1.50	0.002	1.04	0.120	1.74	0.000	1.77	0.001	1.77	0.000	1.76	0.001	No data		1.77	0.000
27 Feb 2004	0.86	0.290	0.96	0.210	1.77	0.000	1.76	0.000	1.77	0.000	1.77	0.000	0.76	0.450	1.78	0.000
19 Apr 2004	1.76	0.000	1.13	0.060	1.68	0.000	1.70	0.000	1.70	0.001	1.71	0.000	1.75	0.000	1.60	0.000
7 Jun 2004	0.96	0.240	0.93	0.262	1.65	0.001	1.77	0.000	1.77	0.000	1.78	0.000	1.74	0.000	1.74	0.000
10 Aug 2004	1.40	0.006	1.04	0.070	1.61	0.001	1.69	0.000	1.68	0.000	1.70	0.000	1.73	0.000	1.51	0.002

W' represents Solow et al.'s (2000) modification of the Kolmogorov–Smirnov statistic. p values >0.05 indicate similar depth distributions.

the blooms should reach the seafloor of Wilkinson Basin 2–3 days after leaving the surface.

There was no strong response in EHAA concentrations to the spring pigment peak, which is in line with the low pigment concentrations. The sum of chlorophyll and pheopigment at the June maximum was approximately $2 \mu\text{g g}^{-1}$ at the sediment–water interface. Assuming a protein:chlorophyll ratio of about 28 for phytoplankton (Montagnes et al., 1994), an increase of only $0.06 \text{ mg EHAA g}^{-1}$ would be expected, which would be difficult to detect against a background of approximately 1 mg EHAA g^{-1} . In intertidal sediments with an order of magnitude higher pigment concentrations, Mayer and Rice (1992) found a strong correlation of protein with pheopigment, but not chlorophyll, concentrations. Thus, if animals are responding to bloom inputs, as suggested by the subsurface chlorophyll peaks (see Section 4.3 below), then this organic nutrient addition is not detectable using the EHAA measurement. Even less variation would be expected in the total organic carbon or nitrogen values.

The nutritional quality of the organic matter in the sediment can be assessed via the ratio of EHAA to total organic matter, i.e., the proportion of organic matter available to consumers (Mayer et al., 2002). Calculating the carbon and nitrogen contents of EHAA as 50% and 16.7%, respectively, virtually all cores yielded EHAA-C:TOC and EHAA-N:TN ratios of <0.03 and 0.06 , respectively. These low values are similar to those of refractory organic matter found in NW Atlantic sediments at slope depths (Mayer et al., 2002). The notable exceptions to these ratios were the 0–0.5 and 3–3.5 cm samples at the August sampling, reflecting accumulation of proteinaceous material at the sediment–water interface from settling detritus and transport of detritus below the sediment surface by animals (see Section 4.3 below).

4.2. Macrofaunal assemblage response

Despite seasonal changes in sediment nutritional quality, the structure of the Wilkinson Basin macrofaunal assemblage remained relatively stable over the course of our study at the taxonomic resolution we employed. There is some indication of a long-term (longer than seasonal) increase in taxonomic diversity (Fig. 4A,C). The data record is short, however, precluding analysis of possible longer-term drivers such as climate oscillations. Dominant taxa were cirratulid, paraonid, and cossurid polychaetes. Eleven taxa, including the three dominant polychaete families, appeared in most of the subsets of taxa whose MDS plots matched those of the entire assemblage. This result suggests that a relatively small number of taxa are driving the observed assemblage pattern. Of the dominant taxa, paraonid and cossurid polychaetes had similar patterns of temporal occurrence, suggesting that these taxa may be responding similarly to seasonal inputs of organic matter.

The only major taxon to show a statistically significant relationship with a measure of sediment nutrition was the polychaete family Cossuridae, whose abundance was positively correlated with freeze-dried EHAA. Maurer and Leathem (1981) noted a positive relationship between the guild containing the Cossuridae (burrowing, motile, non-jawed) and carbon and nitrogen, although cossurids were not a major component of their sample. They noted no relationship between the feeding guilds containing the Paraonidae (surface deposit-feeding, motile, non-jawed) and the Cirratulidae (that they classified as surface deposit-feeding, discretely motile, tentaculate) and carbon and nitrogen, just as we found no relationship between these taxa and measures of sediment nutritional quality.

Predatory taxa had similar patterns of occurrence among cores. Because predator population density should respond to prey population density, the similarity of predator occurrences suggests that the predatory taxa are preying on the same items. Alternatively, various

prey items may have similar temporal patterns of occurrence. General deposit feeders also had similar patterns of occurrence among cores. These taxa may be responding in the same way to the deposition of phytodetritus.

The literature on benthic macrofaunal assemblage response to seasonal variation in sediment nutritional value is equivocal. The lack of a clear relationship may result from relatively long macrofaunal lifespans, or from great spatial variation in macrofaunal abundance (Gooday, 2002). For sites in the tropical northeast Atlantic ranging from 1600 to 4640 m deep, Galéron et al. (2000) reported no seasonal variation in macrofaunal abundance or composition despite variation in primary productivity. For a 4560-m deep site in the Northeast Atlantic, Pfannkuche (1993) reported no seasonal changes in meiofaunal or macrofaunal abundance, despite seasonal variation in sediment chlorophyll. Valderhaug and Gray (1984) also reported no seasonal changes in macrofaunal abundance at a 32-m deep site in the Oslofjord, Norway, again despite a seasonal change in chlorophyll *a*. When their data were broken down by feeding guild or broad taxonomic group, fluctuations did occur, but without clear seasonal pattern. Valderhaug and Gray (1984) attributed the absence of seasonality in macrofaunal abundance to the constancy of the physical environment, as well as to the activities of predatory polychaetes and sediment disturbers such as echinoids. These hypotheses may apply to Wilkinson Basin, which has a relatively constant temperature and a fair number of predatory polychaetes. For a 4100-m deep site in the North Pacific, Drazen et al. (1998) reported temporal variation in chlorophyll *a* and pheopigment, although there was no regular seasonal pattern. Total metazoan density did not vary seasonally, although several major components of the fauna, including polychaetes, increased in density over the winter after detrital aggregates had disappeared and approximately eight months after the peak in particulate organic carbon concentrations. Galéron et al. (2001) also noted a lagged response of macrofaunal polychaete density to summer food input at a 4850-m deep site in the Northeast Atlantic, with density increasing over the winter and into the next summer. Our major polychaete taxa show a similar increase over winter months, perhaps due to a lag between food input and reproductive response. Moodley et al. (1998) noted no lag between food input and macrofaunal density at three much warmer, 18-m deep sites in the Adriatic Sea. Macrofaunal densities were highest in summer, when sediment chlorophyll concentrations were highest.

The relationship between seasonal food input and macrofaunal density may be weak because reproduction may occur some time after food input (Galéron et al., 2001). One might expect the relationship between seasonal food input and biomass or size to be stronger as biomass may respond more quickly than density to pulses of organic matter. The evidence, however, is again equivocal. Of the studies cited above in which macrofaunal biomass was measured, some (Pfannkuche, 1993; Galéron et al., 2000) found no relationship between seasonal food input and macrofaunal biomass. Drazen et al. (1998) found little difference in biomass over the course of their study for all taxa except polychaetes. The polychaete differences were caused by a few large individuals. Valderhaug and Gray (1984) found more pronounced differences over time for biomass compared to density for some species but not others. And where Moodley et al. (1998) found significant differences over time for macrofaunal density, they found no differences over time in macrofaunal biomass.

Despite the confusion over longer-term responses (density and biomass) of macrofauna to pulses of organic matter, it is clear that macrofauna respond to these pulses in the short term. Tracer studies indicate that benthic macrofauna begin to ingest phytodetritus within hours of deposition (e.g., Moodley et al., 2005; Aspetsberger et al., 2007). The rapid uptake of phytodetritus suggests that macrofauna are food-limited.

4.3. Animal and pigment depth distributions

The dominant taxon, cirratulid polychaetes, had a narrow depth distribution close to, but peaking just below, the sediment surface, whereas the other two major taxa (paraonid and cossurid polychaetes) had broader depth distributions. The sessile tubicolous or mudball-building cirratulids (Jumars, 1975; Levin and Edesa, 1997) are surface deposit feeders, but it is clear from recent observations (Shull and Yasuda, 2001, K.M. Dorgan, unpublished data; P.A. Jumars, unpublished data) that burrowing cirratulids are able to deploy both their gills and feeding tentacles in the cracks that they produce at a range of sediment depths. According to Rouse and Pleijel (2001), paraonids are usually found on the surface or burrowing into the upper layers of the sediment. Given that paraonids may be surface or burrowing deposit feeders (Fauchald and Jumars, 1979), a relatively broader depth distribution is to be expected. As primarily subsurface deposit feeders (Jumars et al., 2007), cossurids have the deepest depth distribution of the dominant taxa.

The depth distributions of the dominant taxa may be a function of competition and habitat partitioning. According to Whitlatch (1980), deposit-feeding polychaetes partition habitat by sedimentary organic carbon and either particle size or vertical space. Species occupying habitats over a wide range of sedimentary organic carbon tend to consume a narrow range of particle sizes or have narrow depth distributions. Conversely, species occupying areas within a narrow range of sedimentary organic carbon tend to consume a wider range of particle sizes or have a broader depth distribution. We cannot test this hypothesis using our data because we sampled in only one location and did not examine sediment grain size consumed by the organisms we collected, but it would be interesting to explore further.

The June subsurface peaks of chlorophyll matched subsurface peaks in the distribution of the three dominant taxa found at Wilkinson Basin. All three dominant polychaete families showed June peaks at approximately 5 cm, and the Cossuridae showed an additional peak at 10 cm. This result suggests that these animals are transporting relatively fresh phytodetritus below the sediment surface. Given chlorophyll *a* decay rates (half-life of 28 d at 5 °C in Long Island Sound, Sun et al., 1994) and sedimentation rates for the Gulf of Maine (<1 cm yr⁻¹, Crusius et al., 2004), it is unlikely that the phytodetritus would have been buried by sedimentation alone. There is evidence that macrofauna (Blair et al., 1996; Levin et al., 1997; Levin et al., 1999; van de Bund et al., 2001; Josefson et al., 2002; Moodley et al., 2005; Aspetsberger et al., 2007), and cirratulid worms in particular (George, 1964; Myers, 1977; Shull and Yasuda, 2001) rapidly transport particles downward from the sediment surface (although Witte et al. (2003) considered that Opheliidae and Maldanidae are more important than Cirratulidae in this respect). Jumars et al. (2007) observed that many cirratulids have subterminal expansions at both ends of the body, enabling them to burrow effectively through crack propagation up, down and laterally in the sediment, and Shull and Yasuda (2001) have shown the effectiveness of such burrowing in mixing tracers below the surface. A tracer study by Josefson et al. (2002) showed that 90% or more of phytodetritus transported below the sediment surface was not respired or incorporated into biomass. This buried material may serve as a subsurface food cache to sustain deposit feeders over a longer period of time. Indeed Rudnick (1989) showed that some meiobenthic taxa utilize a large buried reserve of older phytodetritus.

Fucoxanthin shows no subsurface peak, suggesting some decay of the algal material before transport below the sediment surface, decay of the material between being cached by animals and our sampling, or selection by animals for non-diatomaceous material. Pheopigment peaks at 3–5 cm in June and 2.5 cm in August, by contrast, suggest continued nonlocal transport of phytodetritus below the sediment surface by polychaetes, or slow decay of previously transported material.

In addition to transport by animals, other processes may result in subsurface pigment peaks. First, storms may deposit sediment over

the surface layer of phytodetritus. This scenario is unlikely given the depth of Wilkinson Basin, its distance from shore, and the low sedimentation rates for this area. Second, turbidity currents may transport sediment, covering previously deposited phytodetritus. Turbidity currents result in characteristic sediment deposits that are coarsest at the bottom and finest at the top (Gross, 1990). This sediment structure was not apparent in our cores, suggesting a lack of turbidity currents. Third, trawling may also result in transport of phytodetritus below the sediment surface. Wilkinson Basin is intensively trawled (Pilskaln et al., 1998), and profiles of ²¹⁰Pb in our cores (L. Mayer et al., unpublished data) are erratic and consistent with trawling impacts. Trawling, however, would most likely result in a homogenization of the top layers of sediment, including the surface layer of phytodetritus (Mayer et al., 1991), and hence be unlikely to result in subsurface pigment peaks. Given that these scenarios are unlikely, transport by animals remains the probable mechanism by which phytodetritus is transported below the sediment surface at our site.

Mincks et al. (2005) reported much larger interannual than seasonal variation in phytodetrital deposition on the West Antarctic Peninsula shelf. Temporal variability in chlorophyll *a* was confined to the top 2 cm of sediment, however, and although no subsurface peaks were found, substantial amounts of chlorophyll *a* were found deep in the sediment, with concentrations up to 50% of surface values at 8–10 cm. Chlorophyll *a* half-life in this cold water was estimated to be up to 442 days, which, depending on sedimentation rate, may account for the high subsurface values. Mincks et al. (2005) hypothesized that the need for high substrate concentrations for microbial mineralization of organic matter at low (–2.0 to 1.0 °C) Antarctic temperatures may lead to a “food bank” of labile organic matter. This organic matter would represent a temporally stable stock of food for deposit feeders. It is possible that a similar scenario exists in Wilkinson Basin. Although chlorophyll *a* half-lives are likely shorter in Wilkinson Basin (probably more akin to the 28 d value reported by Sun et al. (1994) for Long Island Sound at 5 °C), there is still a substantial concentration of chlorophyll *a* deep in the sediment, exceeding the surface concentration at 10 cm in April, and 15–28% of the surface concentration at 10 cm the rest of the year. It is unclear if the subsurface chlorophyll is the result of low bacterial activity, rapid or persistent animal transport, or a combination of these factors. Regardless, the stability of the benthic assemblage suggests that there may be a relatively constant food stock in Wilkinson Basin.

Alternatively, the low and fairly constant EHAA-N: Total N ratios imply that the proteinaceous material at this site, as assayed by the EHAA measurement, has little nutritional value. Although the benthic assemblage may be relatively constant year-round, the animals may be waiting for pulses of fresh organic matter, detectable with our pigment measurements, but not the EHAA assay. It also suggests that the animals must be able to select fresh particles from refractory ones.

5. Conclusions

Despite seasonal changes in organic input from phytoplankton blooms, the macrofaunal assemblage at Wilkinson Basin remained relatively constant in composition and abundance over the course of a year. This stability may be due to a constant subsurface food stock, the constant temperature at this site, or long generation times (due to low temperature) precluding a rapid response to the input of organic matter. Clearly the spatial variation in abundance and species composition would help to mask any subtle seasonal pattern.

The dominant polychaete families appear to play a major role in transporting phytodetritus from the sediment surface to subsurface depths. They may accomplish it by feeding, burrowing, or both. The rate of phytodetrital burial by animal activity appears to be much greater than the rate of burial by sedimentation. This caching may provide the continuity of food stock through the year to maintain these deeper-

dwelling polychaetes. The tactic of drawing material below the surface for later ingestion clearly lowers subsequent risk from demersal predators as well, affecting both sides of the risk and gain equation.

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