

Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling

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ABSTRACT: Benthic carbon cycling in the northern Bering and Chukchi Seas was hypothesized to be regulated by variable primary production regimes in the overlying water: the highly productive (~ 250 to $300 \text{ g C m}^{-2} \text{ yr}^{-1}$) Bering Shelf-Anadyr Water (BSAW) and the less productive ($\sim 50 \text{ g C m}^{-2} \text{ yr}^{-1}$) Alaska Coastal Water (ACW). Sediment oxygen uptake was correlated with water column parameters and surface sediment C/N ratios characteristic of each water type. Total sediment oxygen uptake rates decreased from a mean $19.2 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in BSAW to a mean $8.7 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in ACW. Mean benthic aerobic respiration rates significantly varied interannually in BSAW, although they were consistently 2 to 3 times greater in BSAW than in ACW within any one year, indicating that interannual variability in water column primary production may have a direct influence on the availability of organic carbon to the benthos. The explanation for higher respiration rates in the benthos beneath BSAW negates an expected reduction due to colder temperatures. A reduction in organic matter to the benthos in ACW apparently limits benthic metabolism even at higher temperatures. Macrofaunal respiration and bioturbation in high benthic biomass regions were important components in benthic carbon cycling.

INTRODUCTION

Past studies have shown a direct relationship between particulate organic matter flux to the benthos and planktonic production in the surface waters of the ocean (Eppley & Peterson 1979, Deuser et al. 1981, Davies & Payne 1984). The quantity and quality of freshly produced or repackaged organic carbon reaching the benthos is influenced by many factors, such as mixed layer and water column depth, zooplankton grazing and bacterial decomposition in the water column (Parsons et al. 1977). Supply of organic matter to the benthos is a major factor influencing benthic community structure, biomass and metabolism (Mills 1975, Graf et al. 1982, Jørgensen 1983, Smith et al. 1983, Smetacek 1984, Wassman 1984, Grebmeier 1987, Grebmeier et al. 1988, 1989).

In this study, we used sediment oxygen uptake rate as an indicator of variability in the supply of organic

carbon to the benthos. We hypothesized that total sediment oxygen uptake would reflect major differences in overlying water column production. Surface sediment C/N ratios are used as an indicator of food quality and, thus, the highest sediment oxygen uptake would reflect areas of increased supply of high quality (low C/N ratio) phytodetritus to the benthos. An ancillary hypothesis was that in regions of high benthic populations, organic carbon turnover in the sediments would be enhanced by increased bioturbation by the dominant fauna. X-radiography of sediment cores, vertical profiles of sediment C/N ratios, and faunal abundance and biomass data are used to investigate potential bioturbation factors. This work was part of an interdisciplinary oceanographic study (ISHTAR: Inner Shelf Transfer and Recycling), which provided supporting data on hydrographic features and water column productivity.

The shallow continental shelf of the northern Bering and Chukchi Seas is characterized by water depths averaging less than 50 m and is ice-covered 7 to 8 mo of the year. Northerly-flowing currents transport Bering Sea water through the Bering Strait and across the shelf in the Chukchi Sea (Fig. 1). The summer season physi-

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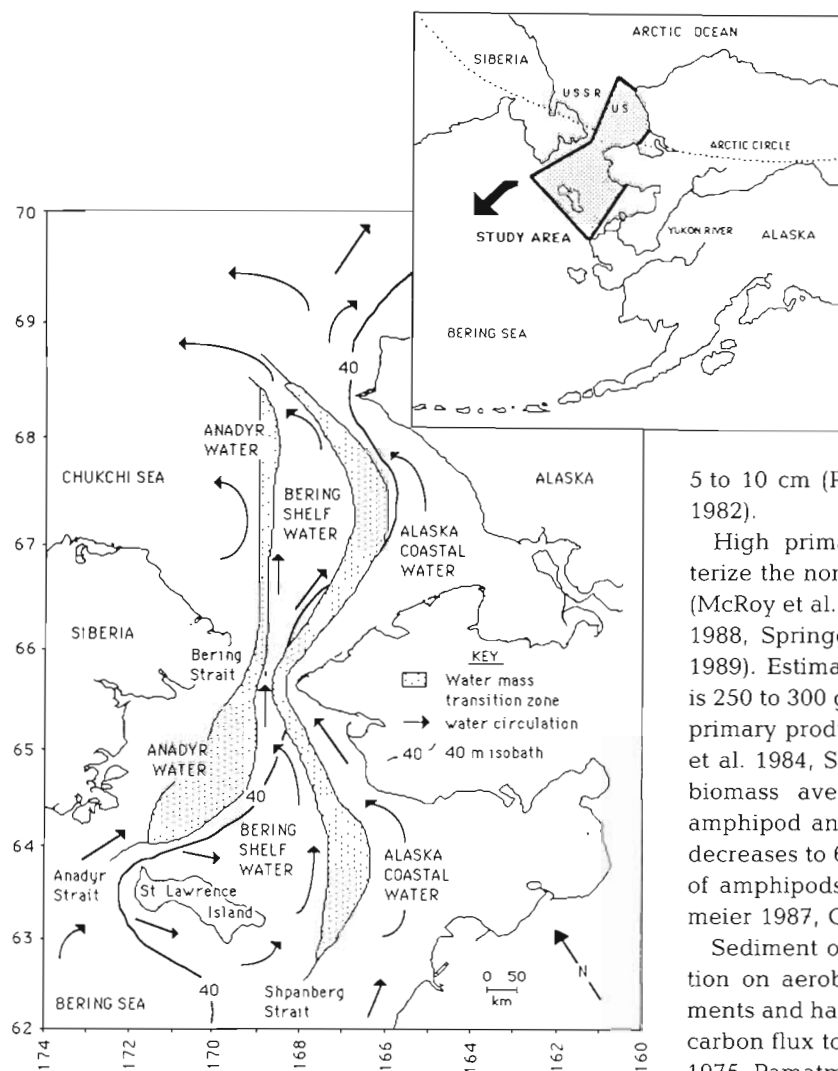


Fig. 1. Study area in the northern Bering and Chukchi Seas showing local water circulation, water masses, and bathymetry (modified from Coachman et al. 1975 and Coachman 1987)

cal oceanographic regime in the area includes 3 water masses defined by T/S profiles (Coachman et al. 1975, Schumacher et al. 1983, Coachman 1987). During the 1985 and 1986 summer season the following bottom water properties characterized these water masses: Anadyr Water ($S \geq 32.5 \text{ ‰}$, $T = -1.0$ to $1.5 \text{ }^\circ\text{C}$) on the western side of the system, Bering Shelf Water ($S = 31.8\text{--}32.5 \text{ ‰}$, $T = 0$ to $1.5 \text{ }^\circ\text{C}$) in the middle region, and Alaska Coastal Water (ACW; $S \leq 31.8 \text{ ‰}$, $T \geq 4 \text{ }^\circ\text{C}$) near the Alaska coast (Coachman 1987). The Bering Shelf and Alaska Coastal waters form a well-defined frontal zone where they meet. However, the interface between Anadyr and Bering Shelf waters is less distinct and forms a more gradual gradient from east to west. Since the salinity, temperature, and nutrient signature of this central water is a combination of both Anadyr and Bering Shelf waters, the combined water hereafter is designated as the Bering Shelf-Anadyr Water (BSAW). The tidal range in the study area is small ca

5 to 10 cm (Pearson et al. 1981, Kowalik & Matthews 1982).

High primary and secondary productivity characterize the northern Bering and Chukchi Seas in BSAW (McRoy et al. 1972, Stoker 1978, 1981, Grebmeier et al. 1988, Springer 1988, Walsh et al. 1988, Walsh et al. 1989). Estimated annual primary production in BSAW is 250 to 300 g C m^{-2} compared to an estimated annual primary production of 50 g C m^{-2} in ACW (Sambrotto et al. 1984, Springer 1988, Walsh et al. 1989). Benthic biomass averages 20 g C m^{-2} in BSAW, where amphipod and bivalve populations are dominant, and decreases to 6 g C m^{-2} in ACW, where a diverse fauna of amphipods, polychaetes and bivalves occur (Grebmeier 1987, Grebmeier et al. 1988, 1989).

Sediment oxygen uptake rates can provide information on aerobic utilization of organic carbon in sediments and have been shown to increase with increased carbon flux to sediments (Hargrave 1969, 1973, Davies 1975, Pamatmat 1977, Deuser & Ross 1980, Suess 1980, Nixon 1981, Smith et al. 1983, Davies & Payne 1984). Although useful in estimating community metabolism in sediments, oxygen respiration rates underestimate total sediment metabolism since they do not directly measure anaerobic processes (Hargrave 1969, Pamatmat 1971a, b, 1977, Davies 1975, Patching & Raine 1983), which can be evaluated by measurement of other oxidants, such as nitrate and sulfate. Higher temperature is known to enhance benthic metabolism (Hargrave 1969, 1973, Davies 1975, Pamatmat 1977, Smith 1978, Smith et al. 1983), but temperature is also often correlated to food supply.

The contribution of macrofaunal respiration to total sediment community metabolism varies with faunal abundance, species composition and season (Kemp & Boyton 1981). Macrofaunal respiration can range from 20 to 90 % of the total community respiration (Smith 1973, Pamatmat 1977, Gray 1981, Blackburn 1987b, Emerson et al. 1988). Blackburn (1987b) found macrofauna could account for up to 70 % of total sediment

metabolism in the northern Bering and Chukchi Seas. The presence of irrigated burrows and tubes in sediment can cause increased oxygen uptake and nutrient flux between the sediment and overlying water, with benthic faunal bioturbation and irrigation being important exchange processes (Goldhaber et al. 1977, Aller & Yingst 1978, Aller 1980, Hylleberg & Henriksen 1980). In addition, bioturbation and irrigation can transport higher organic content surface sediments downwards into the sediment (Fauchald & Jumars 1979). Some species, such as maldanid polychaetes, transport buried organic carbon to the surface, thus stimulating aerobic heterotrophic microorganisms and organic carbon mineralization (Aller 1980, 1982).

MATERIAL AND METHODS

Sediment samples were collected using either a HAPS 0.0133 m² corer or a MK3 0.25 m² box corer. A core incubation technique for benthic metabolism determination was used, following methods described in Pamatmat (1971a), Newrkla (1983), and Patching & Raine (1983). Subsamples for shipboard core incubations were collected with 13 cm diameter, 26 cm long PVC and acrylic cores (8 mm thick walls). Average sediment depth in the cores was 10 to 15 cm, with the remainder of the core overlaid with bottom water. Overlying bottom water was carefully siphoned off and replaced with bottom water collected with a Niskin bottle. The cores were sealed with air-tight lids with a battery-operated stirrer inside that mixed the water to reduce oxygen gradient formation without disturbing the sediments (Newrkla 1983). Control laboratory experiments showed no disturbance of the sediment surface by stirring nor leakage of oxygen through the container walls.

Cores were maintained in the dark at 1 to 2°C for an average 8 to 10 h. This experimental duration was determined an adequate length for measurable depletion of oxygen (average 25%) in the chambers. Oxygen uptake rates, measured in stirred cores for a variety of sediments (both core and in situ methods of measurements) have been found constant for up to 22 h (Patching & Raine 1983, Newrkla 1983). Duplicate 60 ml water samples were collected at the beginning of the experiment from the Niskin bottle and from the sediment cores at the end of the experiment for determination of dissolved oxygen content by Winkler titration. On RV 'Alpha Helix' Cruise 59 (30 June to 10 July 1984) a YSI 49 oxygen electrode and meter were used.

Organic carbon mineralization rates were estimated from the sum of known oxidants in the sediments, oxygen and sulfate, since nitrate is relatively minor as an oxidant (H. Blackburn pers. comm.). Sulfate reduc-

tion rates were obtained from Blackburn & Henriksen (1986) and Blackburn (1987a). Organic carbon mineralization rates were corrected for chemical oxidation at stations with high sulfate reduction rates and high levels of free sulfide (H. Blackburn pers. comm.). At these stations 15% of the measured sediment oxygen uptake rate was subtracted from the original value, based on the assumption that this percentage of oxygen served as a sulfide oxidant and was not available for organic carbon mineralization (Jørgensen 1982, Blackburn & Henriksen 1986). Oxygen is the major oxidant in sediments in the northern Bering Sea under all water masses (Blackburn 1987b), thus organic carbon mineralization rates for stations without high sulfate reduction rates were based on a direct conversion from oxygen to carbon and a respiratory quotient of 1.0 (Nixon et al. 1980).

Thin-section plexiglas boxes (2.5 × 16.0 × 28.0 cm) were used to sample from the box corer and large (13.0 cm diameter × 28.0 cm length) PVC cores were used to collect sediment from the HAPS corer at representative stations in BSAW and ACW and then frozen. Frozen sediment was extracted from the large cores and cut to 2 to 3 cm width slabs. Both frozen plexiglas boxes and sediment slabs were X-rayed to illuminate burrow structure. Minimum burrow surface area was determined for a representative core in the highly bioturbated zone of the BSAW by tracing the inside burrow wall area from the X-ray onto a piece of paper and then passing the 2-dimensional picture through a LiCore Model 3100 area meter. Once X-rayed, the sediment from the plexiglas boxes and large core slabs were sectioned at 1 to 2 cm intervals and the fauna encountered were recorded to species level.

Sediments were sectioned at 1 to 2 cm intervals, dried, and homogenized for organic carbon and nitrogen analyses. Sediments (1 g) were acidified with 2 ml of 1 N HCl and dried at 105°C overnight to obtain carbonate-free sediments, and then homogenized. Duplicate measurements of carbon and nitrogen in sediments were made using a Perkin-Elmer Model 240C CHN elemental analyzer.

Salinity, temperature, and depth data were obtained in conjunction with other investigators using a Niel Brown conductivity-temperature-depth profiler. Data collected as part of the ISHTAR project are available in annual data reports (McRoy & Tripp 1986, 1987). Water column integrated and bottom chlorophyll *a* values were also obtained as part of the ISHTAR project and from Grebmeier (1987).

The parametric Pearson's product-moment correlation test was used to investigate correlations between mean oxygen uptake rates and environmental variables. A nonparametric Mann-Whitney *U*-test was performed on the mean oxygen uptake values for stations in

BSAW and ACW to determine if there was a significant difference in rates between stations in each water type. In addition, a nonparametric Kruskal-Wallis test was used to test for significant differences in oxygen uptake rates between years within BSAW and ACW. A microcomputer statistical package (Brain Power Inc. 1985) was used for these analyses, along with appropriate statistical tables (Rohlf & Sokal 1969, Conover 1980).

Each station designation presented in subsequent tables is composed of 5 numbers; the first 2 numbers designate the cruise, the second 3 numbers designate the actual station.

RESULTS

Benthic stations were occupied over 3 field seasons from July to September 1984 to 1986 in the study area. Temperature and salinity data confirmed the presence of a front dividing BSAW and ACW (McRoy & Tripp 1986, 1987). This front, which varies in location over the open-water season, separates BSAW and ACW with a salinity boundary of 31.8‰ (Coachman 1987). The average location of the front was used to designate station locations relative to BSAW and ACW.

Hydrographic data and sediment oxygen uptake rates were collected at 61 stations in the northern Bering and Chukchi Seas, 45 in BSAW and 16 in ACW, during 5 cruises on the RV 'Alpha Helix' (Fig. 2; Table 1). The cruise dates were as follows: Cruise 59 (30 June to 10 July 1984), Cruise 73 (25 July to 10 August 1985), Cruise 74 (26 August to 9 September 1985), Cruise 85 (11 to 26 July 1986) and Cruise 87 (14 to 24 August 1986).

Oxygen uptake and carbon mineralization rates

Oxygen uptake rates were measured on duplicate sediment cores for 32 of the 45 stations located in BSAW and 12 of the 16 stations located in ACW; the remainder were single core measurements (Table 1). Before pooling average duplicate values with individual measurements, a Mann-Whitney test was performed on the data. There was no significant difference between the mean of duplicate measurements and single measurements for stations in either BSAW ($p > 0.25$) or ACW ($p > 0.25$), thus all stations were subsequently included in the analysis.

Sediment oxygen uptake rates averaged $19.18 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in BSAW and $8.72 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in ACW over the total study period (Table 2). Similarly, the mean organic carbon mineralization rate was 2 to 3 times higher in BSAW ($20.21 \text{ mmol C m}^{-2} \text{ d}^{-1}$) compared to ACW ($9.04 \text{ mmol C m}^{-2} \text{ d}^{-1}$; Table 2). There

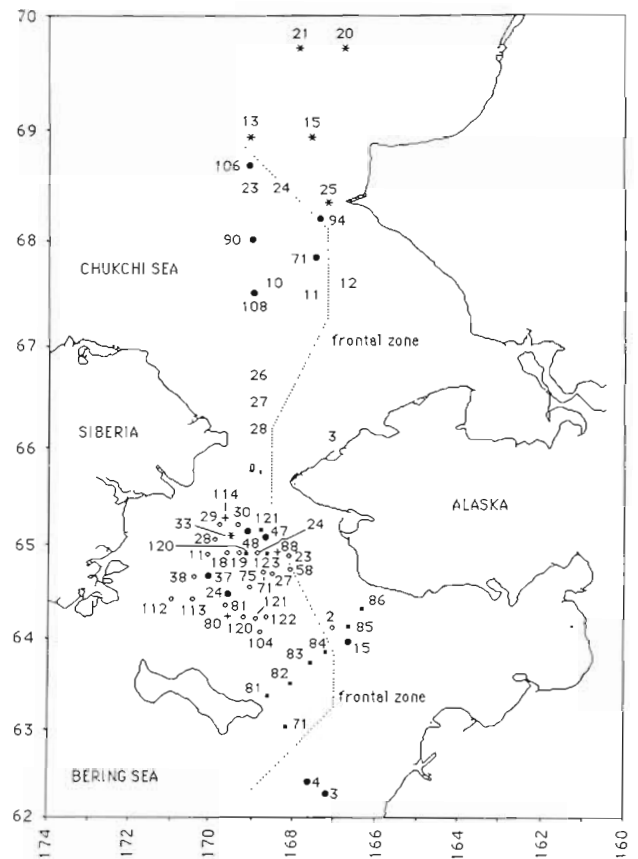


Fig. 2. Location of stations for benthic respiration experiments in the northern Bering and Chukchi Seas for cruises 59 (■), 73 (○), 74 (*), 85 (●) and 87 (+). A frontal zone separates Bering Shelf-Anadyr Water in the west from Alaska Coastal Water in the east

were significant differences between both oxygen uptake and carbon mineralization rates in the 2 water types based on a Mann-Whitney test, stated as a 1-tailed test, $p < 0.001$.

The highest oxygen uptake rates occurred at stations in BSAW, both in the northern Bering and Chukchi Seas (Fig. 3). In the northern Bering Sea high values ($\geq 30 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) were measured northeast of St Lawrence Island and in the central region between St Lawrence Island and Bering Strait, known as the Chirikov Basin. Rates averaged 30 to $40 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in the Chirikov Basin and were lowest ($< 10 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) at stations in ACW and in regions of BSAW northwest of St Lawrence Island and north of Bering Strait. Significant interannual variability in sediment oxygen uptake rates occurred in BSAW (Kruskal-Wallis, $p < 0.001$), but there was no statistical difference between years in ACW (Kruskal-Wallis, $0.05 < p < 0.10$; Table 3).

Oxygen uptake rates underestimated total sediment metabolism in areas where sulfate reduction rates were

Table 1. Hydrographic measurements and oxygen uptake rates for stations occupied during Cruises 59, 73, 74, 85 and 87 (hydrographic data for Cruises 74 and 85 from McRoy & Tripp 1986, 1987). Rates are for duplicate experiments except where standard deviation (SD) is blank, indicating only one sediment core was measured. Other blanks in table indicate no data

Station	Bottom temp. (°C)	Bottom salinity (‰)	Bottom sigma-t	Depth (m)	Sediment oxygen uptake rates (mmol O ₂ m ⁻² d ⁻¹)	
					Mean	SD
59071	-0.24	33.229	26.69	20	12.62	-
59081	-0.68	33.412	26.85	25	22.12	4.46
59082	-0.03	33.269	26.71	30	31.07	16.89
59083	-0.46	33.368	26.81	31	23.86	1.85
59084	-0.33	33.257	26.71	30	17.62	0.74
59085	-0.67	33.311	26.77	28	9.46	0.00
59086	-0.07	33.399	26.82	26	9.93	1.27
59088	4.19	33.179	26.32	23	-	-
59108	-0.16	33.183	26.65	36	-	-
59120	-0.21	32.750	26.30	47	45.62	3.71
59121	0.82	32.635	26.15	50	26.25	9.54
59123	0.07	33.030	26.51	49	18.62	4.82
59132	0.90	32.309	25.89	31	-	-
73002	1.89	32.168	25.71	26	15.74	-
73011	0.31	32.656	26.20	45	23.76	6.29
73018	0.71	32.646	26.17	42	28.56	-
73019	0.65	32.580	26.12	46	2.04	-
73023	-	-	-	42	1.75	0.93
73024	-	-	-	44	15.91	7.67
73027	1.25	-	-	40	21.08	-
73028	1.16	32.756	26.23	46	15.38	0.27
73029	0.16	32.604	26.16	47	8.42	-
73030	0.72	32.559	26.10	49	19.31	11.82
73038	1.42	32.837	26.28	47	16.63	-
73058	0.88	32.432	25.99	28	18.01	-
73071	1.69	32.357	25.88	42	41.60	-
73075	1.12	32.779	26.25	43	16.23	0.37
73081	1.42	32.840	26.28	42	11.18	0.64
73104	1.88	32.522	26.00	34	7.88	0.74
73112	1.99	32.857	26.26	44	1.82	1.01
73113	2.19	32.795	26.19	43	5.53	-
73120	1.95	32.757	26.18	40	10.49	7.52
73121	2.01	32.722	26.19	40	17.96	9.85
73122	2.13	32.777	26.18	40	11.72	-
74003	8.58	28.207	21.87	22	3.63	-
74010	3.01	32.719	26.06	48	14.16	11.50
74011	3.27	32.591	25.94	46	7.95	6.32
74012	5.46	31.972	25.22	48	1.07	0.64
74013	2.70	32.850	26.19	51	11.66	1.33
74015	3.62	32.378	25.74	46	3.65	0.10
74020	4.71	32.064	24.38	42	1.93	0.50
74021	3.33	32.231	25.65	45	2.63	0.83
74023	2.64	32.692	26.07	53	9.20	7.15
73024	2.85	32.421	25.84	49	21.38	0.59
74025	8.51	30.847	23.94	37	0.65	0.37
74026	6.03	31.940	25.13	40	6.41	1.19
74027	5.68	32.006	25.23	43	6.79	-
74028	2.80	32.359	-	52	6.76	0.59
74033	2.33	32.740	26.14	47	2.99	0.45
85003	1.72	31.825	25.45	19	3.19	-
85004	0.31	32.346	25.95	26	18.15	6.19
85015	0.53	32.426	26.00	31	18.15	4.00
85024	1.43	32.470	25.98	37	28.94	-
85037	1.21	32.577	26.09	38	16.66	6.00
85047	2.54	32.476	25.91	48	31.62	-
85048	1.86	32.845	26.26	52	30.80	0.11
85071	2.03	32.517	25.98	54	28.19	3.12
85090	2.97	32.741	26.08	54	24.34	4.21
85094	4.71	32.135	25.44	45	19.37	6.63
85106	2.22	32.475	25.93	52	29.02	1.51
85108	3.21	32.778	26.09	48	30.82	3.60
87080	1.93	32.173	25.71	34	37.92	-
87088	1.97	32.320	25.83	47	28.28	8.63
87114	0.58	32.385	25.97	51	28.19	5.54

Table 3. Mean sediment oxygen uptake rates from 1984 to 1986 for stations located in Bering Shelf-Anadyr Water and Alaska Coastal Water (including number of stations in parentheses and standard deviation, SD)

Year	Date	Bering Shelf-Anadyr Water Oxygen uptake rate (mmol O ₂ m ⁻² d ⁻¹)		Alaska Coastal Water Oxygen uptake rate (mmol O ₂ m ⁻² d ⁻¹)	
		Mean	SD	Mean	SD
1984	30 Jun–10 Jul	24.72 (8)	10.15	9.70 (2)	0.33
1985	25 Jul–10 Aug	15.31 (18)	9.72	11.83 (3)	8.81
	26 Aug–9 Sep	9.46 (8)	5.76	3.60 (7)	3.74
	All stations	13.51 (26)	9.01	6.07 (10)	6.51
1986	11–26 Jul	27.55 (8)	4.95	14.72 (4)	7.71
	14–24 Aug	31.46 (3)	5.59	–	–
	All stations	28.62 (11)	5.17	14.72 (4)	7.71

Table 4. Oxygen uptake, sulfate reduction and organic carbon mineralization rates (sulfate reduction rates from Blackburn & Henriksen 1986, Blackburn 1987a)

Station ^a	Oxygen uptake	Rates (mmol m ⁻² d ⁻¹)			Aerobic respiration (%)
		Sulfate reduction	Organic carbon mineralization ^b		
74–010	14.16	3.0	20.16	70	
74–011 ^c	6.76 ^c	7.0	20.76	33	
74–013	11.66	0.5	12.66	92	
74–015	3.65	0.8	5.25	70	
74–023 ^c	7.82 ^c	8.5	24.82	32	
85–015	18.15	1.2	20.55	88	
85–024	28.94	1.7	32.34	89	
85–037	16.66	2.0	20.66	81	
85–048	30.80	0.6	32.00	96	
85–071	28.19	0.3	28.79	98	
85–090	24.34	1.9	28.10	86	
85–094	19.37	0.5	20.37	95	
85–106	29.02	1.2	31.42	92	

^a RV 'Alpha Helix' Cruise 74 (26 Aug–9 Sep 1985), RV 'Alpha Helix' Cruise 85 (11–26 Jul 1986)
^b Σ Organic carbon mineralized = O₂ uptake rate + 2 (SO₄²⁻ reduction rate)
^c Corrected by 15 % for chemical oxidation (after Jørgensen 1982, Blackburn & Henriksen 1986)

Table 5. Pearson product-moment correlation statistics between sediment oxygen uptake rate and environmental parameters

Environmental parameter (No. of observations)	Sediment oxygen uptake rate	
	Correlation coefficient <i>r</i>	Level of significance <i>p</i>
Bottom water temperature (64)	-0.393	<0.01
Bottom water salinity (63)	0.263	0.01 < <i>p</i> < 0.05
Bottom water density (sigma-t; 62)	0.324	0.01 < <i>p</i> < 0.05
Bottom water chlorophyll <i>a</i> ^a (66)	0.240	0.01 < <i>p</i> < 0.05
Surface sediment C/N ratio ^b (58)	-0.254	0.01 < <i>p</i> < 0.05

^a Bottom water chlorophyll *a* values from McRoy & Tripp (1986, 1987) and Grebmeier (1987)
^b Surface sediment C/N ratios from Grebmeier (1987)

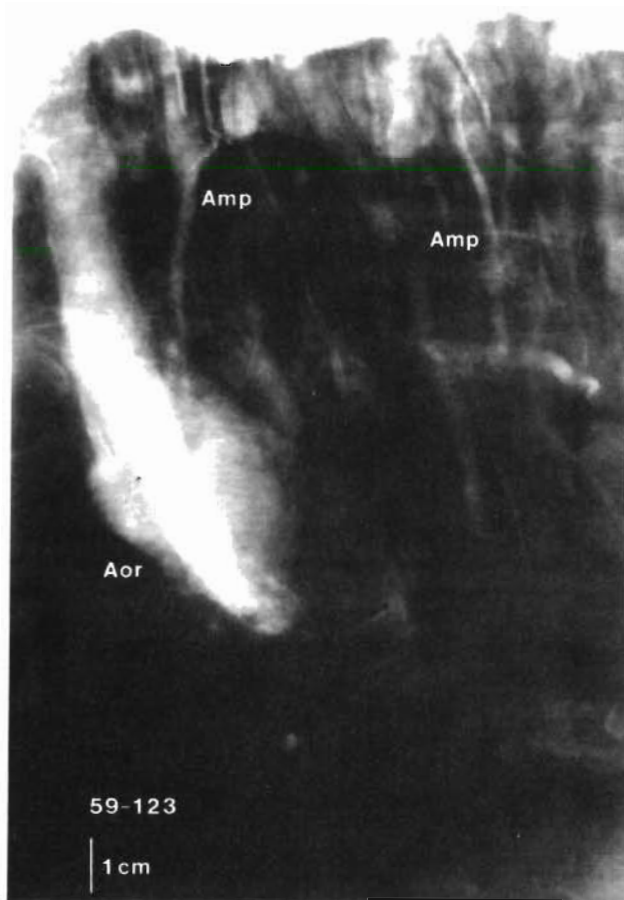


Fig. 4. X-radiograph of sediment core at Stn 59-123 showing infaunal bioturbation zone. Aor: F. Aoridae (*Lembos arcticus*); Amp: F. Ampeliscidae (*Ampelisca macrocephala*)

calcareo; Fig. 5). The bioturbated zone extends 10 cm into the sediment, with empty bivalve shells occupying the sediments below this depth. Empty tellinid bivalve shells form a lag layer (an accumulation of shells with a larger surface area than surrounding sediment) at the base of this core. The sediment type at this station is fine sand, silt and clay.

Stations in ACW have less bioturbation than those in BSAW. The core from Stn 59-085 (Fig. 6) has one suspension-feeding styelid tunicate (*Pelonaia corrugata*) and a venerid bivalve (*Liocyma fluctuosa*). Sediments are primarily fine sand. The core from Stn 59-108 (Fig. 7) is composed of medium sand and is dominated by echinarachnid sand dollars (*Echinarachnius parma*). The zone of bioturbation extends to 6 cm.

Sediment core C/N ratios

Vertical profiles of C/N ratios for 7 BSAW and 4 ACW sediment cores show a trend in the sediments under each water type, with lowest sediment C/N ratios

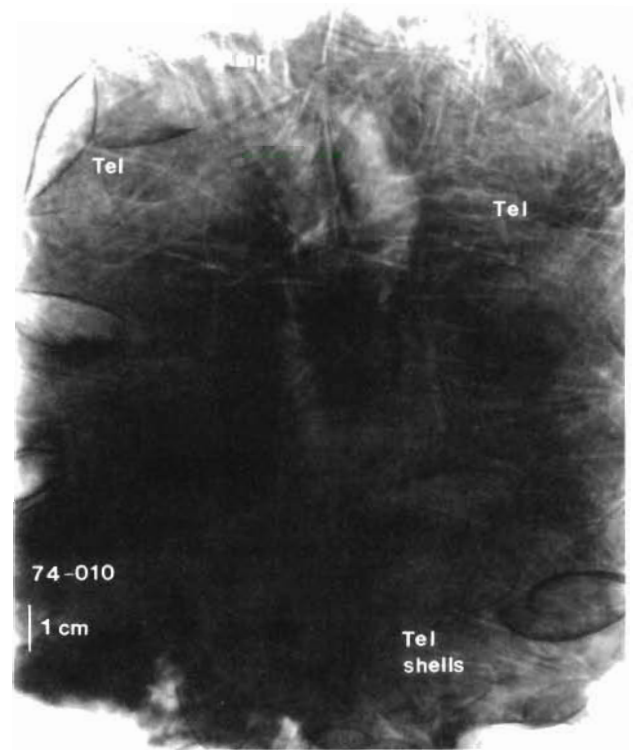


Fig. 5. X-radiograph of sediment core at Stn 74-010 showing infaunal bioturbation zone. Amp: F. Ampeliscidae (*Byblis gaimard*); Tel: F. Tellinidae (*Macoma calcarea*)

occurring in BSAW and highest sediment C/N ratios occurring in ACW (Fig. 8). A bioturbated zone is distinguishable in these data by the vertical profile of similar C/N ratios down to 7 cm, with values rising below this zone.

DISCUSSION

Two factors, temperature and food supply, have a strong limiting influence on benthic metabolism (Graf et al. 1983, Hylleberg & Riis-Vestergaard 1984), but they are often correlated, and therefore hard to separate. Davies (1975) and Wassman (1984) demonstrated that the amount of nutritious, labile organic material supplied to the benthos, rather than temperature, enhanced sediment oxygen uptake rates in fjord ecosystems. Pamatmat & Banse (1969) found that variations in temperature could explain only 30% of the total variation in sediment oxygen uptake rates in Puget Sound, Washington. They proposed that this variance was due to seasonal changes in biological activity responding to a variable organic matter supply.

Both temperature and food supply influence benthic community structure in the northern Bering and Chuk-

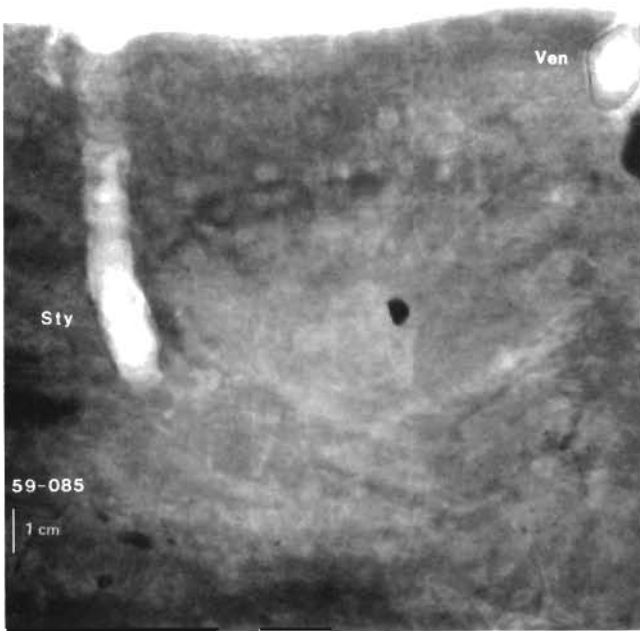


Fig. 6. X-radiograph of sediment core at Stn 59-085 showing infaunal bioturbation zone. Sty: F. Styelidae (*Pelonaia corrugata*); Ven: F. Veneridae (*Liocyma fluctuosa*)

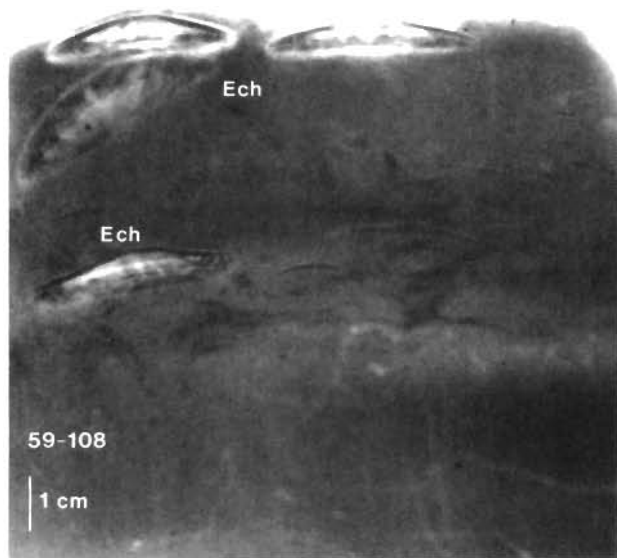


Fig. 7. X-radiograph of sediment core at Stn 59-108 showing infaunal bioturbation zone. Ech: F. Echinarachniidae (*Echinarachnius parma*)

chi Seas (Grebmeier et al. 1989), with food supply determined to have the major influence on benthic biomass (Grebmeier et al. 1988). In the present study, the highest sediment oxygen uptake rate (mean = 19

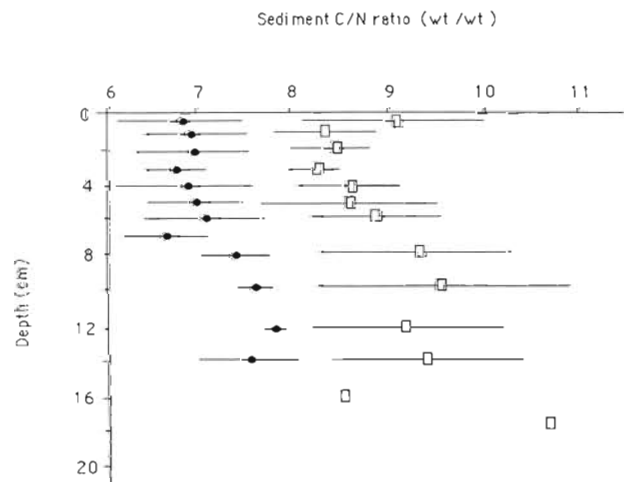


Fig. 8. Mean and range of C/N ratios versus depth of sediments at stations located in Bering Shelf-Anadyr Water (●; 7 stations) and Alaska Coastal Water (□; 4 stations)

mmol O₂ m⁻² d⁻¹) and organic carbon mineralization rate (mean = 20 mmol C m⁻² d⁻¹) occurred in sediments underlying BSAW, characterized by low temperatures and high primary production in the summer (Springer 1988, Walsh et al. 1988, Walsh et al. 1989). The measurement of higher metabolic rates in the lower temperature regime (-1.0 to 1.5°C) in BSAW indicates that bacterial and benthic faunal respiration in these northern waters may not be temperature limited. Comparing the 2 water types, a low mean benthic metabolism rate (9 mmol O₂ m⁻² d⁻¹; Table 1) occurred in the warmer ACW, where mean benthic biomass was also low (6 g C m⁻²) compared to a high mean benthic metabolism rate (19 mmol O₂ m⁻² d⁻¹; Table 2) and mean benthic biomass (20 g C m⁻²) in BSAW (Grebmeier et al. 1988). Although the data imply that the organic carbon flux to the benthos in BSAW was so much greater as to outweigh low temperature effects on benthic metabolism, further studies are needed on the effect of variable temperature regimes on benthic metabolism at the same sites in both BSAW and ACW to differentiate food supply from temperature effects.

Smetacek (1984) suggests that supply of organic matter to the sea floor in shallow coastal environments is a major factor influencing community structure, biomass and metabolism in the benthos; a conclusion supported in our studies (Grebmeier et al. 1988, 1989 this paper). On a global basis, sediment oxygen uptake in BSAW is within the expected range for inner shelf sediments, while the ACW sediment has oxygen uptake closer to those measured in the outer shelf and upper slope regions (Table 6). Inner shelf systems and, in this study, BSAW experience high water column primary production (Parsons et al. 1977, Jørgensen 1983, Springer 1988), along with high sediment oxygen uptake, indi-

Table 6. Comparison of oxygen uptake rates in marine sediments from 5 depth zones and the areal coverage of these zones in the ocean (modified from Jørgensen 1983)

Zone	Depth (m)	Area (10 ¹² m ²)	Oxygen uptake rate (mmol O ₂ m ⁻² d ⁻¹)
Inner shelf	0–50	13 (4%)	20
Outer shelf	50–200	18 (5%)	10
Upper slope	200–1000	15 (4%)	3
Lower slope	1000–4000	106 (29%)	0.3
Deep sea	>4000	208 (58%)	0.05

cating that organic matter supply is a major regulating factor in sediment metabolism rates. In the study area, water column production is 5 to 6 times higher in BSAW than ACW (Springer 1988), which corresponds to a 3- to 4-fold greater benthic biomass in BSAW than ACW (Grebmeier et al. 1988). Differences in the quality and quantity of organic carbon reaching the sediment in these 2 water types suggest that food supply is a major regulating factor in benthic biomass (Grebmeier et al. 1988). The 2 to 3 times higher mean sediment oxygen uptake rate in BSAW compared to ACW supports the hypothesis of an enhanced food supply to the benthos in BSAW relative to the benthos under the less productive ACW.

The factors influencing sediment oxygen uptake may also influence the variability in rates between years. Although differences in sediment oxygen uptake were observed between years in BSAW, the relative difference within each year between BSAW and ACW was the same, that is, 2 to 3 times higher rates in BSAW compared to ACW. The lower 1985 mean oxygen uptake may be the result of reduced organic matter supply, although previous data, both surface sediment C/N ratios and benthic biomass, indicated a seasonally reliable organic matter supply in these waters (Grebmeier et al. 1988). Another possibility is that samples were collected over a larger area, including stations underlying less productive regions of BSAW as well as in areas where organic matter accumulation in the sediments was low due to higher current velocities. Seasonal sampling at designated stations in each water type would clarify the influence of individual environmental parameters upon sediment oxygen uptake rates.

The significant correlations between oxygen uptake and 5 environmental variables (bottom water temperature, salinity, density, chlorophyll *a* concentration, and surface sediment C/N ratio) suggest a relationship between oxygen uptake rates and the quantity and quality of organic matter reaching the sediment. Previous work on microbial respiration in Alaskan marine waters and sediments indicate no direct cause and effect relationship with temperature or salinity (Grif-

fiths et al. 1984); a conclusion supported by this study. Griffiths et al. (1984) concluded that the quality of organic matter could best explain differences in microbial respiration rates. In the present study, the significant relationship between oxygen uptake and bottom chlorophyll *a* concentration indicates the importance of the quantity of organic matter, and the significant correlation with C/N ratios in surface sediments reinforces the conclusion that the quality of organic matter also influences oxygen uptake rates. In combination, these variables indicate that a higher quantity and quality of organic matter reaches the benthos in BSAW than in ACW, thus resulting in higher sediment metabolism.

Total oxygen uptake was highest in the offshore central regions of the northern Bering and Chukchi Seas under BSAW (Fig. 3). These regions are characterized by relatively weak current flow (Creager & McManus 1967, Nihoul 1986, Nihoul et al. 1986) and high phytoplankton biomass and primary production (Springer 1988), which is consistent with a high organic matter flux to the benthos. In addition, the highest oxygen uptake region in the northern Bering Sea coincides with the area of highest benthic biomass (Grebmeier et al. 1988). The bottom here is dominated by tube-dwelling ampeliscid amphipods *Ampelisca macrocephala*, which bind the sediments together through tube formation, and tellinid bivalves (*Macoma calcaria*; Grebmeier 1987 and unpubl.). The high oxygen uptake region off the northeast end of St Lawrence Island (Fig. 3) in fine-grain sediments was also dominated by these same species.

Most stations in ACW are characterized by low oxygen uptake (<10 mmol O₂ m⁻² d⁻¹), except those occurring near the boundary with BSAW. Low oxygen uptake rates also occurred in BSAW just north of both Anadyr and Bering Straits. This could be the result of higher current velocities in this area (Coachman et al. 1975) that decrease the settling of organic material to the sediments. These sediments are characterized by rock, pebble, and gravel and are dominated by epifaunal communities (Stoker 1978). The low surface-to-volume ratio and low organic content of these sedi-

ments (Grebmeier 1987, Grebmeier et al. 1989) as well as reduced levels of bioturbation would be consistent with reduced sediment metabolism.

Aerobic respiration dominates organic carbon mineralization in both BSAW and ACW in the northern Bering Sea (Blackburn & Henriksen 1986, Blackburn 1987b). However, organic carbon mineralization varies under BSAW in the Chukchi Sea depending on the amount of anaerobic respiration occurring there. Blackburn & Henriksen (1986) and Blackburn (1987b) found that macrofaunal respiration accounted for 60 to 70 % of the total aerobic mineralization in BSAW in the northern Bering Sea but only 5 to 50 % in the Chukchi Sea. In ACW, macrofaunal respiration accounted for 10 to 20 % of the total aerobic mineralization. The remainder of aerobic mineralization was due to meio- and micro-fauna and bacteria. Using faunal oxygen uptake rates determined by K. Henriksen (unpubl.) for amphipods and bivalves (maintained in precombusted sediments) and faunal counts made at stations in our study (Grebmeier 1987), an estimate can be made for the dominant macrofaunal respiration component. This estimate indicates that dominant macrofauna account for 61 % of the total sediment oxygen uptake rates measured in high amphipod areas in BSAW, which falls within the 60 to 70 % range found by Blackburn & Henriksen (1986) and Blackburn (1987b).

In the Chirikov Basin, ampeliscid amphipod tubes caused a 200 to 300 % increase in sediment surface area at a representative station (59-123, Fig. 4). As a result, bioturbation must be important in BSAW sediments, thus enabling additional aerobic oxidation of organic material. The abundance and biomass of tubedwelling ampeliscid amphipods at this station were 4695 ind. m^{-2} and 10.7 g C m^{-2} , respectively (Grebmeier 1987). Results (Table 4) show average aerobic respiration accounted for ~88 % of the total organic carbon mineralization in the Chirikov Basin for stations with high benthic biomass (85-024, -037, -048), which is comparable to 80 % reported by Blackburn & Henriksen (1986) and Blackburn (1987b). Ventilation of amphipod tubes by feeding currents and movement of animals allows oxygenated channels to extend 10 to 15 cm into the sediments (Fig. 4). Henriksen (1987) found that mats of *Ampelisca* spp. amphipods can influence uptake and release of nitrate from the sediments, as well as enhance ammonium output, depending on the overlying nutrient concentrations.

The station with the highest faunal standing stock occurred in the Chukchi Sea (Fig. 5) and was dominated by the tellinid bivalve *Macoma calcarea* (abundance = 548 ind. m^{-2} , biomass = 36.0 g C m^{-2} ; Grebmeier 1987 and unpubl.), which lives beneath the sediment surface and extends a siphon to the surface to feed on detritus. *Byblis gaimardi*, a detritus-feeding ampeliscid amphi-

pod, was also dominant (abundance = 4408 ind. m^{-2} , biomass = 7.8 g C m^{-2} ; Grebmeier 1987 and unpubl.), although it builds a shallower, less permanent tube compared to the dominant ampeliscid amphipod (*Ampelisca macrocephala*) in the northern Bering Sea, and thus has less of an effect on altering sediment surface area available for aerobic respiration. Nevertheless, aerobic respiration accounted for 70 % of the total carbon mineralization at this station, which indicates that the high standing stock is important. The increase in anaerobic metabolism at this station is associated with a higher sediment organic content (1.2 %) and finer-grained sediments than found at stations in the Chirikov Basin (Grebmeier 1987, Grebmeier 1989). Areas of high anaerobic metabolism in the Chukchi Sea, such as Stn 74-023, are dominated by tellinid and nuculid bivalves (Grebmeier 1987). The ability of these bivalves to close their shells, thus reducing body exposure to high sulfide sediments, and an ability to feed and respire at the sediment surface, may enable them to compete better in an anoxic environment.

A representative station (59-085, Fig. 6) in ACW also had a bioturbated surface layer (6 to 8 cm), although absolute abundance (1190 ind. m^{-2}) and biomass (10.4 g C m^{-2}) were low compared to BSAW stations (Grebmeier 1987, Grebmeier et al. 1989, and unpubl.). Styelid tunicates *Pelonaia corrugata* and sternaspid polychaetes *Sternaspis scutata* occurred at Stn 59-085, with the dominant fauna being sand dollars *Echinarachnius parma* (abundance = 230 ind. m^{-2} , biomass = 4.6 g C m^{-2} , Grebmeier 1987 and unpubl.). *E. parma* was also dominant (abundance = 160 ind. m^{-2} , biomass = 0.2 g C m^{-2}) at Stn 59-108 (Fig. 7) in ACW (Grebmeier 1987 and unpubl.). The sand dollar *E. parma* is an indicator of hydrodynamic stresses (tidal action) in the Bay of Fundy (Wildish & Peer 1983) which can create impoverished benthic communities. Although tides are minimal in the northern Bering and Chukchi Seas (Pearson et al. 1981, Kowalik & Matthews 1982), faster currents can occur where *E. parma* is dominant (Coachman et al. 1975), and may be responsible for the abundance of *E. parma* to the exclusion of other fauna (Grebmeier et al. 1989). However, at stations where *E. parma* is dominant in both BSAW and ACW, their abundance values are similar but their biomass values are at least 3 to 4 times greater in BSAW than ACW (Grebmeier 1987, Grebmeier et al. 1988). Therefore, although hydrodynamic stresses may influence species composition, food supply regulates benthic biomass. Low primary production and organic carbon supply to the benthos not only limits benthic biomass (Grebmeier et al. 1988), but our study indicates food supply is the regulating factor limiting benthic metabolism in ACW in spite of high bottom water temperatures and low to moderate bioturbation.

In summary, benthic carbon cycling in the northern Bering and Chukchi Seas was influenced by the quantity and quality of organic matter available to the benthos. Highest oxygen uptake rates occurred in BSAW in both basin regions of the northern Bering and Chukchi Seas, indicating a high organic matter flux to the benthos. In addition, the high numbers of macrofauna under portions of BSAW, which enhance bioturbation levels, and the high rate of organic carbon mineralization in the sediments, reflect high benthic food supply to the benthos. We conclude that the low sediment oxygen uptake in ACW is consistent with less organic matter supply to these sediments.

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