THE ECOLOGY OF BENTHIC CARBON CYCLING IN THE NORTHERN BERING AND CHUKCHI SEAS

A

THESIS

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By

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ABSTRACT

Benthic community structure, biomass and carbon cycling in the northern Bering and Chukchi Seas are hypothesized to be regulated by food supplied by variable primary production regimes in the overlying water masses. These water masses transport Pacific Ocean water northward through Bering Strait and across the shelf of the Chukchi Sea. Benthic community structure and metabolism, along with water column and sediment organic carbon, were investigated. Low surface sediment C/N ratios (5.7-7.7) suggest a higher quality, nitrogen-rich marine carbon supply to the benthos in the highly productive (~250 g C m^{-2} yr^{-1}) Bering Shelf/Anadyr (BS/A) water mass compared to lower quality, higher C/N ratios (7.7-14.0), indicative of less labile, more refractory marine and terrestrial organic matter, in sediments under the less productive (~50 g C m^{-2} yr^{-1}) Alaska Coastal (AC) water mass. The benthic communities under BS/A water are dominated by detritus-feeding amphipods (F. Ampeliscidae and F. Isaeidae) and bivalves (F. Nuculidae and F. Tellinidae). A diverse fauna exists under AC water, including a mixture of amphipod (F. Isaeidae and F. Phoxocephalidae), sand dollar (F. Echinarachniidae) and polychaete (F. Sternaspidae and F. Maldanidae) communities. Benthic biomass averaged 20.2 g C m^{-2} under the BS/A water and decreased to an average 6.3 g C m^{-2} under the AC water. Total sediment oxygen uptake rates were highest under BS/A water, averaging 19.2 mmol O_2 m^{-2} d^{-1}, and dropped to an average 8.1 mmol O_2 m^{-2} d^{-1} under the AC water, suggesting a greater organic carbon supply to the BS/A benthos than the AC benthos. Annual benthic carbon consumption associated with the BS/A water is estimated at 67.8 g C m^{-2} yr^{-1} compared to 27.8 g C m^{-2} yr^{-1} in sediments associated with AC water. Combining estimates of zooplankton grazing, microplankton utilization and benthic metabolism, biological consumption accounts for 54% of the BS/A annual carbon production, leaving 46% to be buried in the underlying sediments or transported northward out of the study area. In the AC system all the annual primary production is totally consumed, requiring an external organic carbon source to meet biological demand. The results of the study support the conclusion that the quantity and quality of food supply are major regulating mechanisms in benthic community structure, biomass and carbon cycling in the northern Bering and Chukchi Seas. The seasonally reliable food source leads to stability in this benthic ecosystem in spite of a normally harsh polar environment.

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CHAPTER 1. THE ECOLOGY OF BENTHIC CARBON CYCLING

INTRODUCTION

Shallow marine benthic systems in polar regions may exhibit high faunal abundances and biomass values in spite of low temperatures and seasonal, spring and summer, fluxes of particulate organic matter to the benthos (White 1977; Peterson and Curtis 1980). A major question in marine ecology concerns the mechanisms that regulate benthic community structure. In the Arctic and Antarctic the slow growth, extended time for maturation and long life spans, of benthic fauna, along with variable food supplies and diverse substrate conditions are factors known to influence benthic faunal abundance and biomass (Peterson and Curtis 1980; White 1977 and 1984; Stoker 1978 and 1981; Feder and Jewett 1981). Past studies in shallow sub-arctic and arctic marine systems suggested that high benthic abundance and biomass values often corresponded to areas of enhanced deposition of phytodetritus to the benthos, particularly in low temperature, high salinity water mass regimes (Stoker 1978 and 1981; Jewett and Feder 1981; Haflinger 1981; Feder et al. 1985).

Three major water masses occur in summer in the northern Bering and Chukchi Seas: the low salinity, high temperature Alaska Coastal water near the Alaska coastline in the east, and the high salinity, low temperature Bering Shelf and Anadyr water masses in the central and western portions of this shelf (Coachman et al. 1975). The average standing stock of surface phytoplankton during summer in the region shows a gradient from low values (<2 mg m^{-3}) near the Alaska coastline to high values (up to 16 mg m^{-3}) in the western area of the region (Sambrotto et al. 1984; Walsh et al. 1987). Integrated chlorophyll *a* values during the summer range from below 25 mg C m^{-2} in the Alaska Coastal water and from 300 to 900 mg C m^{-2} in the western sections of both the northern Bering and Chuckchi Seas (Springer and McRoy 1986).

Alaska Coastal (AC) water has an estimated annual primary production of 50 g C m^{-2} compared to an annual value of 250 g C m^{-2} for the combined Bering Shelf/ Anadyr (BS/A) water mass (Springer and McRoy 1986 and unpubl. data; Walsh et al. 1987). The present study addresses the hypothesis that high benthic abundance and biomass regions are correlated with the high primary production in BS/A water.

Standing stock of benthic fauna has been shown to increase with latitude on the continental shelf of the southeastern Bering Sea northward through Bering Strait and into the Chukchi Sea in the Arctic (Stoker 1978 and 1981). In addition, Stoker observed variations in community structure and biomass from east to west in the northern Bering and Chukchi Seas. He suggested four possible explanations for the observed gradient: 1) high primary production; 2) terrestrial detrital input from the Yukon and Kuskokwim rivers; 3) current structure; and 4) the distribution of predators. He also suggested the mechanisms responsible for the observed characteristics of high diversity, benthic community stability, and latitudinal distribution of benthic standing stocks would be found in investigations of the physical and biological interactions which supplied food to the benthos as well as in studies of the fauna itself.

Food supply from high primary production is suggested as a regulating factor in benthic community structure in shallow marine waters in the Antarctic (Clarke 1980). Dayton and Oliver (1977) found benthic biomass to be highest on the east side of McMurdo Sound in nearshore eutrophic regions compared to low faunal biomass values in the oligotrophic west side of the Sound in nearshore regions. They suggested that food supply from phytoplankton had an important impact on benthic community structure. Similar relationships of high water column production and benthic biomass have been observed in the deep sea. Rowe (1969) found a positive correlation of benthic biomass with primary productivity and a negative correlation of bottom fauna with depth. He suggested that the benthos was a better indicator of productivity over a long period of time because highly variable production would be integrated over time and portrayed by benthic community structure. Similar results were found by Smith et al. (1983) on a cruise track between Hawaii and San Diego. Macrofaunal biomass, abundance, and sediment surface organic carbon and nitrogen content increased along an increasing gradient of surface productivity and decreasing depth.

Oxygen uptake by sediments has been shown to increase with increased carbon flux to the benthos (Hargrave 1973; Davies 1975; Smith et al. 1983). These observations suggest that sediment oxygen uptake rates can provide an indication of the quantity of particulate organic carbon reaching the benthos. Davies (1975) found temperature, waterflow, and the type of sediment in a Scottish fjord system also influenced the oxygen consumption by the sediments.

A synoptic view of the location of major water masses during the summer, together with chlorophyll concentrations, differences in annual primary production, and variance in community structure and biomass in the northern Bering and Chukchi Seas suggested a strong coupling between water mass characteristics, food supply and benthic processes. The objective of the present study was to determine whether food supply, influenced directly by variations in water mass primary production and phytoplankton biomass, is a major regulating factor in benthic community structure and standing stock in the region.

STUDY AREA AND HYDROGRAPHY

The study area is located between Alaska and Siberia north of St. Lawrence Island in the Bering Sea (the Chirikov Basin), through Bering Strait, north into the Chukchi Sea to approximately 70° N (Figure 1.1). The western-most limit is defined by the international boundary between the U.S.A. and the Soviet Union. This area is a broad, shallow shelf, with

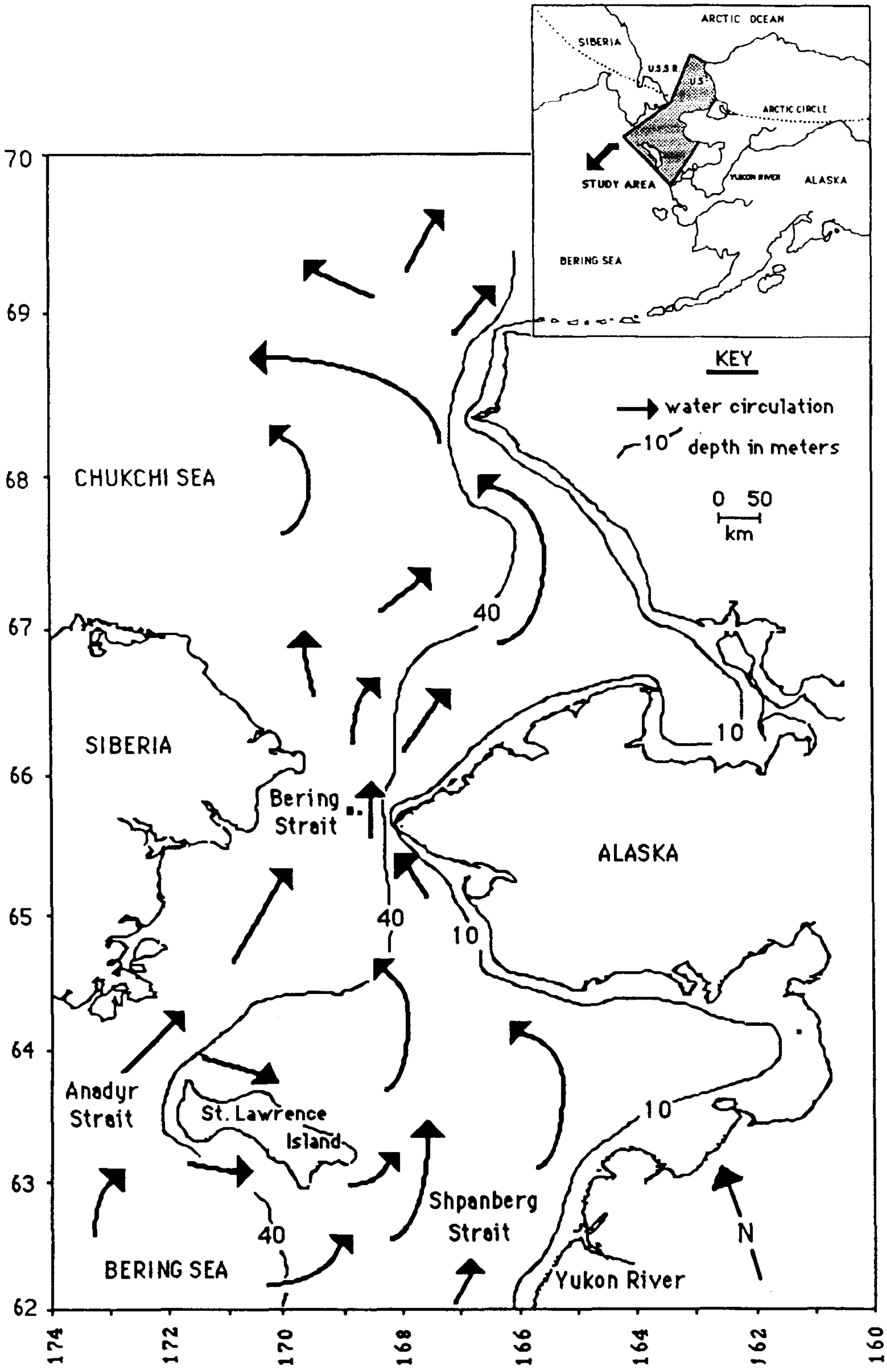


Figure 1.1. Study area in the northern Bering and Chukchi Seas showing local currents and bathymetry (adapted from Coachman et al. 1975; Nelson et al. 1981).

water depths less than 50 meters. Barotropic currents flow northward through the system and are steered by the local bathymetry (Coachman 1975). Average ice coverage extends over the area from November to June (McRoy and Goering 1974). The physical oceanographic regime in the study area in summer includes three major water masses: the Anadyr water (Salinity (S)=32.8 to 33.1°/oo; Temperature (T)=-0.5 to 2.0 °C) and the Bering Shelf water (S=32.4 to 32.7°/oo; T=1-2° C), each flowing northward on the west and east side of St. Lawrence Island, and the Alaska Coastal water (S=31.5-32.1°/oo; T=up to 10°C or more in the summer), which flows northward adjacent to the Alaska mainland (Coachman et al. 1975; Schumacher et al. 1983; Figure 1.2). A persistent frontal zone is maintained during the summer between Bering Shelf and Alaska Coastal water. A second frontal zone occurs between Anadyr and Bering Shelf waters, although varying more in strength and location depending on water transport conditions than the Bering Shelf and Alaska Coastal water frontal zone (Walsh et al. 1987). In the central regions north of St. Lawrence Island the Anadyr water combines with entrained Bering Shelf water to form a Bering Shelf water mass. Unlike the Bering Shelf and Alaska Coastal water frontal zone which maintains a distinctive interface, the Anadyr and Bering Shelf frontal zone 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 is here designated as the Bering Shelf/Anadyr (BS/A) water mass. The Alaska Coastal (AC) water mass designation remains unique.

ORGANIC CARBON SUPPLY TO THE BENTHOS

Primary productivity in shallow marine systems is closely linked to water-sediment-organism processes that occur at the benthic boundary layer (McCave 1976; Gray 1981).

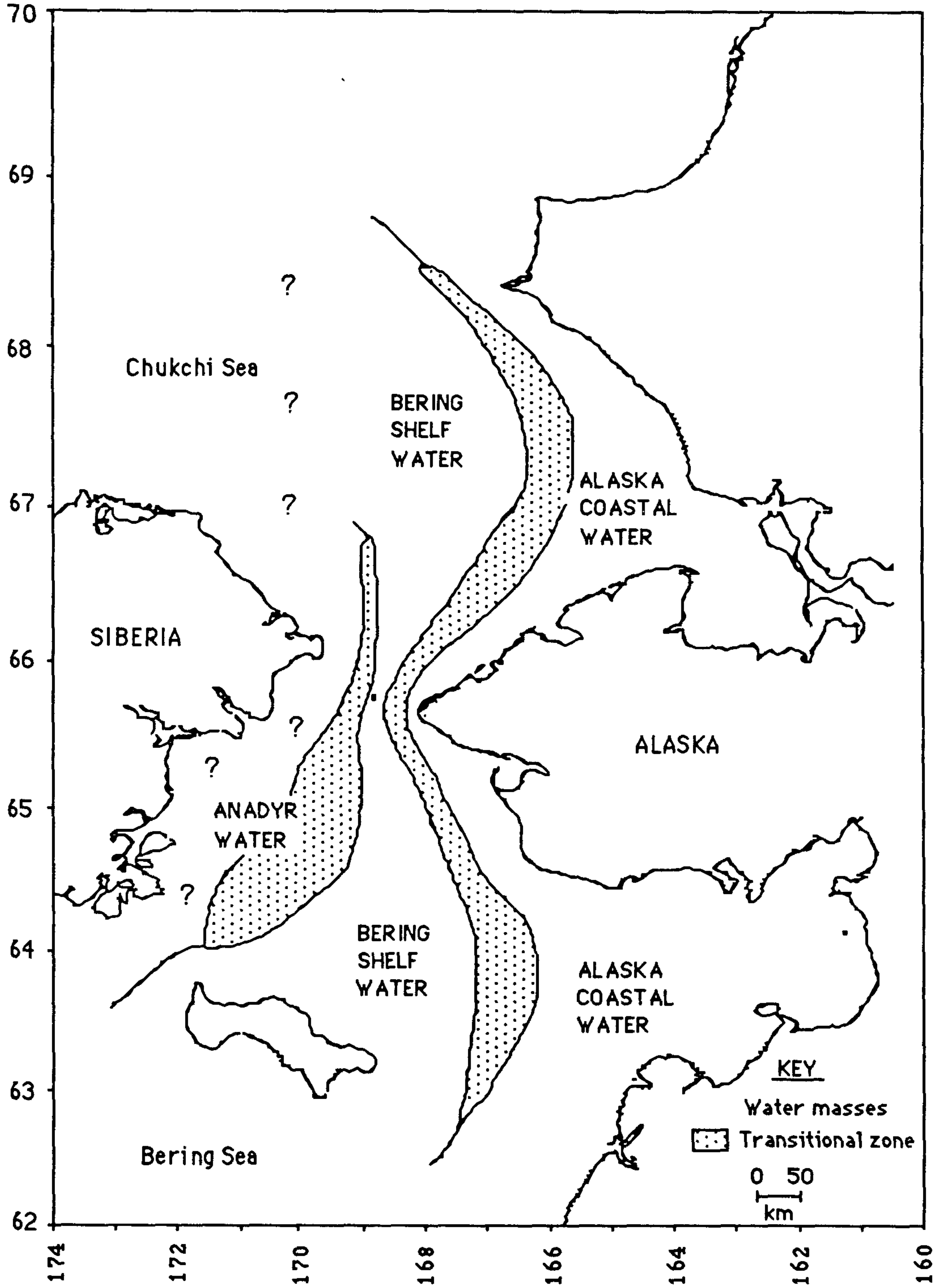


Figure 1.2 Average water mass location in the northern Bering and Chukchi Seas based on bottom temperature and salinity values during the summer season (modified from Coachman et al. 1975; Nelson et al. 1981; ISHTAR Data Report 1986,1987, and unpubl. data). Question marks indicate areas of unknown water type.

Organic matter, settling to the benthos from the euphotic zone, provides the major energy source for organisms associated with the sediments. In turn, benthic microfauna, along with bioturbation by macrofauna, enhance carbon utilization and subsequent inorganic nutrient flux from the benthos back into the water column. A direct relationship between carbon flux and benthic biomass has been shown by a variety of investigators. Boesch (1982) documented temporal variations in benthic ampeliscid amphipod species off Long Island and related this to the episodic enrichment of the overlying water column by a heavy phytoplankton bloom. A threefold increase in the amphipod *Pontoporeia* sp. in the Baltic Sea was correlated with an intense phytoplankton bloom in 1972 (Elmgren 1978). Davies and Payne (1984), working on organic carbon flux and benthic interactions in the North Sea, suggested that the increased rate of fresh organic carbon input to the benthos from a bloom provided a stimulatory effect on the growth and reproduction of benthic animals, acting as a "trigger mechanism" for their life cycles. This process may be occurring in the northern Bering and Chukchi Seas where the pulse of organic carbon during the summer period is believed to descend intact to the sea floor, either as phytodetritus or fecal pellets, especially in areas where a high biomass of benthic fauna has been observed (Stoker 1978 and 1981).

No carbon flux values are available for the northern Bering and Chukchi Seas. However, sediment oxygen uptake rates can provide an indication of the quality and quantity of particulate organic carbon reaching the benthos (Hargrave 1973; Davies 1975; Smith et al. 1983). In addition to a relationship between carbon flux and sediment oxygen uptake rates, Hargrave (1973) determined that more organic carbon reached the benthos in systems that had less efficient pelagic communities to crop the falling carbon. The northern Bering and Chukchi Seas support a zooplankton population that can crop approximately 1-20% of the available phytoplankton (Zenkevitch 1963; Walsh et al. 1987). Walsh et al. (1987) estimated that microplankton consumed 8 to 9% of the available particulate organic carbon in BS/A water, which when combined with their estimate of zooplankton consumption in this water mass provides a large phytodetritus and fecal pellet detrital pool to the benthos. This information, in combination with known high standing stock levels in the benthos, suggests a high probability that labile organic material reaches the benthos in the northern Bering and Chukchi Seas. Therefore, it is hypothesized that sediment oxygen uptake rates will be higher under the more productive BS/A water due to enhanced flux of labile organic carbon to the benthos compared to lower particulate organic carbon supply to the benthos in AC water.

BENTHIC COMMUNITY STRUCTURE AND BIOMASS

The rich benthos in the northern Bering and Chukchi Seas has been related to a high supply of nutrients brought into the area by the currents, thus influencing primary production, and by typically reduced bottomfish predation pressure associated with low bottom water temperatures (Neiman 1963; Alton 1974; Stoker 1978 and 1981; Jewett and Feder 1980 and 1981). The northern Bering and Chukchi Seas are considered to be primarily a detritus-based trophic system, supporting both deposit and suspension feeders (Stoker 1981). Stoker concluded that the high species diversity and stability of the benthic communities seen on the Bering/Chukchi continental shelf indicates that a relatively reliable food supply is maintained by northerly flowing currents providing food across the shallow shelf. Recent evidence suggests that BS/A water can accumulate for days to weeks north of St. Lawrence Island due to variabilities in physical transport mechanisms in the region, thus potentially allowing phytoplankton enough time to grow and settle out to the benthos (Walsh et al. 1987).

Recent studies in the southeastern Bering Sea as part of the Processes and Resources of the Bering Sea shelf (PROBES) project have shown that the physical oceanographic regime influences the type of food web found on the shelf (Iverson 1979; Niebauer, Alexander and Cooney 1981; Feder and Jewett 1981; Haflinger 1981; McDonald et al. 1981; Walsh and McRoy 1986). In the southeast Bering Sea, three domains occur from nearshore to offshore waters on the shelf: the inner shelf domain (0-50 m), the middle shelf domain (50-100 m), and the outer shelf domain (100 m-shelf break). The middle shelf domain is characterized by high benthic biomass, with lower benthic biomass occurring in the outer domain. Slow cross-shelf advection, high phytoplankton concentrations and low water column grazing by zooplankton suggest a decoupled system where labile organic material settles ungrazed to the bottom. In contrast, the outer shelf domain supports a pelagic food web with a low benthic biomass. The coupled system in the outer domain, where pelagic grazers crop the available phytoplankton, results in a food-limited situation for the underlying benthic fauna in contrast to the decoupled system in the middle domain. Experimental measurements of sediment oxygen consumption on the middle shelf showed high oxygen uptake and inorganic nutrient flux rates from the sediments, suggesting both enhanced phytodetrital flux to the benthos as well as the importance of benthic bacteria and macrofauna on carbon mineralization (Walsh and McRoy 1986). All these factors are suggested to enhance benthic populations on the middle shelf.

Bioturbation of sediments by infaunal feeding organisms is known to enhance sediment transport, increase porewater nutrient mixing, and influence the flux of organic matter within the sediments and across the benthic boundary layer (McCave 1976 ; Gray 1981; Aller 1982; Blackburn and Henriksen 1983). Bioturbation by marine mammal feeding behavior also appears to be an important process in the northern Bering and Chukchi Seas (Nelson et al. 1981; Oliver et al. 1983 a and b; Nerini 1984; Oliver and Slattery 1985; Nelson and Johnson 1987). The mixing of organic carbon and oxygen downwards into the sediment during bioturbation enhances carbon utilization by bacteria and detritivores. In addition, buried carbon is brought towards the surface where oxic conditions exist, enabling remineralization processes to occur (Gray 1981).

SEDIMENT PATTERNS

Surface sediment organic carbon values in the northern Bering Sea are low (0.5%), but rise to 1.5% organic carbon in the southern Chukchi Sea sediments, suggesting a depositional regime in the southern Chukchi Sea (Walsh et al. 1987). Fine-grained sand occurs in the northern Bering Sea, with coarse-grained sand and gravel occurring near the Alaska coastline (McManus et al. 1977; Nelson et al. 1981). Sediment grain size decreases to finer-grained silt and mud in the Chukchi Sea due to reduced current speeds (McManus et al. 1977). Coarse-grained sediments (gravel, pebbles, and rocks) occur in regions of higher current flows, primarily in straits, off headlands, and on the outer edges of the northern Bering Sea (McManus et al. 1977; Nelson et al. 1981). These coarser-grained sediments typically support sessile epifaunal communities whereas soft bottom sediments (sand and mud) support primarily infaunal communities (Nelson et al. 1981).

HYPOTHESES

The following chapters address the hypothesis that food supply from water column primary production is a regulating mechanism in benthic community structure, biomass, and carbon cycling in the northern Bering and Chukchi Seas. The following sub-hypotheses are addressed individually by chapter:

1. The carbon:nitrogen ratios and stable carbon isotope values of particulate organic matter in surface sediments provide an indication of the quality of organic matter reaching the benthos, reflecting processes occurring in the overlying water mass. Sediments underlying the nutrient-rich, productive BS/A water will maintain values close to labile phytoplankton, thus being of higher food quality (high nitrogen content), whereas sediments underlying the less productive, more terrigenous carbon influenced AC water will reflect a lower food quality

(low nitrogen content).

2. Benthic community structure is responsive to sediment grain size. However, benthic faunal biomass is directly influenced by the quantity and quality of the food supply, such that communities underlying the highly productive BS/A water maintain larger standing stocks than those underlying the less productive AC water mass.

3. Sediment oxygen uptake and carbon mineralization rates are an indication of the quantity and quality of organic matter reaching the benthos and reflect carbon flux differences to the benthos in each water mass. Therefore, these rates will be higher under the more eutrophic BS/A water compared to rates measured under the oligotrophic AC water.

CHAPTER 2. BENTHIC CARBON CYCLING: I. SEDIMENT ORGANIC MATTER

INTRODUCTION

The distribution of organic matter in sediments is a function of hydrodynamics, water column productivity, terrestrial input, sedimentation rates and bioturbation (Jørgensen 1983). Finer grain sediments, indicative of low current velocities, generally have a higher total organic carbon content (Bordovskiy 1965b; Gray 1981). The organic carbon content in the northern Bering Sea averages 0.5%, increasing to 1 to 2% in the Chukchi Sea in response to reduced current velocities (Walsh et al. 1987). Fine and very fine sand grain size patterns are characteristic of the central regions of the northern Bering Sea, with coarser grained sand and pebbles and rock near the outer boundaries of the Chirikov Basin and in Anadyr and Bering Straits (Creager and McManus 1967; McManus et al. 1977; Figure 2.1a, b). A higher percentage of very fine sand and silt and clay characterize the offshore regions in the Chukchi Sea, where the largest percentage of Yukon River sediment and organic particulates settle out of the water column (McManus and Smyth 1970; McManus et al. 1974 and 1977).

Carbon/nitrogen (C/N) ratios in surface sediments can provide an indication of the quality of organic matter arriving at the sea bottom (Parsons et al. 1977). Average C/N ratios for marine phytoplankton are 5-7, zooplankton 3-8, bacteria 5.7, river particulate organic matter 8-12, land plants≥ 69, marine surface sediments 8-12, and biochemically-resistant organic carbon buried in marine sediments>15 (Müller 1977; Parsons et al. 1977; Smetacek et al. 1978; Walsh et al. 1981; Meybeck 1982; Valiela 1984; Table 2.1). The C/N ratio of particulate organic matter increases over time as nitrogen is depleted due to autolysis and bacterial degradation of soluble and labile cell components during decomposition (both in the water column and sediments; Jørgenson 1983). The composition of organic matter that

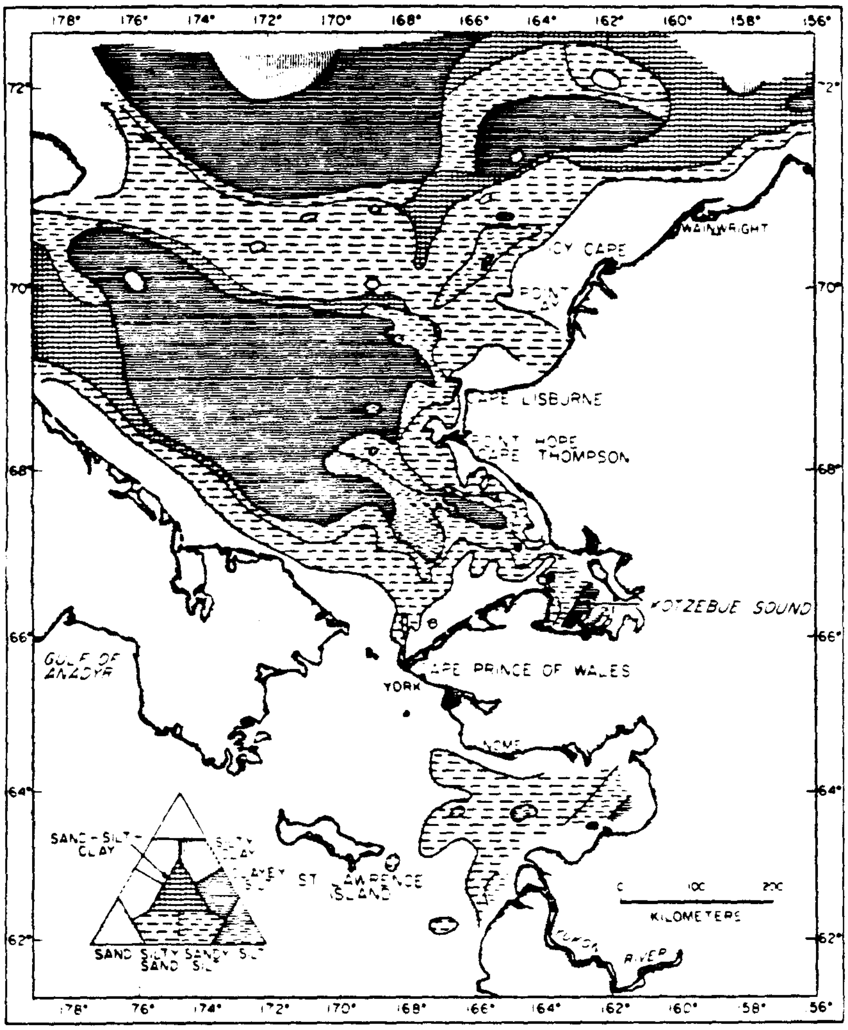


Figure 2.1a. Distribution of sediment texture expressed in terms of three-end member relationship of Shepard (1954) in the northern Bering and Chukchi Seas (from Creager and McManus 1967).

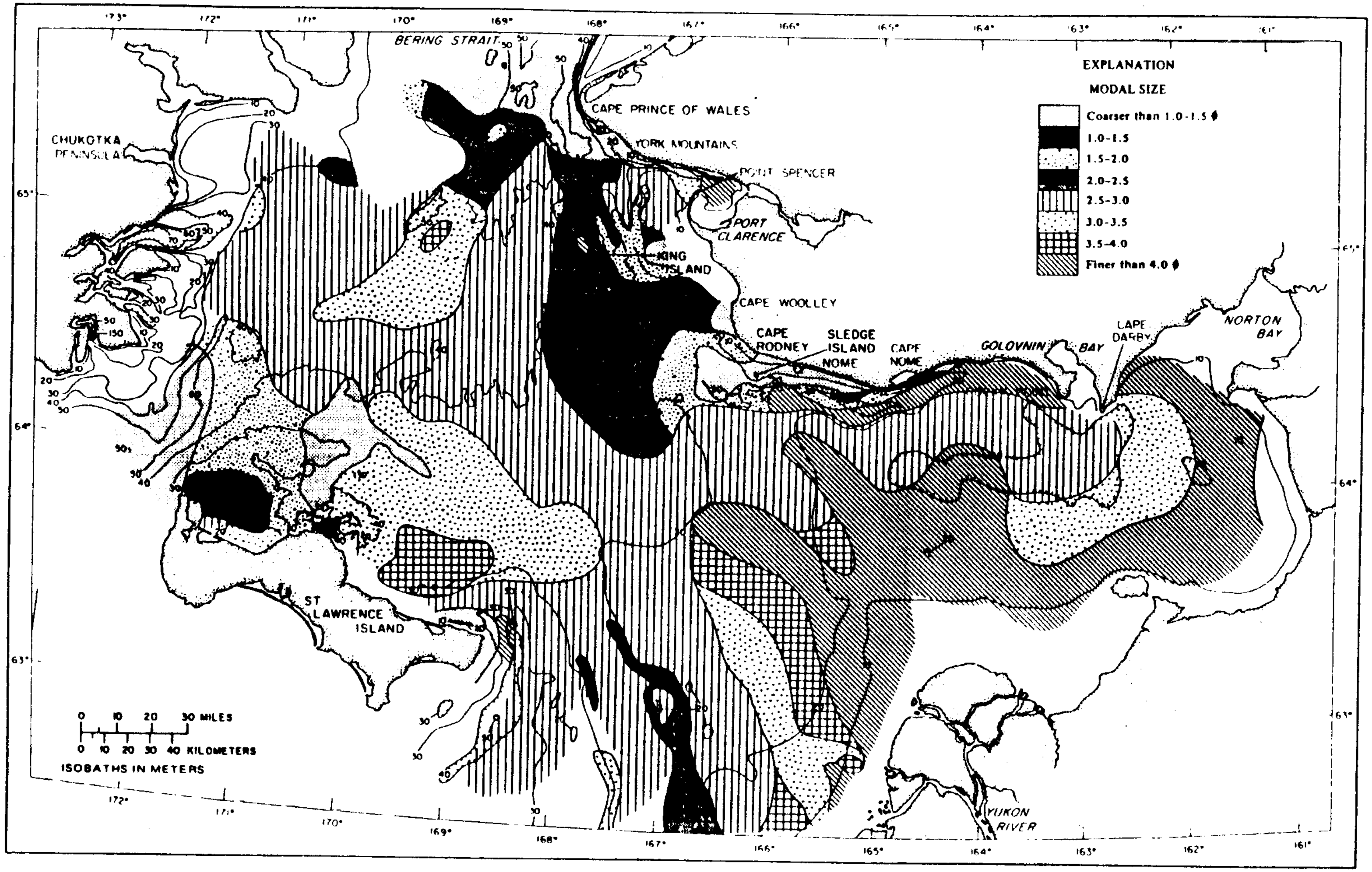


Figure 2.1b. Distribution of modal classes of sand in the northern Bering Sea (from McManus et al. 1977).

Table 2.1. Average C/N weight ratios in plants and sediments (from Müller 1977; Parsons et al. 1977; Smetacek et al. 1978; Walsh et al. 1981; Meybeck 1982; Valiela 1984).

Type of material	C/N
Marine phytoplankton	5-7
Marine zooplankton	3-8
Bacteria	5.7
Marine sediments	
Long Island Sound (surficial)	8.5
Basin sediment (surficial)	8-11
Bering Sea (surficial)	8.4
Terrestrial plants	69-105
Soil humus	18
River material	
dissolved organic	20
particulate organic	8.8
total organic	12

reaches the sediments thus depends on water depth, with organic matter being the least depleted in nitrogen at shallower depths (Bordovskiy 1965 a; Martens et al. 1978; Suess and Müller 1980). This process continues at the sediment surface through the activity of benthic microorganisms and animals. However, another process can occur in the water column and at the sediment-water interface that decreases organic matter C/N ratios. Bacteria grown on detritus in the laboratory have been shown to assimilate ammonia (Fenchel and Harrison 1976; Jørgensen 1983), thus increasing detrital nitrogen content and lowering C/N values. In both the laboratory and in seawater the availability of nitrogen can limit mineralization rates. These nutrients are not normally limiting in marine sediments since they accumulate in sediment porewaters below the oxic layer (Jørgensen 1983). In spite of nutrient availability, preferential loss of nitrogen often occurs in sediments, with C/N values increasing to a plateau value of 12, which may be the balance between organic matter decomposition and bacterial assimilation of nutrients into their own cellular structure (Jørgensen 1983).

The quality of detritus available to the benthos is largely determined by source and degree of decomposition when it reaches the bottom (Tenore et al. 1982). Phytoplankton and marine algal detritus, unlike vascular plant material, can be readily assimilated by some detritivores (e.g. the polychaete *Capitella capitata*) without requiring bacterial breakdown activities (Findlay and Tenore 1982; Tenore et al. 1982). In addition, low water temperatures have been shown to reduce bacterial decomposition rates in some marine systems, thus reducing the bacterial loop component in those food webs (Iturriaga 1979; Hobbie and Cole 1984; Pomeroy and Diebel 1986). In the Bering Shelf/Anadyr (BS/A) water column microheterotrophs (including bacteria) have a minimal effect on detrital decomposition in the water column due to the overwhelmingly large amount of phytoplankton available (P. Andersen, pers. comm.; Andersen and Fenchel 1986). However, in the terrestrially-influenced Alaska Coastal (AC) water, where primary production is low and particulate organic matter river input occurs, the microheterotrophs play a more important role in utilizing both a reduced marine organic carbon supply and terrestrial carbon load (Andersen and Fenchel 1986), thus influencing the quality and quantity of organic matter reaching the benthos.

Low C/N ratios (6-8) in surface sediments can indicate regions of recent marine phytodetritus deposition. Areas with higher sediment C/N values (>10) indicate either older, more refractory detrital material or terrestrial deposits (Parsons et al. 1977; Walsh 1980). Walsh et al. (1981), in their description of various marine shelf systems (ie. Peru, the Atlantic Ocean, the Gulf of Mexico, and the Bering Sea), used surface sediment C/N ratios to trace areas of high nutrient concentrations in the water column and subsequent downstream utilization by phytoplankton, and delineated areas of loss of particulate material to the benthos. Walsh et al. (1981) and Walsh and McRoy (1986) document processes in the southeastern Bering Sea where differential organic carbon inputs to the shelf were observed in the cross-shelf distribution of C/N ratios in surface sediments. The middle shelf, characterized by high sedimentation rates and benthic biomass (Feder and Jewett 1981; McDonald et al. 1981), had C/N ratios near 6, with C/N ratios increasing to 10 in the outer shelf where sedimentation is low and pelagic grazing dominates.

Recent ecological studies using stable carbon isotopes have addressed the role of marine and terrestrial organic carbon in marine food webs (Fry and Sherr 1984; Mills et al. 1984). The use of stable carbon isotope measurements provides a tracing method in an ecological system since the isotopic value of source materials is relatively constant through the food chain. Marine phytoplankton has an average $\delta^{13}C$ value of -21‰, although temperature has an effect on isotope ratios (Sackett et al. 1965). Temperate values range from -18‰ to -24‰ (Parker and Calder 1970; Fry and Sherr 1984), whereas McConnaughey and McRoy (1979) found a $\delta^{13}C$ value of -24.4 °/₀₀ for phytoplankton in the southeastern Bering Sea. Recent data from the southeast Bering Sea (Schell and Saupe 1987) also show a mean $\delta^{13}C$ phytoplankton value of -23.8 °/₀₀, although the range was from -20.0 to -25.0 °/₀₀. The $\delta^{13}C$ values of the southeastern Bering Shelf sediments were -22.0 °/₀₀ to -22.9 °/₀₀, indicative of marine origin (Peters et al. 1978). In general, southeast Bering Sea organic carbon $\delta^{13}C$ values between -20 and -25 °/₀₀ indicate marine origin and $\delta^{13}C$ <- 25°/₀₀ indicate carbon of terrestrial origin (Walsh et al. 1981; Fry and Scherr 1984; Schell and Saupe 1987).

Multiple sources of organic carbon into sediments can alter the resultant ratio although $\delta^{13}C$ can provide information on the relative importance of marine vs. terrestrial sources in conjunction with other data. Sediments show a small but consistent increase in $\delta^{13}C$ between particulate organic carbon (POC) in the water column and in the sediments, with surface sediments being about 2° /₀₀ more enriched in the heavier ^{13}C isotope than water column POC (Fry and Sherr 1984). Thus, the influence of bacterial metabolism and terrestrial carbon in the benthos complicate the differentiation between marine and terrestrial input. The use of multiple indices, such as $\delta^{13}C$ and C/N ratios, can more accurately distinguish point sources of organic carbon in sediments (Fry and Sherr 1984).

This chapter addresses the hypothesis that C/N and stable carbon isotope ratios of particulate organic matter in surface sediments provide an indication of the quality of organic matter reaching the benthos in the northern Bering and Chukchi Seas, thus reflecting processes occurring in the overlying water column. Sediments underlying the relatively productive BS/A water (Chapter 1) are predicted to show a low C/N signature (high organic matter quality) compared to a high C/N signature (low organic matter quality) in sediments under the less productive AC water.

MATERIALS AND METHODS

Bottom salinity, temperature, and depth data were obtained from a Niel Brown conductivity-temperature-depth (CTD) profiler. Sediment samples were collected using a Haps benthic corer or a MK3 box corer. Sediment subsamples were taken with either 6 cm or 13 cm diameter plexiglas cores, 26 cm in length, and frozen for later laboratory analysis. Preliminary data at select stations in both water masses showed no change of sediment grain size with depth in the top 5-10 cm, so only surface sediment values were determined for subsequent stations. Surface sediments (0-1 cm) were sectioned, dried, homogenized and subsampled for sediment grain size analysis by dry sieving, using standard geological sieves (1-4 phi sizes) and a Ro-tap machine (Folk 1980). Sediments were weighed after sieving and a modal sediment size and percent composition were determined. Areas dominated by gravel and rock, which precluded box coring and grab sampling, were given a qualitative phi size of less than 1 for comparison of sediment zones in the study area. One gram subsamples of surface sediments for carbon and nitrogen analyses were acidified with two ml of 1N HCl and dried at 105 °C overnight to obtain carbonate-free sediments, and then homogenized. Duplicate carbon and nitrogen content measurements were determined on a Perkin-Elmer Model 240C CHN elemental analyzer.

Thin-section plexiglas boxes (2.5 cm x 16.0 cm x 28.0 cm) or large PVC sediment cores (133 cm^2 by 28 cm long) were collected at selected stations in each water mass and frozen for later laboratory analyses. The large sediment cores were removed from the PVC core and cut to 2.5-3.0 cm widths. Sediment from both the plexiglas boxes and the large PVC cores was sectioned at 1 cm intervals for carbon and nitrogen analyses.

Water samples for particulate organic carbon (POC) and particulate organic nitrogen (PON) determinations were collected from 1.7 liter Niskin bottles into 250 ml subsamples and filtered through 0.43µ Gelman™ precombusted glass fiber filters and frozen. In the laboratory, filters were placed flat in precombusted glass containers in a vacuum desiccator and fume acidified with HCl for 24-48 hours to obtain carbonate-free samples and retained until analyzed.

Sediments for stable carbon isotope analysis were processed following the methodology of Dunton and Schell (1987). Surface sections of 500 mg of carbonate-free dry weight sediment were combined with 700 mg Cuprox™ copper wire and isolated with 6 mm Pyrex™ glass tubing in a vacuum. Samples were subsequently combusted at 585°C for 2 hours. Liquid nitrogen and cryogenically cooled alcohol were used to isolate liberated carbon dioxide after combustion, which was then transferred via a new sealed glass tube to the VG Instruments Sira-9™ mass spectrometer.

The $\delta^{13}C$ (°/oo) ratios reported are relative to the Peedee Belemnite (PDB) standard (Craig 1953), with 2 internal standards automatically used to calibrate the mass spectrometer. Precision was estimated to be ±0.22 °/oo (Cooper 1987). The $\delta^{13}C$ value is a standard means of expressing carbon isotope ratios where:

$$\delta^{13}C = \{ [({}^{13}C/{}^{12}C_{sample}) / ({}^{13}C/{}^{12}C_{standard})] - 1 \} \times 10^{3}.$$

More negative values indicate material more depleted in the heavier ^{13}C isotope.

Correlations between station variables and sediment parameters were investigated using both parametric (Pearson product-moment r) and nonparametric (Spearman's rho) correlation tests. Parametric tests were utilized when a large enough sample size was available to assume a normal distribution. The nonparametric Kruskal-Wallis test was used to investigate between year differences in mean surface sediment C/N values. The statistical program StatView™ (BrainPower 1985) was utilized on a Macintosh™ computer.

Each station designation presented in subsequent tables is composed of 5 numbers: the first two numbers designate the cruise, the second three numbers designate the actual station, e.g. 59023 means cruise 59, station 023.

RESULTS

Seventy-seven stations were occupied in the northern Bering and Chukchi Seas (Figure 2.2 a and b; Appendix A). Salinity, temperature and depth data were collected from R/V Alpha Helix cruises 73 and 87 (this study) and combined with data collected during the Inner Shelf Transfer and Recycling (ISHTAR) project cruises (ISHTAR Data Report 1986, 1987 and unpubl. data; Appendix B). Carbon and nitrogen values were determined for all 77 stations, whereas sediment grain size was determined for 33 of these stations (Appendix C). Water column POC, PON, and C/N ratios were determined for 13 stations in the northern Bering Sea (Figure 2.3). Nineteen stations were analyzed for stable carbon isotope ($\delta^{13}C$) ratios in surface sediments (Appendix C).

Sediment zones

The distribution of surface sediment grain size varied in the study area (Figure 2.4). The Chirikov Basin north of St. Lawrence Island is characterized by fine and very fine sand grain-size zones. Gravel and cobble areas are found within Anadyr Strait, north of Bering Strait, and southeast of St. Lawrence Island. Coarse-grained sand, in addition to fine and very fine sand zones, occur at various places under AC water. The southern Chukchi Sea contains very fine sand regimes along with areas of silt and clay occurring in the central region.

The percent composition of various grain size classes in the surface sediments shows a separation of stations between northern Bering and Chukchi Seas (Figure 2.5). A majority of stations in the northern Bering Sea are in the >70% sand substrate class, with stations in the southern Chukchi Sea occurring near the 50% fine sand/silt and clay substrate class. In the northern Bering Sea, a large percentage of the BS/A stations occur in fine sand areas, with AC stations occupying both sand and coarse sand and gravel areas.

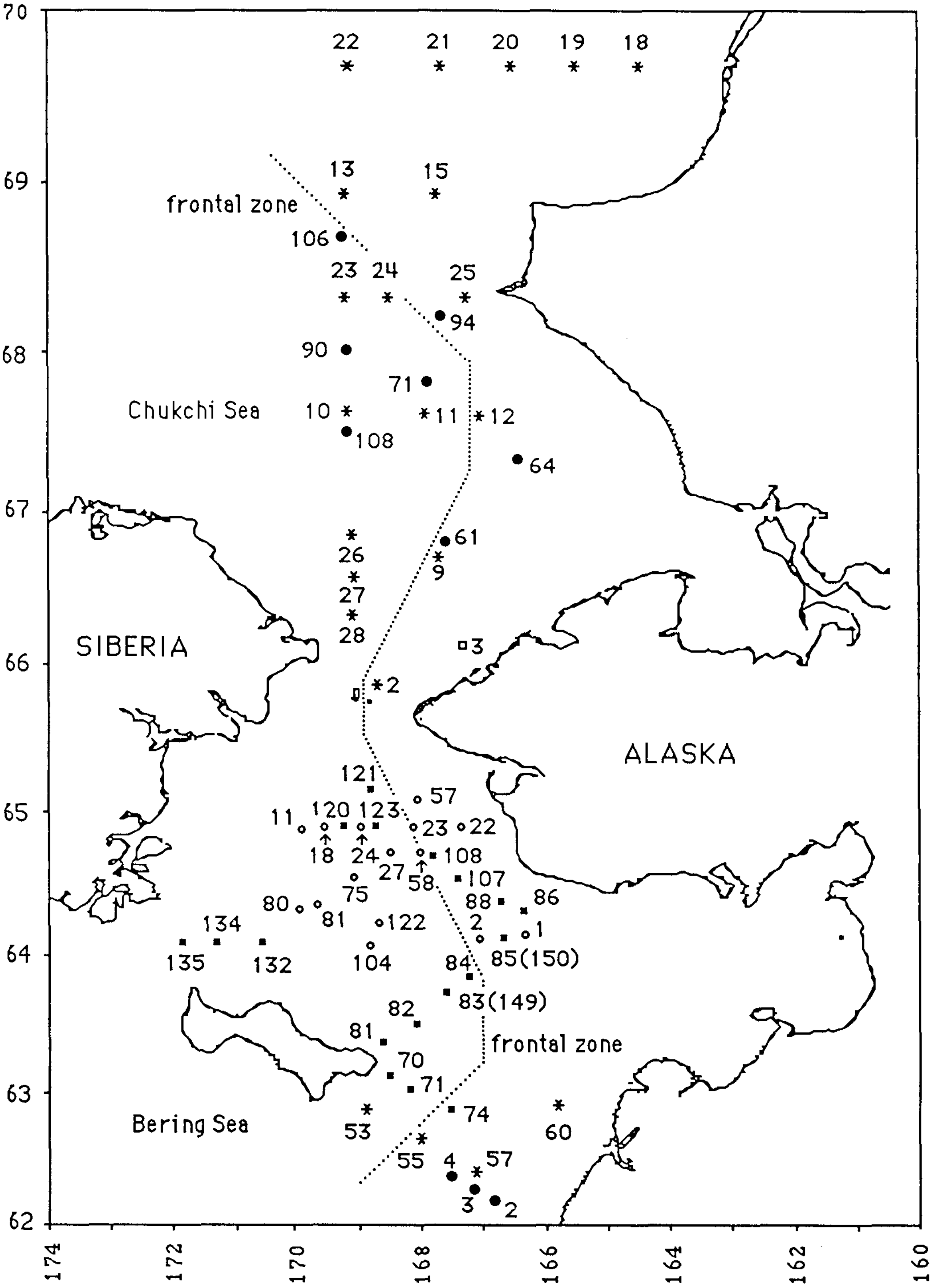


Figure 2.2a. Location of sediment stations in the northern Bering and Chukchi Seas for R/V Alpha Helix cruises 59(▪), 73(∘), 74(*), 85(●), and 87(+).

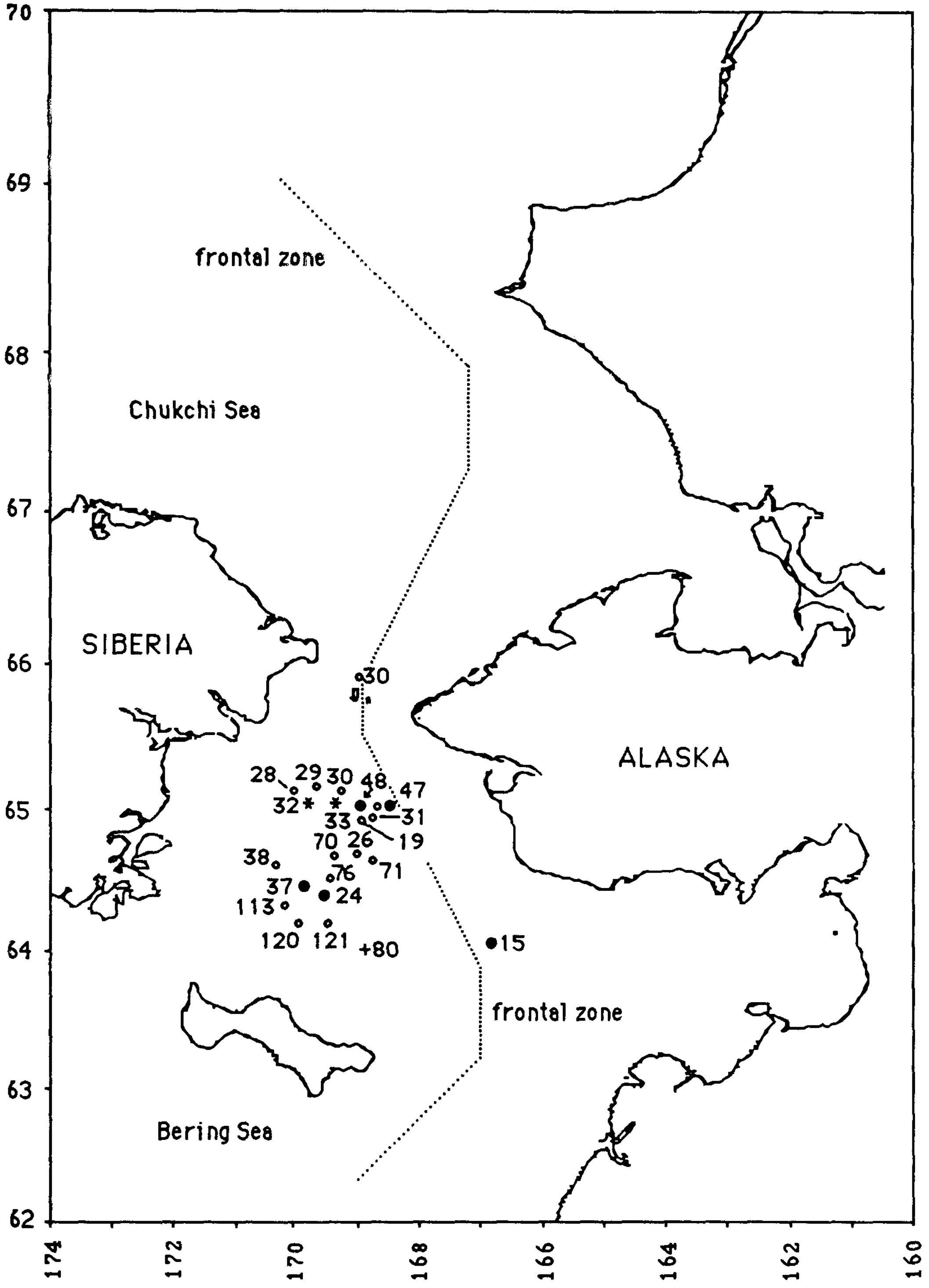


Figure 2.2b. Location of sediment stations (Figure 2.2a Continued).

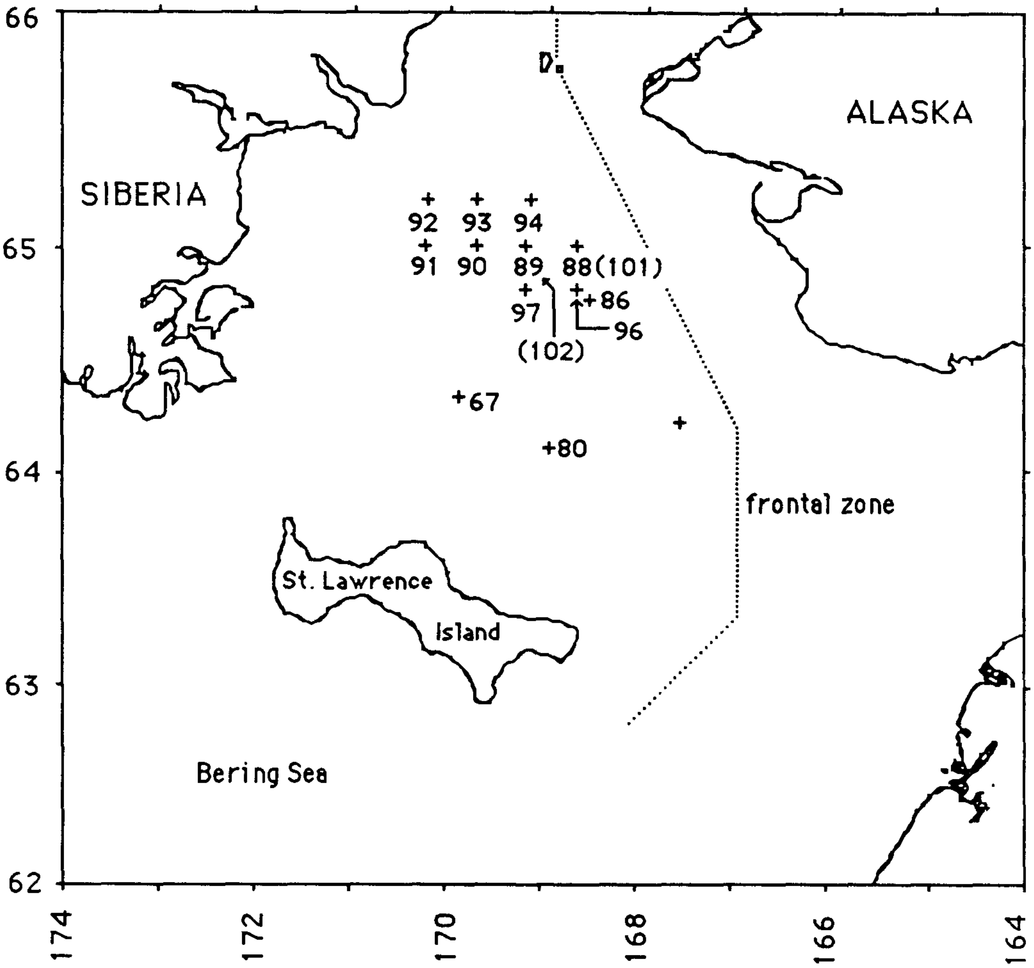


Figure 2.3. Location of stations for water column POC and PON measurements during R/V Alpha Helix cruise 87 (+).

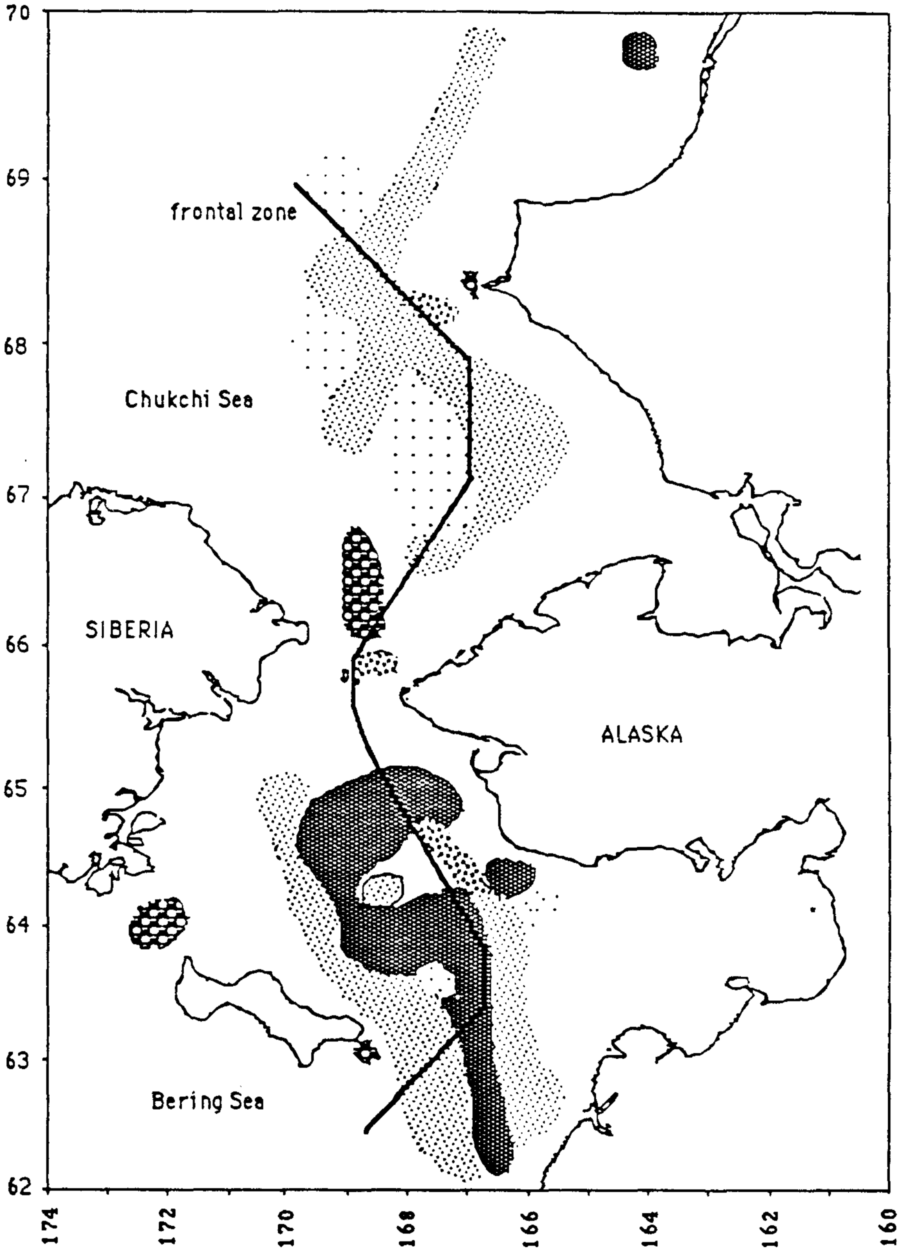


Figure 2.4. Distribution of modal grain size (phi) classes for surface sediments in the northern Bering and Chukchi Seas in relation to frontal zone between BS/A and AC waters.

Key: Sediment modal phi size

<1	▩	coarse sand, gravel, and cobbles (qualitative observations)
2	▨	medium sand
3	■	fine sand
4	▒	very fine sand
>4	☐	silt and clay

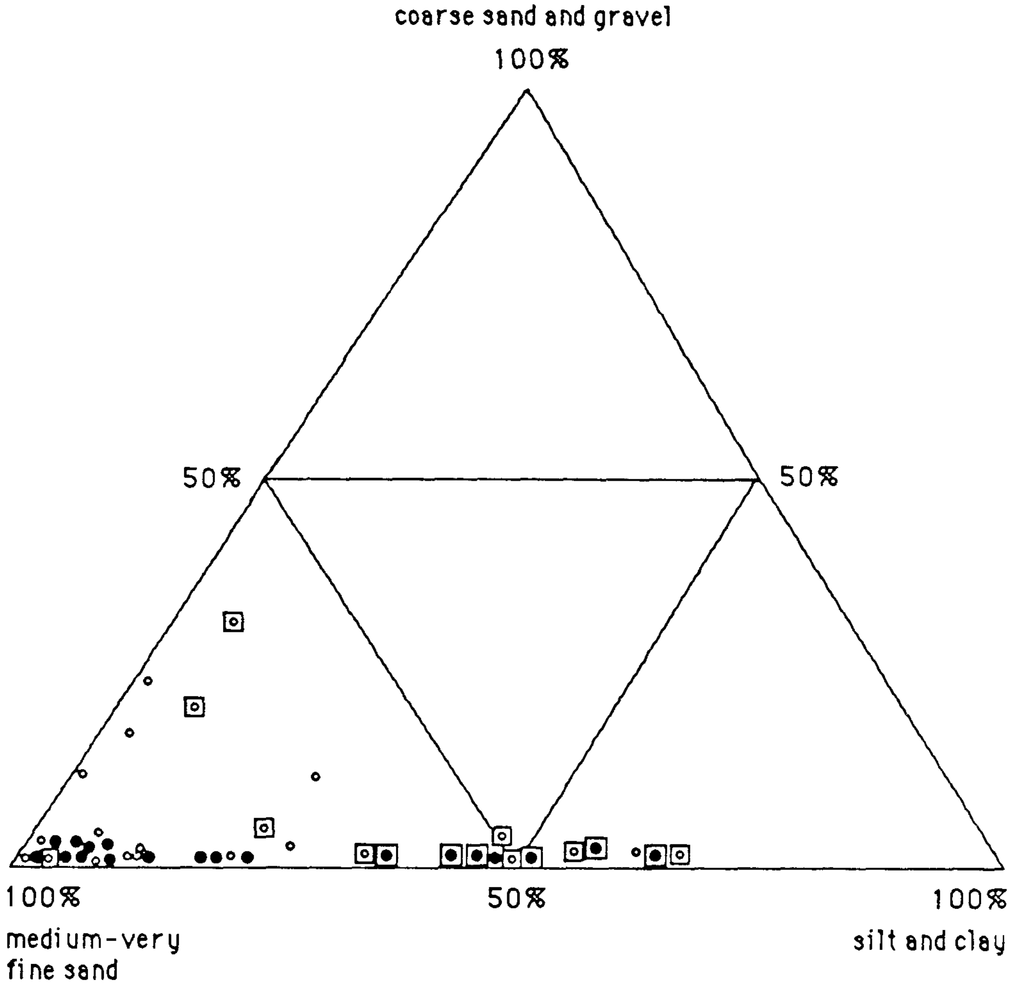


Figure 2.5. Ternary diagram for surface sediment grain size class composition at stations in the northern Bering and Chukchi Seas. Stations located in the Bering Shelf/Anadyr water are designated by the symbol (•) and stations in the Alaska Coastal water are designated by the symbol (°). All stations located in the Chukchi Sea are boxed, unboxed are in the Bering Sea.

Total organic carbon in surface sediments

The distribution of total organic carbon (TOC) in surface sediments delineates a low value region in the central northern Bering Sea and a high value region in the southern Chukchi Sea (Figure 2.6). Organic carbon averages 0.5% in the northern Bering Sea and rises to an average 1.5% in the Chukchi Sea. The highest sediment organic carbon content occurs in the basins of both shelves in the northern Bering and Chukchi Seas. An area of organic carbon accumulation is indicated in the Central Chukchi Sea, where maximum surface sediment TOC reaches 1.9%. TOC and TON content in surface sediments are positively correlated to sediment phi size ($r=0.573$, $p=0.01$ and $r=0.529$, $p=0.01$, respectively). This relationship agrees with other research where the increased surface area of finer sediments provides more area for adherence of organic material (Bordovskiy 1965; Gray 1981).

Carbon:nitrogen ratios in surface sediments

Carbon:nitrogen ratios in the surface sediments show a gradient of low values (mean=6.7), indicative of labile phytodetritus, in the central regions of the northern Bering and Chukchi Seas to higher values (mean≥8.5), indicative of more refractory and/or terrestrial carbon, near the Alaska coastline (Figure 2.7). There is no significant difference between years of mean C/N ratios in surface sediment underlying BS/A water (Kruskal-Wallis, $p>0.25$.; Table 2.2) However, a significant difference in C/N ratios was found between years for surface sediments underlying AC water (Kruskal-Wallis, $0.025<p<0.05$). Surface sediment C/N ratios were significantly correlated with water depth ($r=0.361$, $p=0.01$) and sediment modal phi size ($r=-0.398$, $p=0.05$; Appendix E).

Sediment core C/N ratios

Vertical profiles of C/N ratios for 7 cores show a vertical trend in the sediments under each water mass similar to the horizontal gradient in C/N ratios seen for surface sediments

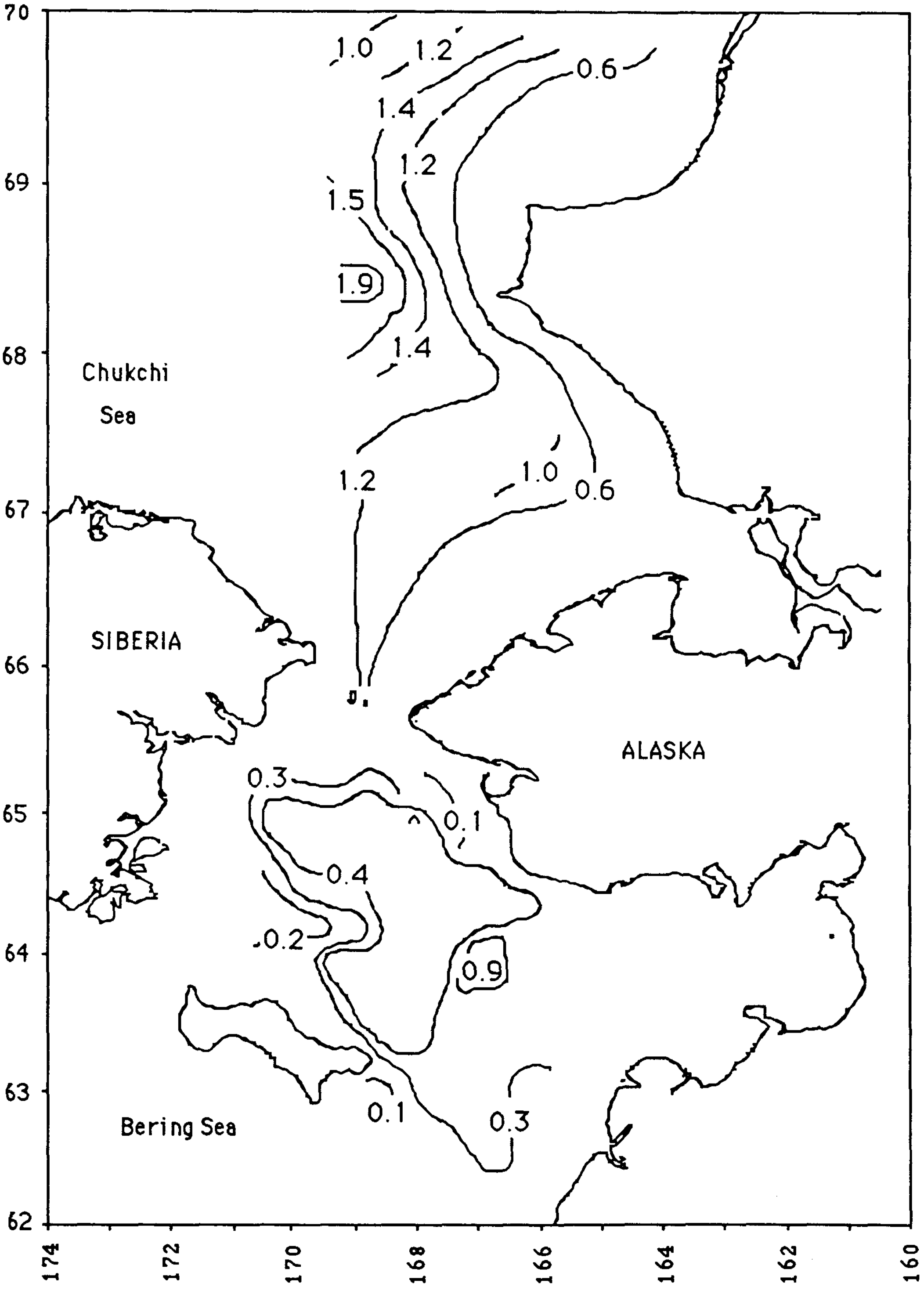


Figure 2.6. Distribution of total organic carbon (%) in surface sediments in the northern Bering and Chukchi Seas.

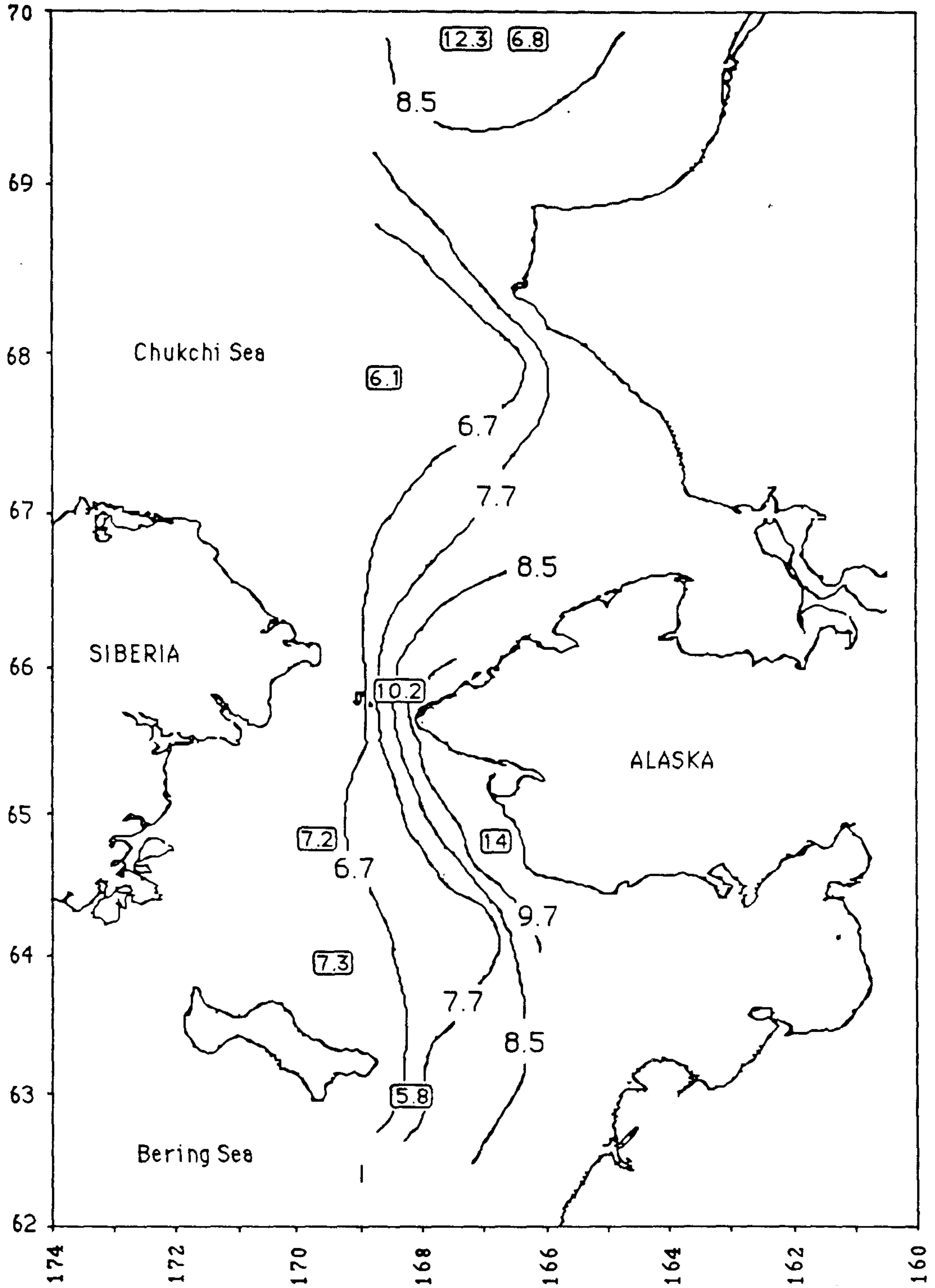


Figure 2.7. Distribution of average C/N ratios in surface sediments in the northern Bering and Chukchi Seas. Boxed values indicate individual station ratios.

Table 2.2. Mean surface sediment C/N ratios from 1984-86 for the Bering Shelf/Anadyr and Alaska Coastal water masses (including number of stations sampled in parentheses and s.d.=standard deviation).

	Water Mass			
	Bering Shelf/Anadyr		Alaska Coastal	
Year	Mean surface sediment C/N ratios	s.d.	Mean surface sediment C/N ratios	s.d.
1984	7.02 (9)	0.52	8.40 (5)	1.63
1985	6.73 (31)	0.32	8.93 (15)	1.93
1986	6.76 (10)	0.22	7.54 (7)	0.47

(Figure 2. 8). The lowest C/N ratios occurred in BS/A sediments and the highest C/N ratios in AC sediment. 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 (Figure 2.8; Appendix D).

Water column particulate organic carbon (POC) and nitrogen (PON)

POC and PON were analyzed in water column samples from 13 stations in BS/A water (Figure 2.3; Table 2.3). A Mann-Whitney test indicated that there was no significant difference between C/N ratios at surface and bottom depths ($p>0.10$). The average C/N ratio for all stations ($n=26$) at all depths was 6.20 ± 1.34.

Stable carbon isotope ratios ($\delta^{13}C$)

Surface sediments from 19 stations were analyzed for stable carbon isotope ratios (Figure 2.9). On the average, the most negative values occur in AC water off the Yukon River (-23.5 ‰) and in the northern part of the study area in the Chukchi Sea (-23.4 ‰ and -23.8 ‰). The least negative values (-21.0 ‰ to -21.3 ‰) occurred under BS/A water in the northern Bering and Chukchi Seas. In the northern Bering Sea the average $\delta^{13}C$ ratio in BS/A water was -22.0 (±1.0) ‰ compared to -22.5 (±0.6) ‰ in AC water. In the Chukchi Sea the average $\delta^{13}C$ in BS/A water was -22.1 (±1.0) ‰ compared to -23.6 (±0.3) ‰ in AC water.

A nonparametric Spearman rank correlation test was performed to test the hypothesis that $\delta^{13}C$ ratios become more negative with increasing C/N ratios in sediments, suggesting more terrestrial carbon input to these sediments. The results (Figure 2.10) show a significant correlation ($0.05\leq p\leq0.10$) but the scatter in the plot indicates the need for further sampling.

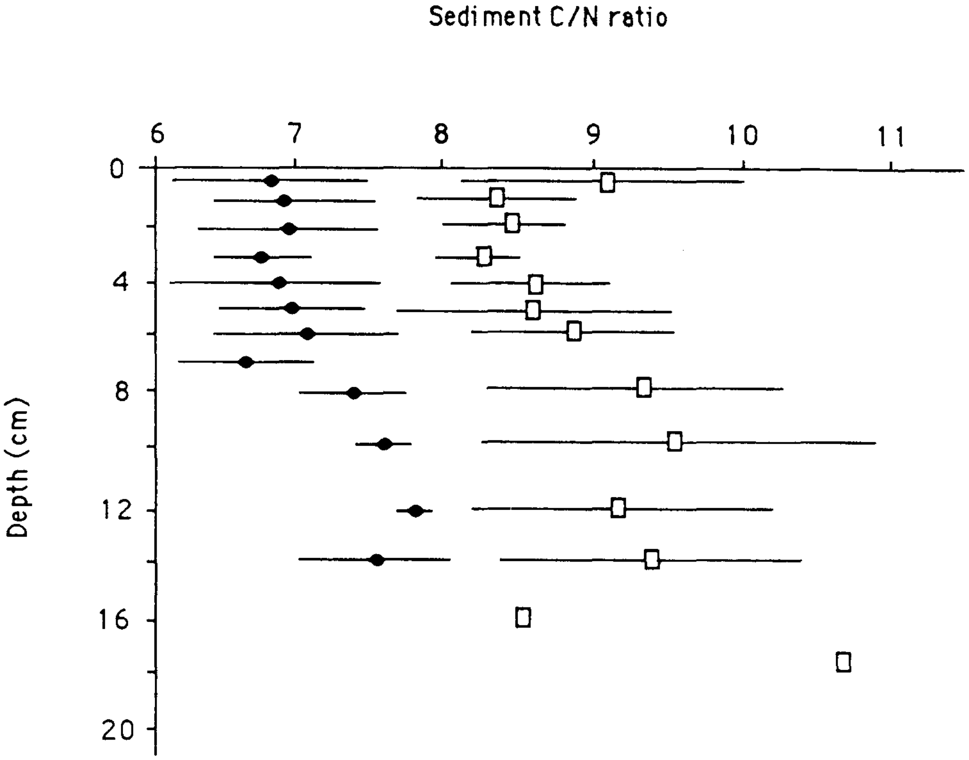


Figure 2.8. Mean and range of C/N ratios versus depth of sediments at stations in the Bering Shelf/Anadyr (●; 7 stations) and Alaska Coastal (☐; 4 stations) water masses.

Table 2.3. Particulate organic carbon and nitrogen concentrations (μg l^{-1}) and C/N ratios in the Bering Shelf/Anadyr water (R/V Alpha Helix Cruise 87, 10-24 August, 1987).

Station	Depth (m)	Carbon	Nitrogen	C/N
67	35	300.70	58.45	5.14
	42	261.07	46.88	5.57
80	0	344.55	48.41	7.12
	15	241.87	49.62	4.87
	30	219.05	32.68	6.70
	34	219.05	33.89	6.46
86	0	437.03	74.53	5.86
	15	340.15	64.05	5.31
88	0	422.13	105.90	3.99
	15	552.20	136.16	4.06
	25	235.03	44.18	5.32
	47	339.99	49.02	6.94
89	0	778.55	100.46	7.75
90	10	494.17	96.19	5.14
92	0	1960.37	263.01	7.45
	10	1132.87	201.52	5.62
93	0	1986.01	236.83	8.39
94	0	831.00	160.70	5.17
	10	755.65	142.56	5.30
96	0	777.18	100.15	7.76
	15	421.96	84.43	5.00
97	0	895.59	151.38	5.92
	15	465.02	64.05	7.26
101	15	650.16	110.63	5.88
	44	230.36	27.95	8.24
102	10	820.51	92.54	8.87
Mean (n=26)				6.20±1.34

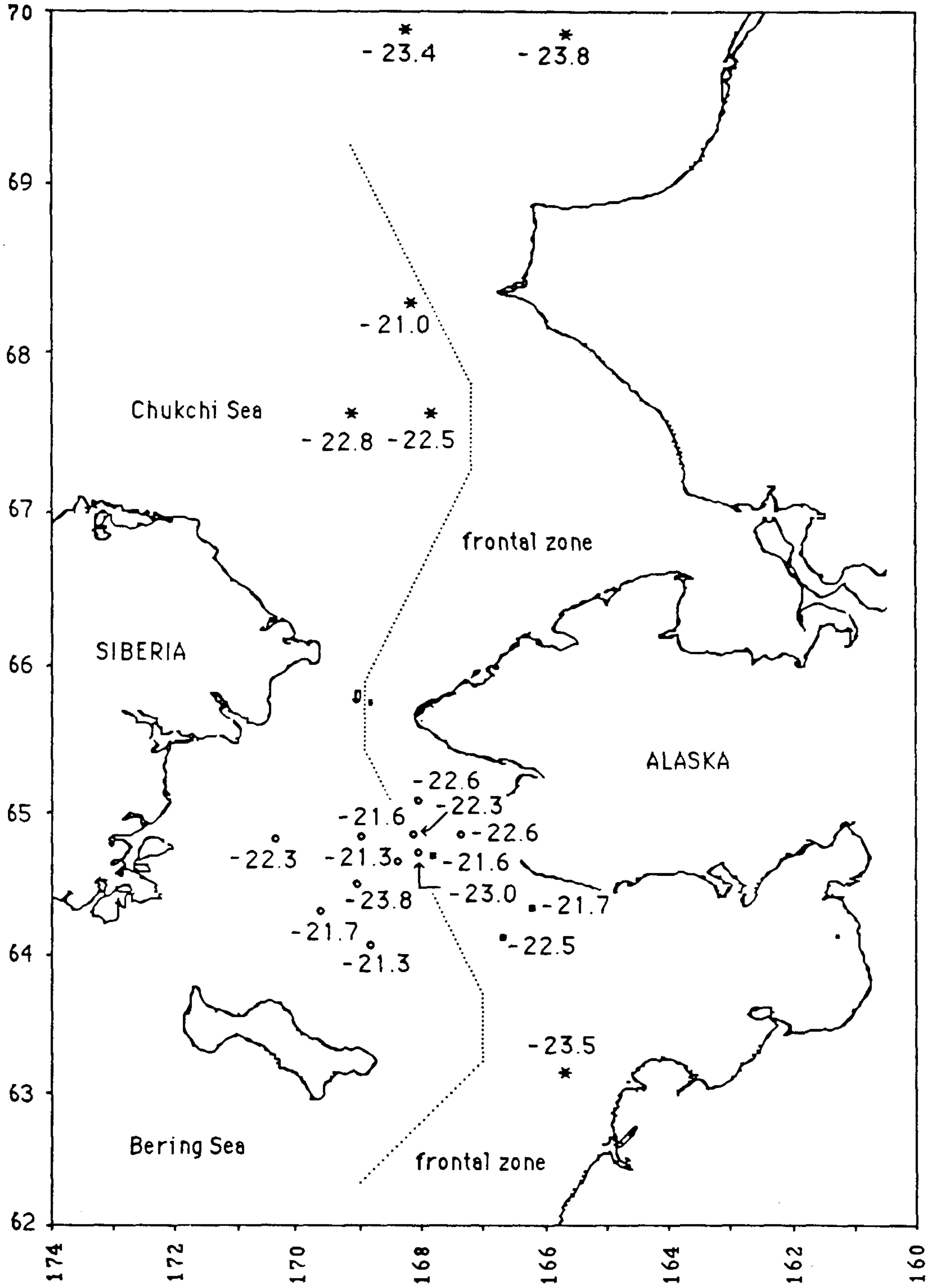


Figure 2.9. Distribution of $\delta^{13}C$ ratios in surface sediments for cruises 59(▪), 73(∘), and 74(∗) in the northern Bering and Chukchi Seas.

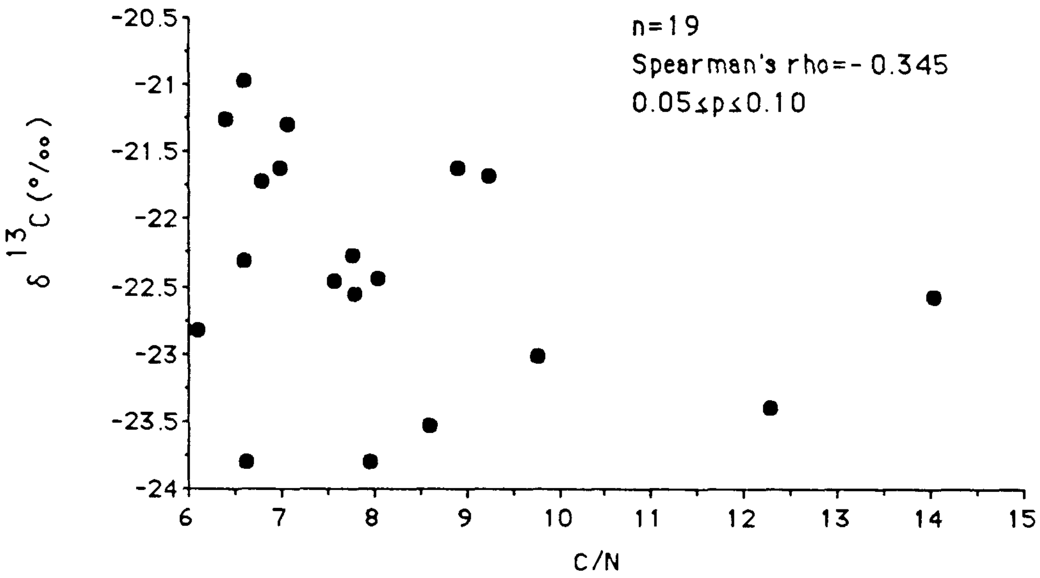


Figure 2.10. Relationship between $\delta^{13}C$ and C/N ratios in surface sediments in the northern Bering and Chukchi Seas.

DISCUSSION

If food is a major regulating mechanism controlling benthic structure and biomass, then both the quality and quantity of available organic matter should be important. The relatively stable C/N ratio of descending POC seen in the BS/A water column (Table 2.3), along with low C/N ratios in the underlying sediments, suggests a nitrogen-rich food source reaches the benthos. In comparison, sediments underlying the nutrient-depleted AC water exhibit high C/N ratios, suggesting the associated organic detritus is relatively nutrient-depleted compared to that available in surface sediments in BS/A water. The organic matter available to benthic populations is thus of a higher quality (lower C/N ratios) in BS/A water than in AC water. Recent research suggests a lower bacterial and microheterotrophic grazing rate (1-2%) occurs in the more eutrophic BS/A water compared to up to 50% in the more oligotrophic AC water (Andersen and Fenchel 1986). In addition, zooplankton grazing rates are relatively low (about 20%) in proportion to the available phytoplankton biomass in BS/A water, suggesting a larger food supply reaches the benthos in BS/A water than AC water (Cooney 1981; Walsh et al. 1987).

The sediments appear to mirror processes occurring in the overlying water column. Low C/N ratios in the surface sediments, indicative of a high quality (high nitrogen) source of organic matter, occur under the highly productive, cold and saline BS/A water mass. Inorganic nutrient supply to the euphotic zone is higher in BS/A compared AC waters (Whitledge 1986), which could reduce the relative amount of nitrogen lost from phytodetritus during its descent to the benthos in BS/A water. Phytoplankton blooms occur periodically throughout the summer in BS/A water (Springer and McRoy 1986) and, in conjunction with the low C/N ratios measured in the surface sediments, suggest a continual input of highly labile organic matter to the benthos. Stable carbon isotope data support a marine origin for this detritus. More intense sampling has shown a clear relationship between less negative

$\delta^{13}C$ and low C/N ratios in surface sediments (r=0.80, n=52; Parker and Scalan 1987). The low C/N ratios recorded during the summer (July-September) in the surface sediments underlying BS/A water do not vary significantly between years over three field seasons, suggesting a high quality food supply is available to benthic populations on a regular basis interannually.

In contrast, high C/N ratios occur in surface sediments near the Alaska coastline, probably due to a mixture of marine and terrestrial organic matter. Average C/N ratios for suspended material from the Yukon River are 14.5, decreasing to 10.5 at the mouth (Table 2.4). Average C/N ratios for particulate matter near the bottom in Norton Sound and the northeastern Bering Sea shelf ranged from 8.0-9.5 (Table 2.4). Most of the Yukon River suspended load remains in AC water, with primary deposition sites occurring in Norton Sound and downstream in the Chukchi Sea ((McManus and Smyth 1970; McManus et al. 1974 and 1977). The average C/N values for surface sediments in AC water range from 8.5-14.5, suggesting a lower quality (low nitrogen) terrestrial organic matter signature in these sediments, which can dilute the low C/N signature of phytodetritus. Addition of some terrestrial organic matter is suggested by the more negative $\delta^{13}C$ values measured in sediments in the present study and in data of Parker and Scalan (1986 and 1987). The data from the present study (Figure 2.10), together with that of Parker and Scalan (1987), clearly show the relationship between stable carbon isotope variation and C/N ratios in surface sediments. The mixing of decomposing marine phytoplankton in the nutrient-depleted AC water mass (which could have high or low C/N values depending on the degree of its decomposition and remineralization) and terrestrial organic matter input from rivers (high C/N ratios) would result in the higher C/N ratios measured in these sediments than those under BS/A water. The suspended material in Norton Sound and nearshore marine waters has higher C/N ratios near the bottom than at the surface (Table 2.4), suggesting depletion of

Table 2.4. Average C/N ratios for suspended materials from the Yukon River Estuary, Norton Sound, and northeastern Bering Sea Shelf (from Feeley et al. 1981).

Sample Location	C/N Ratio
Yukon River Estuary (0-15 °/oo)	14.5
Yukon River Estuary (15-25 °/oo)	10.5
East Norton Sound	
surface	6.4
5 m above bottom	9.2
Central Norton Sound	
surface	7.7
5 m above bottom	8.0
Western Norton Sound-northeastern Bering Sea shelf	
surface	6.4
5 m above bottom	9.5

nitrogen during descent through the water column. This differs from BS/A water, where C/N ratios of particulate detritus remained unchanged on its way to the bottom.

Unlike sediment underlying BS/A water, there was a significant difference in surface sediment C/N ratios measured during summer between years in AC water. This is reasonable considering the suspended particulate matter load from the Yukon River into the northern Bering Sea can be highly variable and the amount of maximum runoff is dependent on yearly ice cover and the timing of ice break-up (U.S.G.S. Water Resource Data 1975-1979, 1985). Thus, there is an inherent interannual variability in the coastal system due to discharge rates which can influence the supply and quality of organic matter.

Sediment is primarily composed of fine and very fine sand in the central Chirikov Basin in the northern Bering Sea under BS/A water, with sediments decreasing in average grain size to very fine sand and silt and clay in the southern Chukchi Sea. Sediment type is most variable under AC water, ranging from gravel and medium sand to silt and clay modal size classes. These observed sediment patterns appear related to the slower current regimes occurring in the central, offshore regions of the northern Bering and Chukchi Seas and the relatively faster current regime in AC water (Creager and McManus 1967; Coachman et al. 1975; Nihoul et al. 1986). Variabililty in northward-flowing current velocities in AC water, due to seasonal freshwater runoff and changes in transport conditions (Coachman et al. 1975), may influence the residence time of terrestrial organic matter in this water mass, thus influencing the time available for bacterial mineralization of detritus both in the water column and on the bottom. Reduced currents in the southern Chukchi Sea allow enhanced deposition of fine organic material with a concurrent increase in organic carbon accumulation in surface sediments relative to the northern Bering Sea.

In summary, the quality of organic matter arriving at the sediment-water interface in the northern Bering and Chukchi Seas is influenced by variations in primary production, riverine carbon input, grazing and decomposition processes occurring in the overlying water column. The BS/A water mass is a relatively eutrophic system compared to the AC water mass, and a higher quality and quantity of labile organic matter is available annually in the underlying surface sediments for benthic consumption and mineralization processes. The benthic communities underlying BS/A water are exposed to a persistent, high quality food supply, whereas benthic communities in AC water are exposed to a greater variation of terrestrial organic matter input, such that the quality of organic matter can fluctuate within and between years. Sediment grain size patchiness is more evident underlying AC water compared to BS/A water, which can also influence the pattern of benthic community structure.

CHAPTER 3. BENTHIC CARBON CYCLING: II. BENTHIC COMMUNITY STRUCTURE

INTRODUCTION

The relationship between high abundance and biomass of benthic fauna and enhanced carbon flux to the sediments has been well documented (Zenkevitch 1963; Rowe 1969; Elmgren 1978; Smith et al. 1983; Davies and Payne 1984). The quantity and quality of organic matter that descends to the sea floor is dependent on a variety of factors, including primary production, sinking rate of phytoplankton, levels of zooplankton grazing, mixed layer depth, and overall water column depth (Parsons et al. 1977; Pace et al. 1984; Wassman 1984). The structure of benthic communities and their relative abundance and biomass, therefore, can reflect processes occurring in the overlying water. In addition, the benthos averages water column processes over a longer time period, thus providing a mirror of trends that occur annually (Rowe 1969; Elmgren 1978; Graf et al. 1982; Jones 1984).

The shallow shelf of the northern Bering and Chukchi Seas, with water depths averaging less than 50 meters, can be ice covered for 7 to 8 months of the year. This area contains three northward flowing water masses: the Anadyr and Bering Shelf water masses, forming a modified Bering Shelf/Anadyr (BS/A) water to the west, characterized by low temperatures (-0.1 to 2 .0 °C) and high salinity (32.2 to 33.0 ‰), and the Alaska Coastal (AC) water mass to the east, characterized by high temperatures (2.0 to 10.0 °C) and low salinity (<32.0 ‰; Figure 1.2). The tidal range throughout the area is small, ranging from 5 to 10 cm (Pearson et al. 1981; Kowalik and Matthews 1982).

High primary and secondary productivity characterize the northern Bering and Chukchi Seas in BS/A water (McRoy et al. 1972; Alton 1974; Stoker 1978 and 1981; Springer and

McRoy 1986; Walsh et al. 1987). The largest benthic biomass (905 g m^{-2}) in the Bering Sea was found in the Chirikov Basin (Alton 1974). Stoker (1978) found a similar pattern, with highest benthic standing stock observed in Bering Strait and the southern Chukchi region (465 g m^{-2}), which corresponds with high primary productivity values (200 to 300 g C m^{-2} yr^{-1}) in the region (Springer and McRoy 1986; Walsh et al. 1987). Low standing stocks of benthic fauna occur in the regions covered by AC water (Stoker 1978). Zooplankton populations vary between large oceanic species in BS/A waters (ie. *Neocalanus* spp.) to small, neritic species in AC waters (ie. *Pseudocalanus* spp.; Zenkevitch 1963; Cooney 1981; Springer 1986).

An increasing gradient of benthic biomass with latitude has been observed for the northern shelf of the Bering and Chukchi Seas (Figure 3.1). This gradient was correlated with sediment grain size and temperature (Stoker 1978 and 1981). In addition, Stoker (1978) observed a change in community structure in the northern Bering and Chukchi Seas with the eastern marine system near the Alaska coastline characterized by a low biomass of polychaetes, bivalves, and echiuroids compared to benthic communities to the west, which were characterized by a high biomass of amphipods and different species of bivalves.

Although Stoker qualitatively concluded that species distribution and feeding type were correlated with substrate type, he had limited environmental data available to address quantitative reasons for variability in benthic standing stock. He suggested four potential factors which could influence benthic structure and standing stock: primary productivity, terrestrial detritus input, current regimes, and distribution of predators.

An important predator group on benthic invertebrates in the study area are marine mammals, primarily the gray whale, *Eschrichtius robustus*, the Pacific walrus, *Odobenus*

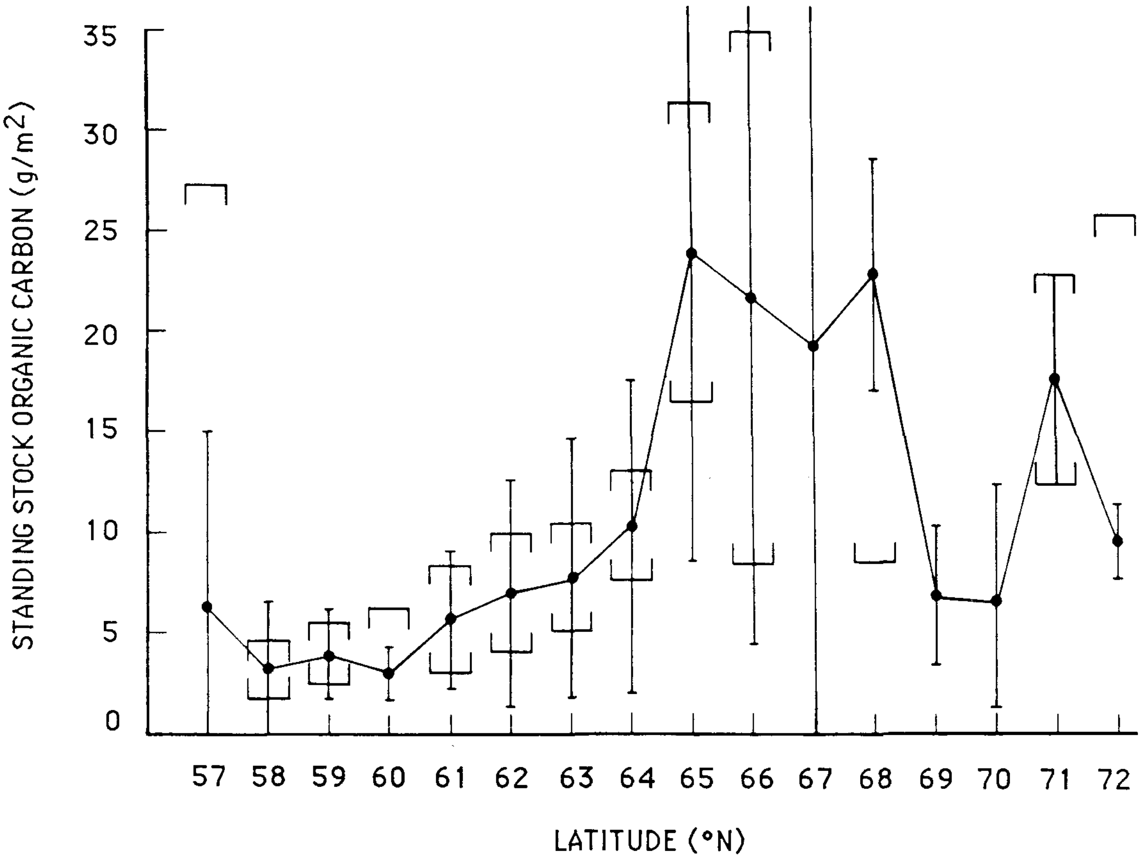


Figure 3.1. Variation of benthic biomass with latitude on the Bering and Chukchi Sea shelves (from Stoker 1978). Vertical lines indicate standard deviation and brackets indicate the coefficient of variation around the mean. The study area is located from 62° to 70° N.

rosmarus, and the bearded seal, *Erignathus barbatus* (Johnson et al. 1966; Feder and Jewett 1981; Nelson et al. 1981; Fay et al.1977 and 1984; Johnson and Nelson 1984; Lowry and Frost 1981; Nerini 1984; Oliver et al. 1983 *a* and *b* ; Fukuyama and Oliver 1985; Miller et al. 1985; Oliver and Slattery 1985). These animals disturb the sediments during feeding activities and deplete the invertebrate food resource as well as possibly enhance secondary productivity through sediment reworking and subsequent inorganic nutrient release to the water column. They also may be influencing successional processes through opening up space for recolonization (Nelson and Johnson 1987).

Epifaunal biomass in the northern Bering and southeastern Chukchi Sea is much lower than that observed in the southeastern Bering Sea (Feder and Jewett 1978; Jewett and Feder 1981). Echinoderms are dominant in total biomass (primarily by members of the sea star family Asteridae) in the northern Bering and Chukchi Seas, although molluscs are dominant in numbers of species (Feder and Jewett 1978). Demersal fishes are generally absent from the study area, presumably due to extremely low temperatures (Neiman 1963; Jewett and Feder 1980 and 1981) which can reach -1.8°C at various times of the year (Ahlnäs and Garrison 1984).

This paper addresses the hypothesis that food supply and sediment grain size are important regulating factors for benthic community structure, abundance and biomass in the northern Bering and Chukchi Seas.

MATERIALS AND METHODS

Four replicate 0.1 m^2 van Veen grabs (with penetration facilitated by 32 kg of lead weight) were taken at each station for quantitative sampling of benthic populations. Each sample was washed through 1 mm sieve screens and animals subsequently were preserved in 10% hexamethyltetramine-buffered formalin, stored in plastic Whirl-Pak™ bags, and returned for laboratory analysis in Fairbanks. Animals were keyed to family level, then counted and weighed to determine abundance and wet weight biomass. Past research on the continental shelf of the Bering and Chukchi Seas presented evidence that only 1 to 5 individual species occurred in each dominant faunal family, with a majority of families containing only 1 or 2 species (Stoker 1978; Appendix F). Therefore the familial level determinations are considered an adequate measure of faunal composition in the study area and the clustering program presented a valid methodology for this analysis.

Preserved wet weight faunal biomass was converted to carbon (C) biomass using the conversion values of Stoker (1978). The C conversions enable a standardization for comparison of biomass between stations by reducing the influence of the calcium carbonate tests of echinoids on total biomass. In order to support the decision to convert wet weight to carbon biomass as a direct measure of biomass measured during this analysis, the hypothesis that carbon biomass (using Stoker's 1978 conversion values) positively correlated with formalin wet weight data collected in this study, was tested using the parametric Pearson's product-moment correlation statistic (Sokal and Rolff 1969).

Stoker (1978) determined that organic carbon values averaged only 0.9% higher (per wet weight measurement) for frozen samples compared to formalin-preserved samples for all taxa. In addition, he determined carbon conversion values for animals to the species level, which were extrapolated to the familial level in the present study. When multiple species in the same family occurred, the mean value for all inclusive species was used (Appendix G).

A limitation in the sampling scheme was the inability of the van Veen grab to capture deep-dwelling bivalves in the families Myidae and Mactridae which has prevented complete sampling by all researchers in this area (Stoker 1978 and 1981; Feder et al. 1985).

Highly motile epifaunal organisms (crabs, sea stars and predatory gastropods) were excluded from the analysis. Stations dominated by relatively sessile and sessile epifaunal organisms, such as barnacles, sea anenomes, sea urchins, and bryozoans, were included in the community analysis. Colonial organisms (ectoprocts, sponges, and anthozoans) were given an abundance count of one for each colony observed. Fragments were given an abundance value of one and then weighed as a sum total of fragments for that taxa determination. A nonparametric Mann-Whitney U test was used to determine whether there was a significant difference between benthic biomass values for stations occurring in each water mass. The nonparametric Kruskal-Wallis test was used to test whether there was a significant difference in mean benthic biomass for stations in each water mass between years. A statistical package (StatView™, BrainPower 1985) was utilized on a MacIntosh™ computer, with the resultant test statistic being compared to standard tables to address levels of significance (Rohlf and Sokal 1969; Conover 1980).

Natural log-transformed abundance information was used in a numerical clustering procedure to group stations according to faunal similarities (Feder et al.1985; Stoker 1981). The program clusters stations on the basis of similarities in relative percent of faunal composition using the Czekanowski similarity coefficient (Stephenson et al. 1972). Log transformation [ln(x+1)] was used because the Czekanowski coefficient is sensitive to extremely large abundance values which occur'in a large percentage of the data (Boesch 1973). The benthic fauna occurring at all stations within a cluster group (100%) are considered co-occurring benthic fauna. When only a few families co-occur in a cluster group the list of faunal families is expanded to include those occurring in a majority of the stations, indicated by the percent occurrence within a cluster group. A mean biomass value was calculated for individual and combined cluster groups by determining the mean biomass of the stations combined by the similarity cluster analysis.

Each station number designation presented in subsequent tables is composed of five numbers: the first two numbers designate the cruise, the second three numbers designate the actual station, e.g. 59023 means cruise 59, station 023.

RESULTS

Benthic stations were occupied over three summer field seasons from July-September between 1984-1986 in the study area on the R/V Alpha Helix (Figure 1.1; Appendix A). The temperature and salinity data confirmed the presence of the front dividing the two major water masses in the study: the combined Bering Shelf/Anadyr (BS/A) water and the Alaska Coastal (AC) water (Appendix B). This front, which varies seasonally, separates the water masses with a salinity boundary of 32.0 °/oo (Figure 1.2). Over the three field seasons bottom salinity and temperature ranged from 32.2 to 33.0 °/oo and -1.0 to 2.0 °C, respectively, in BS/A water and AC water ranged from 28.0 to 32.0 °/oo and 2.0 to 9.0 °C. These values, in conjunction with the average location of the seasonal front, were used to designate station locations relative to water masses.

BENTHIC COMMUNITY STRUCTURE

Faunal abundance and biomass were determined for 49 benthic stations occupied over the 3 field seasons (Figure 3.2; Table 3.1; Appendix H, I). Individual faunal abundances were used in a clustering program to form 17 cluster groups, 6 being individual stations (Figure 3.3). The majority of the multiple station groups clustered at the 53 to 74% level, with only one group (Group XI) separating at only a 43% similarity level. There were a total of 10 combined cluster groups, 3 being individual stations, at a lower similarity level.

Cluster Groups

The following section describes the dominant co-occurring families that make up greater than 50% of the top 95% of ranked faunal abundance in each cluster group (Figure 3.4; Table 3.2). The boundaries of the cluster groups were drawn around all the stations within the group. When a large number of families co-occurred within a cluster group, only the

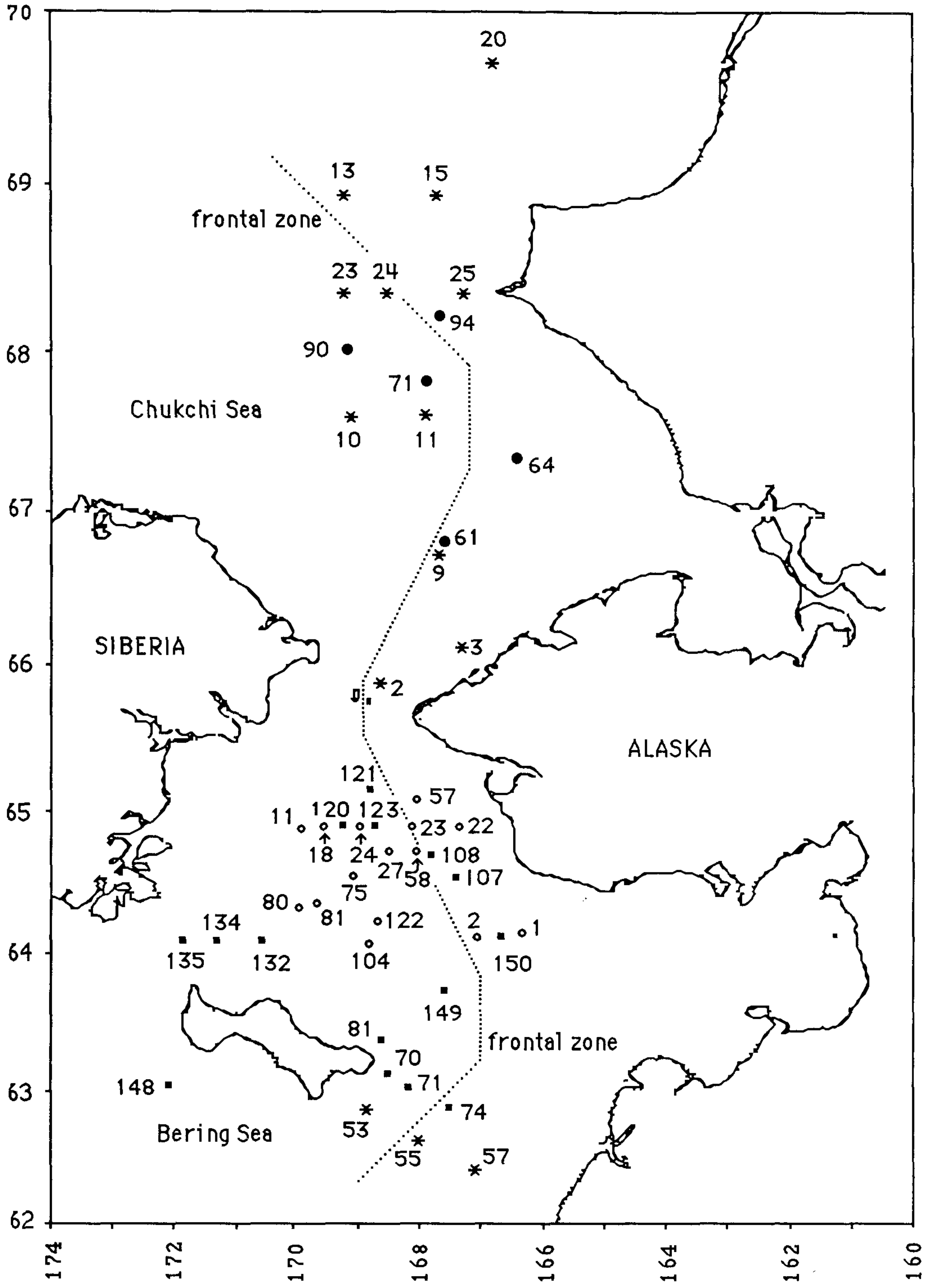


Figure 3.2. Location of benthic sampling stations in the northern Bering and Chukchi Seas for cruises 59(▪), 73(◦), 74(*) and 85(●). Frontal zone separates BS/A water in the west from AC water in the east.

Table 3.1. Abundance and biomass for benthic fauna collected during cruises 59 (30 June-10 July 1984), 73 (25 July-10 August 1985), 74 (26 August-9 September 1985), and 85 (11-26 July 1986).

Station	Abundance (no. m^{-2})	Biomass (g m^{-2})	Biomass (g C m^{-2})
59070	313	549.60	22.90
59071	463	2143.76	18.57
59074	140	41.99	2.61
59081	900	388.84	13.65
59107	7770	35.32	1.95
59108	315	108.61	3.04
59120	7383	725.42	32.24
59121	2865	739.49	29.52
59123	5548	685.47	26.82
59132	188	2376.97	20.92
59134	1558	744.84	11.27
59135	1810	517.48	13.67
59148	2293	405.13	13.30
59149	3195	180.03	9.02
59150	1190	699.30	10.44
73001	1418	257.43	7.36
73002	1190	290.96	8.49
73011	5845	405.20	19.65
73018	7628	520.22	21.29
73022	1535	39.00	1.82
73023	2510	894.40	22.33
73024	6398	706.67	25.91
73027	8605	289.30	12.84
73057	305	17.58	1.03
73058	5785	97.22	2.89
73075	8908	505.85	24.50
73080	1668	493.14	17.70
73081	3245	308.18	17.43
73104	14365	342.17	20.05
73122	5555	241.97	13.99
74002	1080	318.94	11.58
74003	2765	86.29	3.23
74009	2623	196.52	4.61
74010	9188	1593.22	58.95
74011	2548	330.84	15.11
74013	488	51.65	1.33
74015	890	29.68	1.73
74020	545	17.04	9.91
74023	2068	484.31	20.14
74024	2178	190.06	7.86
74025	193	71.28	3.86
74053	7923	485.53	16.67
74055	4423	160.94	4.53

Table 3.1. Continued.

Station	Abundance (no. m^{-2})	Biomass (g m^{-2})	Biomass (g C m^{-2})
74057	2370	883.76	8.34
85061	2433	411.99	7.44
85064	785	34.97	1.69
85071	2048	118.01	8.52
85090	12115	629.60	32.36
85094	687	423.30	19.15

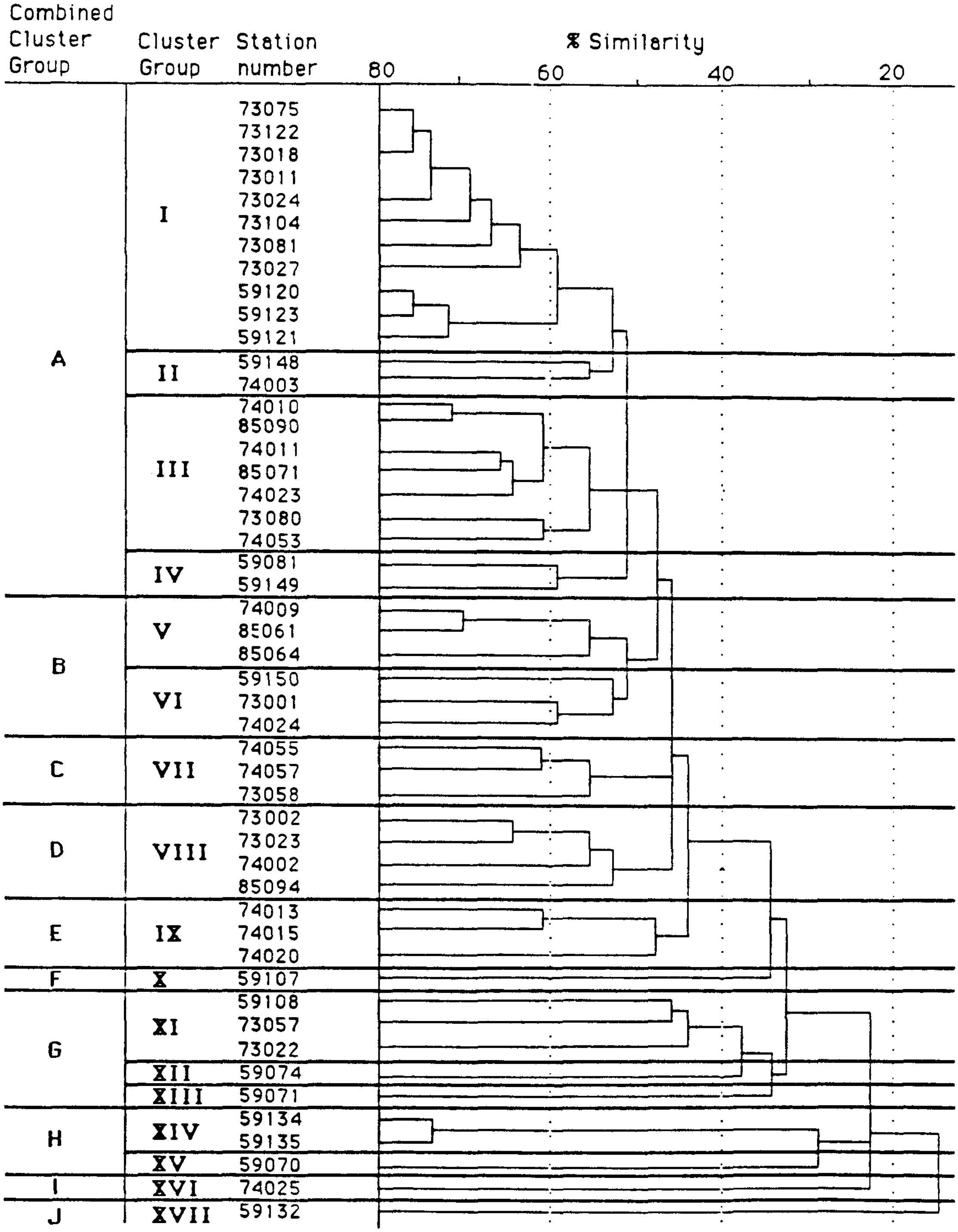


Figure 3.3 Dendrogram showing cluster analysis of abundance data based on station to station faunal similarities. The combined cluster groups were formed at a lower similarity level than the individual cluster groups.

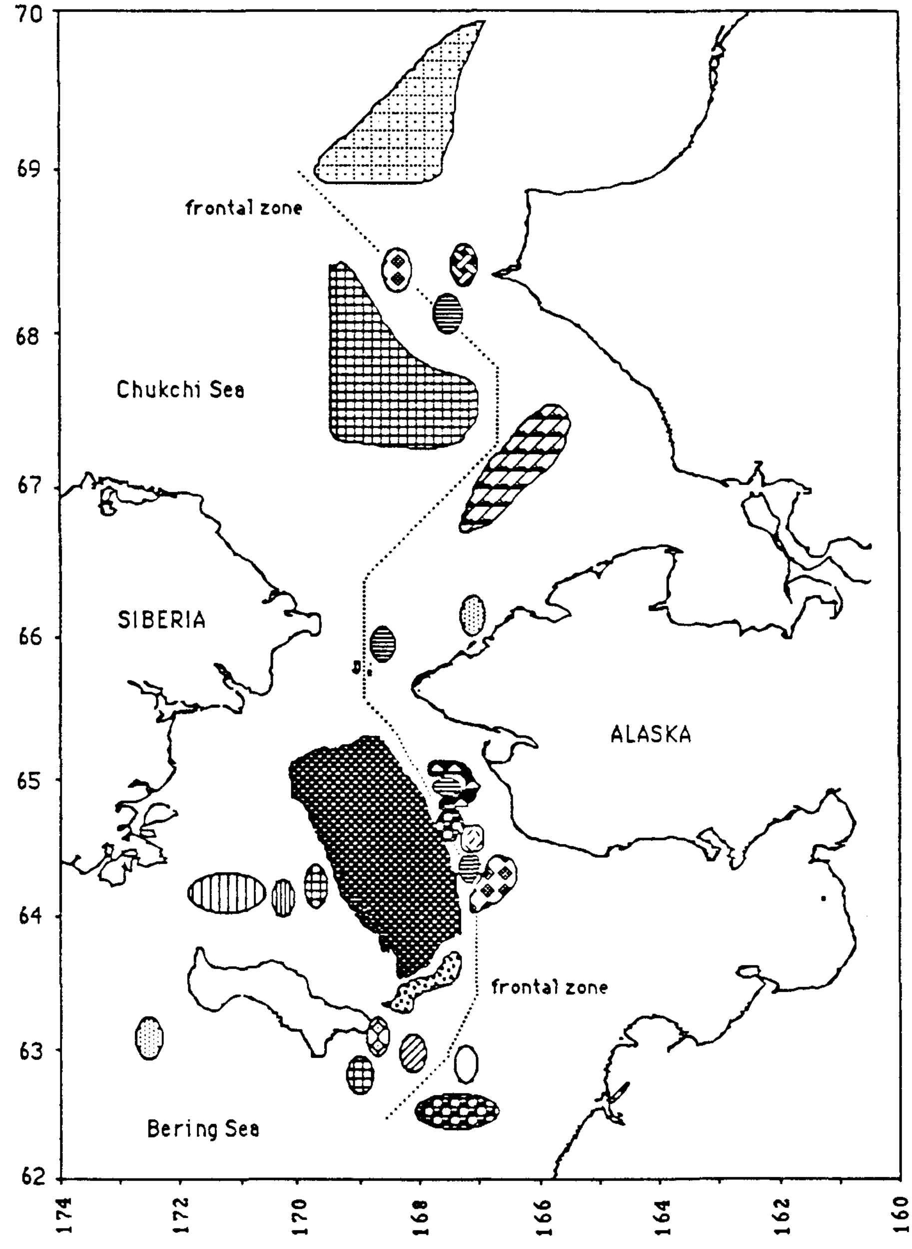


Figure 3.4. Distribution of faunal communities based on individual cluster group analysis (see Table 3.2 for list of dominant fauna):

- ▓ I
- ░ II
- ▦ III
- ▧ IV
- ▨ V
- ◆ VI
- ▩ VII
- ▤ VIII
- ⁘ IX
- ◸ X
- ▲ XI
- ☐ XII
- ▨ XIII
- ▥ XIV
- ◇ XV
- ▚ XVI
- ▥ XVII

Table 3.2. Dominant benthic fauna co-occurring in the top 95% of ranked abundance of individual groups for station-station cluster analysis. Percent occurrence is the combined value for that family within the cluster group.

Cluster Group	Percent Similarity	Stations	Dominant families	Percent occurrence within group
I	59	73075	Ampeliscidae	100
		73122	Isaeidae	100
		73018	Phoxocephalidae	100
		73011	Lysianassidae	91
		73024	Tellinidae	82
		73104	Ampharetidae	64
		73081	Capitellidae	55
		73027	Nuculidae	55
		59120		
		59123		
		59121		
II	56	59148	Goniadidae	100
		74003	Orbiniidae	100
			Oweniidae	100
			Ampeliscidae	100
			Haustoridae	100
			Isaeidae	100
			Leuconidae	100
			Tellinidae	100
			Nuculidae	100
			Ophiuridae	100
III	56	74010	Isaeidae	100
		85090	Haustoridae	100
		74011	Nuculidae	100
		85071	Ampeliscidae	86
		74023	Phoxocephalidae	86
		73080	Leuconidae	86
		74053	Capitellidae	71
			Polynoidae	71
			Tellinidae	71
			Maldanidae	57
			Nephtyidae	57
			Phyllodocidae	57

Table 3.2. Continued.

Cluster Group	Percent Similarity	Stations	Dominant families	Percent occurrence within group
IV	59	59081	Ampeliscidae	100
		59149	Isaeidae	100
			Phoxocephalidae	100
			Nuculidae	100
			Tellinidae	100
			Thyasiridae	100
V	56	74009	Orbiniidae	100
		85061	Sigalionidae	100
		85064	Phoxocephalidae	100
			Oediceratidae	100
			Nuculidae	100
			Thyasiridae	100
			Ophiuridae	100
VI	53	59150	Capitellidae	100
		73001	Maldanidae	100
		74024	Nephtyidae	100
			Sigalionidae	100
			Sternaspidae	100
			Ampeliscidae	100
			Phoxocephalidae	100
			Leuconidae	100
			Nuculidae	100
			Amphiuridae	100
			Ophiuridae	100
VII	56	74055	Orbiniidae	100
		74057	Isaeidae	100
		74058	Oediceratidae	100
			Phoxocephalidae	100
			Leuconidae	100
			Echinarachniidae	100

Table 3.2. Continued.

Cluster Group	Percent Similarity	Stations	Dominant families	Percent occurrence within group
VIII	53	73002	Ampharetidae	100
		73023	Capitellidae	100
		74002	Goniadidae	100
		85094	Maldanidae	100
			Polynoidae	100
			Sabellidae	100
			Syllidae	100
			Phoxocephalidae	100
			Nuculanidae	100
			Tellinidae	100
			Ophiuridae	100
			Golfingiidae	100
IX	48	74013	Goniadidae	100
		74015	Nephtyidae	100
		74020	Polynoidae	100
			Sternaspidae	100
			Ampeliscidae	100
			Phoxocephalidae	100
			Nuculidae	100
			Tellinidae	100
			Ophiuridae	100
X	< 35%	59107	Isaeidae Ampeliscidae Phoxocephalidae Orbiniidae	95.7% of total station
XI	43%	59108	Ampeliscidae	100
		73057	Isaeidae	100
		73022	Phoxocephalidae	100
			Nuculidae	100
			Tellinidae	100
			Echinarachniidae	100

Table 3.2. Continued.

Cluster group	Percent similarity	Stations	Dominant families	Percent occurrence within group
XII	<38	59074	Phoxocephalidae	>69.6% of total station
			Nuculidae	
			Tellinidae	
			Maldanidae	
			Nephtyidae	
			Orbiniidae	
XIII	<35	59071	Echinarachniidae	>89.8% of total station
			Alyconidiidae	
			Trochidae	
			Phoxocephalidae	
			Isaeidae	
			Nephtyidae	
			Lysianassidae	
XIV	74	59134 59135	Pectinariidae	100
			Nephtyidae	100
			Terebellidae	100
			Polyplacophora sp.	100
			Gastropod sp.	100
			Holothuroidea sp.	100
			Ophiuridae	100
			Ophiactidae	100
			Strongylocentrotidae	100
XV	<28	59070	Terebellidae	>75.2% of total station
			Sabellidae	
			Nephtyidae	
			Polynoidae	
			Ampharetidae	
			Isaeidae	
			Pyuridae	
			Styelidae	

Table 3.2. (Continued).

Cluster Group	Percent Similarity	Stations	Dominant families	Percent occurrence within group
XVI	<23	74025	Golfingiidae Maldanidae Syllidae Amphiuridae Ampeliscidae Rhynchocoela sp. Ectoprocta sp. Anthozoa	>62.3% of total station
XVII	<15	59132	Echinarachniidae Nephtyidae Strongylocentrotidae Veneridae Cardiidae Gastropoda sp.	>93.3% of total station

families occurring at 100% of the inclusive stations are listed in subsequent tables. In addition, feeding types for dominant fauna are presented (Table 3.3). The top three families present in 95% of the ranked abundance and biomass for each station in the individual cluster groups are listed in Appendix I.

Cluster Group I is composed of 11 stations located in the central Chirikov Basin north of St. Lawrence Island which are located under BS/A water. Selective detritus-feeding amphipods (Ampeliscidae, Isaeidae, and Phoxocephalidae) occurred in 100% of the stations. Ampeliscid amphipods can also be suspension feeders. Other scavenger amphipods (Lysianassidae) occurred in 91% of the stations. Bivalves (Tellinidae and Nuculidae) occurred in 55-82% of the stations. Selective detritus-feeding polychaetes (Ampharetidae) occurred in 64% of the stations and deposit-feeding polychaetes (Capitellidae) occurred in 55% of the stations.

Cluster Group II is composed of two stations (one in BS/A and one in AC water) in widely different locations. However, they clustered at the 56% similarity, having ten families in common. Deposit-feeding polychaetes (Oweniidae and Orbiniidae) occurred at both stations, as did predatory polychaetes (Goniadidae). Amphipods (Ampeliscidae, Isaeidae and Haustoriidae) were present. Selective-detritus feeding cumaceans (Leuconidae), bivalves (Tellinidae and Nuculidae), and brittle stars (Ophiuridae, which are scavenger/predator/suspension-feeding animals) also occurred at both stations.

Cluster Group III contains 7 stations, five occurring in the Chukchi Sea and two in the northern Bering Sea . The stations clustered together at the 56% similiarity level and were all located under BS/A water mass. Selective detritus-feeding bivalves (Nuculidae) are dominant at all the stations in this group. Two amphipod families (Isaeidae and Haustoriidae) occurred in 100% of the stations, with the remaining amphipods (Ampeliscidae and

Table 3.3. Feeding mode of dominant faunal families in 95% of ranked abundance and biomass for stations in the northern Bering and Chukchi Seas (based on descriptions by Stoker 1978; Fauchald and Jumars 1979; Barnes 1980; Feder et al. 1985).

Taxa	Feeding Mode
Foraminifera	carnivore/scavenger
Cnidaria	
Anthozoa	carnivore
Rhynchocoela	carnivore
Annelida	
Polychaeta	
F. Ampharetidae	selective detritus feeder
F. Capitellidae	deposit feeder
F. Cirratulidae	selective detritus feeder
F. Flabelligeridae	selective detritus feeder
F. Goniadidae	carnivore/scavenger
F. Lumbrineridae	carnivore/scavenger/selective detritus feeder
F. Maldanidae	deposit feeder
F. Magelonidae	selective detritus/deposit feeder
F. Nephtyidae	carnivore/scavenger/selective detritus feeder
F. Ophelidae	deposit feeder
F. Orbiniidae	deposit feeder
F. Oweniidae	deposit feeder
F. Pectinariidae	selective detritus feeder
F. Phyllodocidae	carnivore/scavenger
F. Polynoidae	carnivore/scavenger
F. Sabellidae	suspension feeder
F. Sigalionidae	carnivore/scavenger
F. Spionidae	selective detritus/suspension feeder
F. Sternaspidae	deposit feeder
F. Syllidae	carnivore/scavenger feeder
F. Terebellidae	selective detritus feeder
Arthropoda	
Crustacea	
F. Balanidae	suspension feeder
Amphipoda	
F. Ampeliscidae	selective detritus/suspension feeder
F. Corophiidae	selective detritus/suspension feeder
F. Gammaridae	selective detritus feeder
F. Haustoriidae	selective detritus feeder
F. Isaeidae	selective detritus feeder
F. Lysianassidae	carnivore/scavenger/selective detritus feeder
F. Oediceratidae	selective detritus feeder
F. Phoxocephalidae	selective detritus feeder
F. Pleustidae	selective detritus feeder
Cumacea	
F. Diastylidae	selective detritus feeder

Table 3.3. Continued.

Taxa	Feeding Mode
F. Lampropidae	selective detritus feeder
F. Leuconidae	selective detritus feeder
Isopoda	
F. Anthuridae	selective detritus feeder
Mollusca	
Bivalvia	
F. Astartidae	suspension feeder
F. Cardiidae	suspension/selective detritus feeder
F. Montacutidae	selective detritus feeder
F. Myidae	suspension/selective detritus feeder
F. Nuculidae	selective detritus feeder
F. Nuculanidae	selective detritus feeder
F. Tellinidae	selective detritus/suspension feeder
F. Thyasiridae	suspension feeder
F. Veneridae	suspension feeder
Gastropoda	
F. Cylichnidae	carnivore/scavenger
F. Muricidae	carnivore/scavenger
F. Trochidae	carnivore/scavenger
F. Turridae	carnivore/scavenger
Polyplacophora	scavenger
Ectoprocta	
F. Alyconidiidae	suspension feeder
Ectoprocta sp.	suspension feeder
Echinodermata	
Echinoidea	
F. Echinarachniidae	selective detritus feeder/suspension feeder
F. Strongylocentrotidae	selective detritus feeder/scavenger
Holothuroidea	
F. Synaptidae	selective detritus/suspension feeder
Ophiuroidea	
F. Amphiuridae	selective detritus/suspension feeder
F. Ophiactidae	selective detritus/suspension feeder
F. Ophiuridae	selective detritus/carnivore
Priapulida	carnivore/scavenger
Sipunculida	
F. Golfingiidae	selective detritus feeder
Echiurida	
F. Echiuridae	selective detritus feeder
Chordata	
Ascidiacea	
F. Mogulidae	suspension feeder
F. Pyuridae	suspension feeder
F. Styelidae	suspension feeder

Phoxocephalidae) and cumaceans (Leuconidae) occurring in 86% of the stations. Bivalves (Tellinidae) occurred in 71% of the stations, with the remainder of the within group ranked abundance being composed of 5 polychaete families. Deposit-feeding polychaetes (Capitellidae and Maldanidae) occurred in 57-71% of the stations. The carnivorous polychaetes (Polynoidae, Phyllodocidae, and Nephtyidae) also occurred in 57-71% of the stations. Some species of Nepthyidae can also be selective detritus feeders.

Cluster Group IV (59% similarity level) is composed of two stations located northwest of St. Lawrence Island in the Chirikov Basin under BS/A water. Amphipods (Ampeliscidae, Isaeidae, and Phoxocephalidae) occurred in both stations. The remainder of the co-occurring dominant fauna include detritus-feeding bivalves (Nuculidae and Tellinidae) and filter-feeding bivalves (Thyasiridae).

Cluster Group V is composed of three stations that are located under AC water in the Chukchi Sea. Seven dominant families co-occurred in all stations. Deposit-feeding polychaetes (Orbiniidae) and carnivorous predators (Sigalionidae) are abundant. Amphipods (Phoxocephalidae and Oediceratidae) are present as well as bivalves (Nuculidae and Thyasiridae). In addition, carnivorous/detrital-feeding brittle stars (Ophiuridae) are present.

Cluster Group VI is composed of three stations, two in the Chirikov Basin under AC water and one in the southern Chukchi Sea under BS/A water. Various polychaetes (Capitellidae, Maldanidae, Nephtyidae, and Sigalionidae) are present. Amphipods (Ampeliscidae and Phoxocephalidae), cumaceans (Leuconidae), bivalves (Nuculidae), and brittle stars (Ophiuridae and Amphiuridae) also co-occurred.

Cluster Group VII (56% similarity) is composed of three stations located in the Chirikov Basin and southeast of St. Lawrence Island under AC water. Six faunal families in the top 95% of the ranked abundance co-occurred at these stations. These include polychaetes (Orbiniidae), amphipods (Isaeidae, Oediceratidae, and Phoxocephalidae) and cumaceans

(Leuconidae). Selective detritus-feeding sand dollars (Echinarachniidae) were also present.

Four stations make up Cluster Group VIII, which has a 53% similarity level. Two stations occur in the Chirikov Basin and two in the southern Chukchi Sea, all under AC water. Various polychaetes (Capitellidae, Maldanidae, Ampharetidae, Syllidae, Polynoidae, Goniadidae, and Sabellidae) were dominant. Syllid polychaetes are predators and sabellid polychaetes are suspension feeders. Amphipods (Phoxocephalidae) also co-occurred as did bivalves (Tellinidae and Nuculanidae). Deposit-feeding sipunculids (Golfingiidae) and brittle stars (Ophiuridae) were also present.

Cluster Group IX (48% similarity level) is composed of three stations located in the southern Chukchi Sea in AC water. Co-occurring fauna include polychaetes (Goniadidae, Nephtyidae, Polynoidae, and Sternaspidae), amphipods (Phoxocephalidae and Ampeliscidae), bivalves (Nuculidae and Tellinidae), and brittle stars (Ophiuridae).

One station occurs in Cluster Group X, which only combines with other groups below the 35% similarity level. This station occurs under AC water in the Chirikov Basin. Ninety-five percent of the ranked abundance at this station includes polychaetes (Orbiniidae) and amphipods (Isaeidae, Ampeliscidae and Phoxocephalidae).

Cluster Group XI (43% similarity level) is composed of three stations located under AC water in the Chirikov Basin. Amphipods (Isaeidae, Phoxocephalidae and Ampeliscidae) and bivalves (Nuculidae and Tellinidae) are co-occurring fauna. In addition, sand dollars (Echinarachniidae) are also present.

Cluster Group XII is composed of one station southeast of St. Lawrence Island (with <38% similarity level to any other station) located in AC water. Six families make up >69.6% of the total faunal abundance at this station, with the remainder of the station abundance being composed of many faunal families with low individual abundance values. The station is dominated by polychaetes (Maldanidae, Nephtyidae, and Orbiniidae), amphipods

(Phoxocephalidae) , and bivalves (Nuculidae and Tellinidae).

Cluster Group XIII contains one station in BS/A water southeast of St. Lawrence Island. Seven families make up >89.8% of the total station abundance, with the remainder of the abundance composed of many families with small counts. Sand dollars (Echinarachniidae) dominate by abundace. Disc bryozoans (Alyconidiidae) are abundant as are gastropods (Trochidae). Polychaetes (Nephtyidae) and amphipods (Phoxocephalidae, Lysianassidae and Isaeidae) are also numerically dominant.

Two stations in the Chirikov Basin under BS/A water make up Cluster Group XIV at the 74% similarity level. Nine families co-occur at these stations. These include polychaetes (Nephtyidae, Pectinariidae and Terebellidae), brittle stars (Ophiuridae and Ophiactidae), polyplacophorans (chitons) and gastropods. Sea urchins (Strongylocentrotidae) are abundant as well as species of holothuroideans (sea cucumbers).

A single station (Cluster Group XV) located on coarse, gravel sediments at the southeastern end of St. Lawrence Island in BS/A water only combines with other groups at the 28% similarity level. Eight families make up 75.2% of the total station abundance; the remainder of the ranked abundance is composed of a large number of families, each containing only a few animials. Abundance is dominated by amphipods (Isaeidae) and polychaetes (Terebellidae, Sabellidae, Nephtyidae, Polynoidae, and Ampharetidae). Tunicates (Pyuridae and Styelidae) are also abundant at this station.

Cluster Group XVI is a lone station located off Point Hope in the Chukchi Sea under AC water in coarse sand and gravel. It does not group with any other station until below a 23% similarity level. Eight diverse families dominate 62.3% of the total station abundance, with the remaining abundance composed of a wide variety of families with only a few animals in each. Polychaetes (Maldanidae and Syllidae) are dominant as are sipunculids (Golfingiidae). Amphipods (Ampeliscidae) and brittle stars (Amphiuridae) are abundant. Proboscis worms, (*Rhynchocoela* spp.), sea anenomes and encrusting bryozoans are also present.

The final Cluster Group XVII is made up of one station in the Chirikov Basin under BS/A water. This station is the least similar to the other 48 stations analyzed as it does not combine with the other groups until below a 15% similarity level. Six faunal taxa dominate 93.3% of the stations ranked abundance. Sand dollars (Echinarachniidae) are dominant, with polychaetes (Nephtyidae) second in abundance. Sea urchins (F. Strongylocentrotidae) are abundant as are bivalves (Veneridae and Cardiidae).

Combined Cluster Groups

By combining cluster groups at the lowest similarity level possible, while still retaining separations between major groups, 10 Combined Cluster Groups (six still being individual stations) were obtained (Figure 3.3 and Figure 3.5). Cluster Groups I-IV, which all occur under BS/A water, combine as the large Group A at a 51% similarity level. Within the combined Group A four dominant faunal families co-occur: Ampeliscidae, Isaeidae, Tellinidae and Nuculidae (Table 3.4).

Combined Group B is composed of Cluster Groups V and VI which group together at a the 51% similarity level and occur primarily in AC water. The dominant co-occurring families in this combined group are Sigalionidae, Phoxocephalidae, Nuculidae, and Ophiuridae.

Combined Groups C, D, E, and F correspond to Cluster Groups VII,VIII, IX, and X, respectively, and all occur in AC water.

Combined Group G is composed of Cluster Groups XI, XII and XIII, which combines 5 stations at the 35% similarity level, and occurs primarily in AC water. Only one family, Phoxocephalide, co-occurs at all stations at this low level. However, if considered at a 67% co-occurrence level, four dominant families are found in a majority of the combined stations. These are Isaeidae, Nuculidae, Tellinidae, and Echinarachniidae.

The Combined Group H joins the Cluster Groups XIV and XV and occurs in BS/A

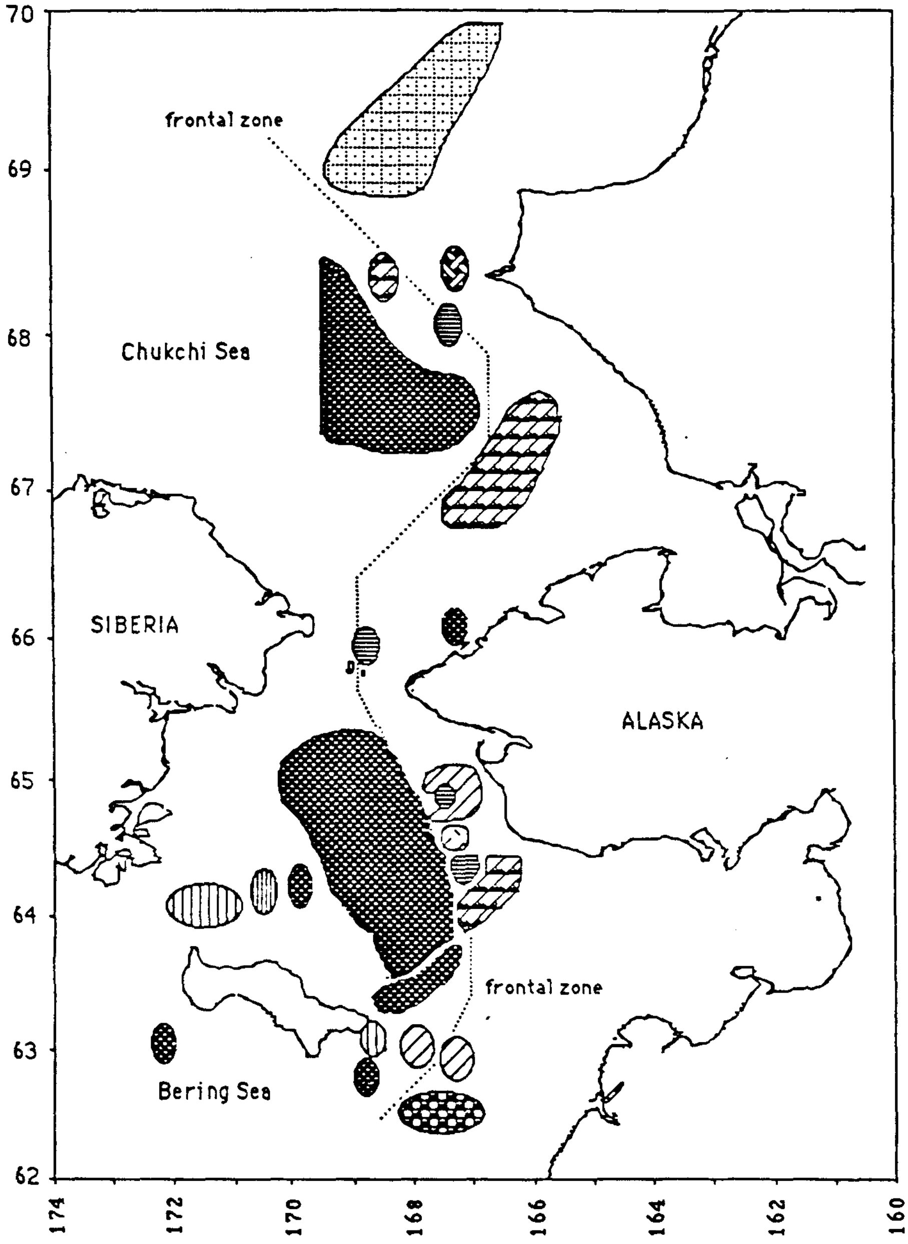


Figure 3.5. Distribution of faunal communities based on combined cluster group analysis (see Table 3.4 for list of dominant fauna):

A ▩ (I,II,III,IV)
B ▨ (V,VI)
C ▦ (VII)
D ▤ (VIII)
E ▦ (IX)
F ▨ (X)
G ▨ (XI,XII,XIII)
H ▥ (XIV,XV)
I ▩ (XVI)
J ▥ (XVII)

Table 3.4. Dominant benthic fauna co-occurring in the top 95% of ranked abundance of combined groups for station-station cluster analysis. Water mass type is designated as Bering Shelf/Anadyr=BS/A or Alaska Coastal=AC.

Combined Group	Water mass	Cluster Group	No. of Stations	Dominant families
A	BS/A	I,II,III and IV	22	Ampeliscidae Isaeidae Nuculidae Tellinidae
B	AC (except 1 BS/A)	V,VI	6	Sigalionidae Phoxocephalidae Nuculidae Ophiuridae
C	AC	VII	3	Orbiniidae Isaeidae Oediceratidae Phoxocephalidae Leuconidae Echinarachniidae
D	AC	VIII	4	Ampharetidae Capitellidae Goniadidae Maldanidae Polynoidae Sabellidae Syllidae Phoxocephalidae Nuculanidae Tellinidae Ophiuridae Golfingiidae
E	AC	IX	3	Goniadidae Nephtyidae Polynoidae Sternaspidae Ampeliscidae Phoxocephalidae Nuculidae Tellinidae Ophiuridae

Table 3.4. Continued.

Combined Group	Water mass	Cluster Group	No. of Stations	Dominant families
F	AC	X	1	Isaeidae Ampeliscidae Phoxocephalidae Orbiniidae
G	AC (except 1 BS/A)	XI,XII,XIII	6	Phoxocephalidae [†] Isaeidae [†] Nuculidae [†] Tellinidae [†] Echinarachniidae
H	BS/A	XIV,XV	3	Nephtyidae Terebellidae
I	AC	XVI	1	Sipunculidae Maldanidae Syllidae Ampeliscidae Rhynchocoela sp. Ectoprocta sp. Anthozoa sp.
J	AC	XVII	1	Echinarachniidae Nephtyidae Strongylocentrotidae Veneridae Cardiidae Gastropoda sp.

[†] 67% co-occurrence between stations

water. Three stations are grouped at a low 28% similarity level, with only two families (Nephtyidae and Terebellidae) co-occurring at all stations within the combined group.

Group I is Cluster Group XVI and occurs in AC water. Group J is Cluster Group XVII and occurs in BS/A water.

BENTHIC BIOMASS

Results of the statistical analysis comparing the two measurements of biomass showed that there is a significant correlation between wet weight biomass and C biomass ($r=0.617, p<0.005$; Figure 3.6). If the 5 stations (59071, 59132, 59134, 59150 and 74057) where echinoids (families Echinarachniidae and Strongylocentrotidae) dominate are deleted, the correlation coefficient r increases to 0.948, $p<0.005$, indicating a very strong correlation between preserved wet weight and carbon weight. Although subsequent tables will include wet weights for comparison, the remainder of the text will use carbon when discussing biomass.

Mean benthic biomass was 3-4 fold higher under BS/A water compared to stations under AC water (Figures 3.7 and 3.8). Benthic biomass did not vary significantly between years (1984-86) in each water mass (Kruskal-Wallis test, $p>0.25$; Table 3.5). Biomass values averaged 20.15 g C m^{-2} in the BS/A water and decreased to 6.31 g C m^{-2} in the AC water (Table 3.6). The decrease in mean benthic biomass between water mass type was significant (Mann-Whitney U test, $p<0.0001$). There was no significant difference of mean benthic biomass by location within the BS/A water or AC water (Mann-Whitney U test, $p>0.25$).

Biomass of Individual Cluster Groups

Cluster Groups I, III, IV, XIII, XIV, XV, and XVII all occur under BS/A water and generally have the highest biomass of all the groups, ranging from 11.34-24.21 g C m^{-2} (Table 3.7). Five of the seven cluster groups determined to be under the BS/A water mass

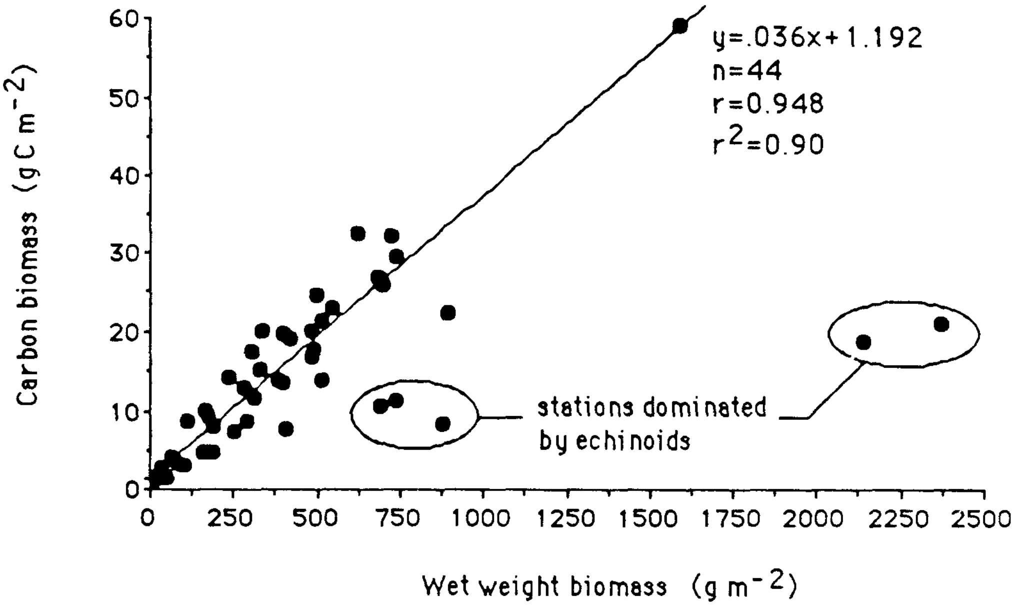


Figure 3.6. Wet weight biomass versus carbon biomass for benthic fauna at the same stations. The correlation does not include five stations that are dominated by the echinoid families Echinarachniidae and Strongylocentrotidae.

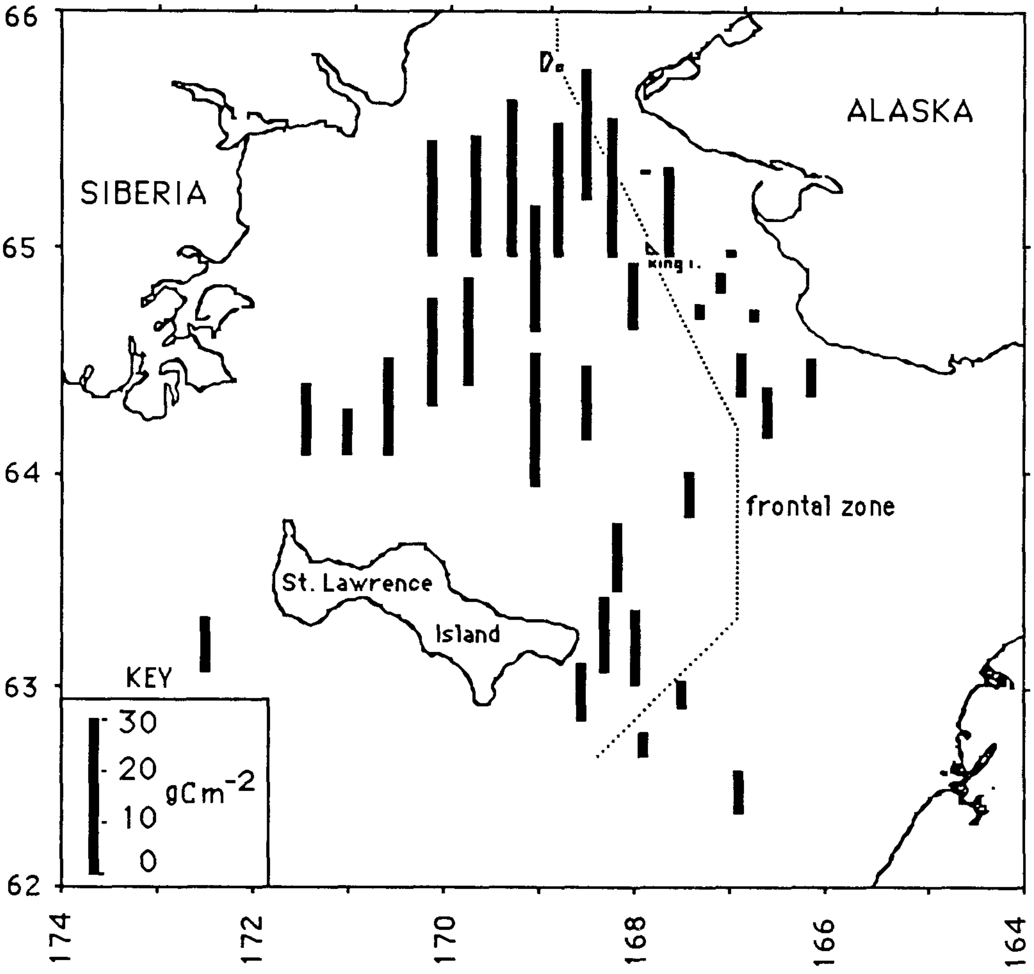


Figure 3.7. Distribution of biomass (g C m^{-2}) of benthic fauna in the Chirikov Basin and surrounding areas in the northern Bering Sea. The frontal zone separates Bering Shelf/Anadyr water in the west from Alaska Coastal water in the east.

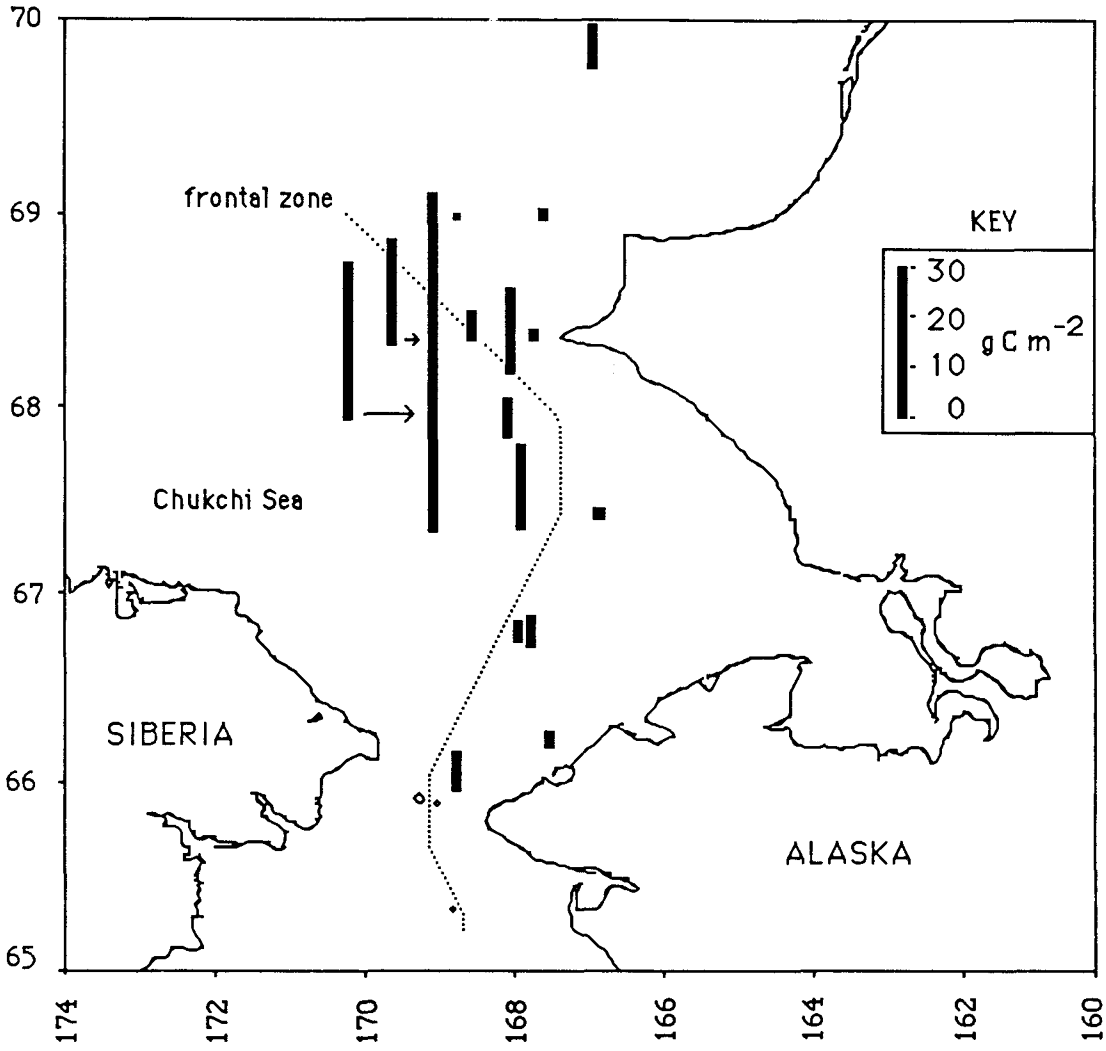


Figure 3.8. Distribution of biomass (g C m^{-2}) of benthic fauna in the Chukchi Sea. The frontal zone separates Bering Shelf/Anadyr water in the west from Alaska Coastal water in the east.

Table 3.5. Mean benthic biomass for Bering Shelf/Anadyr and Alaska Coastal water masses (number of stations sampled given in parentheses and s.d.=standard deviation).

	Water Mass			
	Bering Shelf/Anadyr		Alaska Coastal	
Year	Mean benthic biomass (g C m^{-2})	s.d.	Mean benthic biomass (g C m^{-2})	s.d.
1984	19.26 (11)	7.84	4.51 (4)	3.80
1985	20.86 (14)	11.91	6.20 (15)	5.57
1986	20.44 (2)	16.86	9.43 (3)	8.90

Table 3.6. Mean benthic biomass for all stations in the northern Bering and Chukchi Seas according to water mass (number of stations sampled given in parentheses and s.d.=standard deviation).

	Water Mass			
	Bering Shelf/Anadyr		Alaska Coastal	
Location	Mean benthic biomass ($g\ C\ m^{-2}$)	s.d.	Mean benthic biomass ($g\ C\ m^{-2}$)	s.d.
Northern Bering Sea	19.10 (21)	6.20	6.19 (12)	5.99
Chukchi Sea	23.82 (6)	19.42	6.45 (10)	5.70
COMBINED	20.15 (27)	10.30	6.31 (22)	5.72

Table 3.7. Mean abundance and biomass for individual cluster groups located in the Bering Shelf/Anadyr (BS/A) and Alaska Coastal (AC) water masses.

Cluster Group	Number of stations	Water mass	Abundance no.m^{-2}		Biomass			
					gm^{-2}		g Cm^{-2}	
			Mean	s.d.	Mean	s.d.	Mean	s.d.
I	11	BS/A	6940	3131	497.27	191.65	22.20	6.20
II	2	both	2529	338	245.72	225.46	8.27	7.12
III	7	BS/A	5365	4286	590.66	470.71	24.21	16.92
IV	2	BS/A	2048	1623	284.44	147.65	11.34	3.27
V	3	AC	1947	1011	214.49	189.15	4.58	2.88
VI	3	both	1595	517	382.26	276.62	8.55	1.65
VII	3	AC	4193	1719	380.64	436.88	5.25	2.80
VIII	4	AC	1367	792	481.90	290.97	15.39	6.44
IX	3	AC	641	218	83.92	75.72	4.32	4.84
X	1	AC	7770	-	35.32	-	1.95	-
XI	3	AC	718	707	55.06	47.59	1.96	1.01
XII	1	AC	140	-	42.00	-	2.01	-
XIII	1	BS/A	463	-	2143.76	-	18.57	-
XIV	2	BS/A	1684	178	631.16	160.77	12.47	1.70
XV	1	BS/A	313	-	549.60	-	22.90	-
XVI	1	AC	193	-	71.28	-	3.86	-
XVII	1	BS/A	188	-	2376.97	-	20.92	-

(I, III, XIII, XV, and XVII) are all located in the central region of the water mass and range from 18.57-24.21 g C m^{-2}. Cluster Groups XIII and XVII (each individual stations) located in BS/A water are notable for their extremely high mean wet weight biomass (Table 3.7). The dominant fauna (both in abundance and biomass) in these cluster groups was the sand dollar F. Echinarachniidae (*Echinarachnius parma*; Grebmeier unpubl. data; Appendix I). *E. parma* made up 72% of the abundance and 88% of the biomass in Cluster Group XIII , whereas it made up 63% of the abundance and 80% of the biomass in Cluster Group XVII. The remaining groups IV and XIV range from 11.34-12.47 g C m^{-2} and are located at the edge of the water mass in the BS/A and AC frontal zone.

Cluster Groups II and VI , which contain stations in both water masses, have biomass values ranging from 8.27-8.55 g C m^{-2}. Within these groups, two stations are located in BS/A water. Station 59148 (in Cluster Group II) is southwest of St. Lawrence Island and has a benthic biomass of 13.30 g C m-^{2} and station 74024 (in Cluster Group VI) in the Chukchi Sea has a biomass of 7.86 g Cm^{-2}.

The majority of the cluster groups under the AC water mass (V,VII,VIX,X,XI,XII,XVI) have low biomass, ranging from 1.95-5.25 g C m^{-2}. The exception is Cluster Group VIII, which is composed of four stations that occur near the front between BS/A and AC water. These stations range from 8.49-22.33 g Cm^{-2}. Cluster Groups II and VI, which contain stations in both water masses, range from 8.27-8.55 g C m^{-2}. However, station 74003, in Cluster Group II, occurs in AC water and has a biomass of only 3.23 g C m^{-2}. Stations 59150 and 73001 occur in Cluster Group VI under AC water and have a biomass range of 7.36 to 10.44 g C m^{-2}. These two latter stations occur in the frontal zone between BS/A and AC water.

Biomass of Combined Cluster Groups

The mean biomass for the 10 Combined Cluster Groups followed the same trends as the individual group biomass measurements (Table 3.8). Combined Groups A, H, and J all occurred in BS/A water and their biomass ranged from 15.95 to 20.59 g C m^{-2}.

Combined Groups C,D,E,F, and I all occurred in AC water and had values ranging from 1.95 to 15.39 g C m^{-2}. The highest values are for Cluster Group VIII, with the remaining four combined groups having values ranging from 1.95 to 5.25 g m^{-2}. Combined Groups B and G ranged from 5.29-6.57 g C m^{-2}. A majority of the stations in these two groups were located in AC water.

DISCUSSION

Water mass characteristics have been used previously to delineate faunal boundaries since they can influence dispersal of planktonic larval stages (Ekman 1953; Thorson 1957). Stewart et al. (1985) investigated benthic macrofaunal groupings using similarity analyses on the Canadian continental shelf and slope and determined that they corresponded with major water mass and temperature regimes in the area. However, they did not investigate the influence of overlying water mass productivity on benthic faunal abundance and biomass. Stoker (1978 and 1981) showed that major faunal groups in Bering and Chukchi Seas correlated most highly with sediment grain size and temperature, although neither primary production nor phytoplankton biomass were investigated. The distribution of faunal groups due to substrate preference is influenced both by larval and adult substrate requirements (Wilson 1953; Gray 1981).

Stoker (1978) determined faunal groupings for this area based on data collected from 1970-1974 (both summer and winter). These faunal groupings correspond in general location and composition to those groupings found here, although the sampling was 10-14 years earlier (Figure 3.9 and Table 3.9). Stoker's Cluster Group (SCG) I is similar to Cluster

Table 3.8. Mean abundance and biomass for combined cluster groups located in Bering Shelf/Anadyr (BS/A) and Alaska Coastal (AC) water masses.

Combined Cluster Group	Number of stations	Water mass	Abundance		Biomass			
			no. m^{-2}		g m^{-2}		gC m^{-2}	
			mean	s.d.	mean	s.d.	mean	s.d.
A (I,II,III,IV)	22	BS/A	5593	3620	484.77	311.99	20.59	11.46
B (V,VI)	6	both	1771	744	298.38	231.00	6.57	3.02
C (VII)	3	AC	4193	1719	380.64	436.88	5.25	2.80
D (VIII)	4	AC	1367	792	481.90	290.97	15.39	6.44
E (IX)	3	AC	641	218	83.92	75.72	4.32	4.84
F (X)	1	AC	7770	-	35.32	-	1.95	-
G (XI,XII,XIII)	5	both	552	562	470.19	936.18	5.29	7.46
H (XIV,XV)	3	BS/A	1227	802	603.97	123.05	15.95	6.14
I (XVI)	1	AC	193	-	71.28	-	3.86	-
J (XVII)	1	BS/A	188	-	2376.97	-	20.92	-

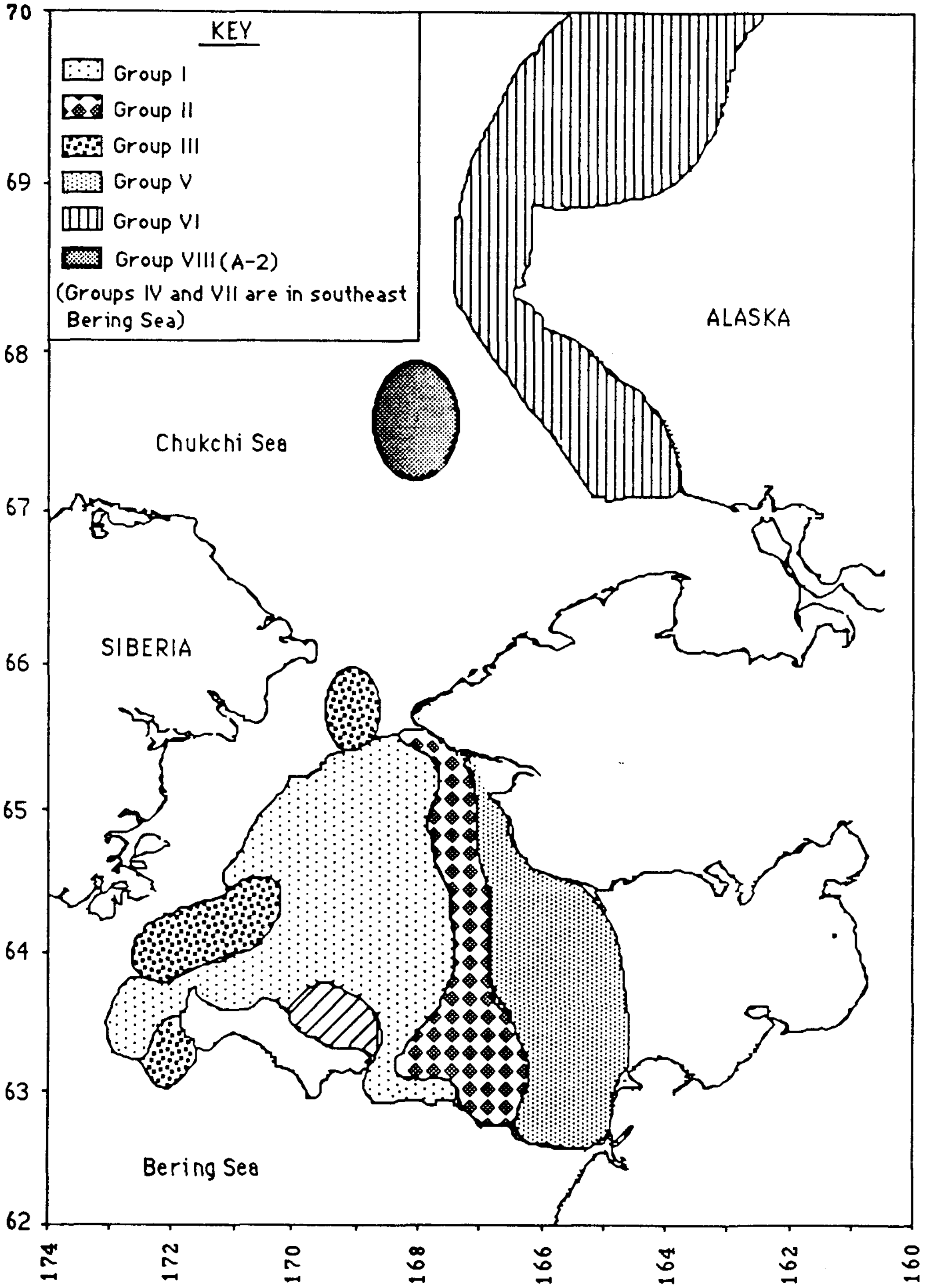


Figure 3.9. Station cluster groups as determined by benthic faunal similarities on the Bering/Chukchi shelf (based on Stoker 1978).

Table 3.9. Comparison of cluster groups from Stoker's collections (1970-74) and present study (1984-1986) in Bering Shelf/Anadyr (BS/A) and Alaska Coastal water masses.

Source: Stoker 1978					Source: This study				
Cluster Group (no. of stations)	Water mass	Benthic biomass (gC m^{-2}) Mean	s.d.	Dominant faunal families	Cluster Group (no. of stations)	Water mass	Benthic biomass (gC m^{-2}) Mean	s.d.	Dominant faunal families
I (28)	BS/A	23.1	14.3	Ampeliscidae Tellinidae Astartidae	I (11)	BS/A	22.2	6.2	Ampeliscidae Isaeidae Tellinidae
II (33)	AC	4.4	1.4	Tellinidae Echinarachniidae	VII, VIII, X, XI (11)	AC	6.1	6.4	Tellinidae Echinarachniidae Isaeidae
III (10)	BS/A	14.1	11.3	Ophiuridae Strongylocentrotidae Pectinariidae	XIV (2)	BS/A	12.5	1.7	Ophiuridae Strongylocentrotidae
V (20)	AC	7.5	8.6	Cardiidae Oweniidae Sternaspidae Amphiuridae Gorgonocephalidae	VI (3)	both	8.6	1.7	Nuculidae Nepthyidae Cirratulidae Echinarachniidae Echiuridae
VI (12)	AC	11.1	7.6	Astartidae Ophiuridae Golfingiidae Maldanidae	V, VIII, IX, XVI (11)	AC	8.4	7.1	Cardiidae Tellinidae Ophiuridae Golfingiidae Maldanidae
VIII -A2 (4)	BS/A	26.6	14.8	Tellinidae Nuculidae Nuculanidae Haustoriidae	III (7)	BS/A	24.2	16.9	Tellinidae Nuculidae Ampeliscidae Isaeidae

Group I in the present analysis (Figure 3.4) and both occurred in BS/A water. Most of the same dominant animals (based on ranked abundance and biomass) were present, amphipods in the Family (F.) Ampeliscidae and bivalves in the F. Tellinidae. However, in contrast to this study, Stoker found that bivalves in the F. Astartidae were dominant in SCG I, whereas here amphipods in the F. Isaeidae were dominant in Cluster Group I. This difference could be due to sampling techniques, since Stoker utilized a 3 mm screen mesh during sieving whereas a 1 mm mesh was used in this study. Isaeid amphipods are 1-5 mm long and many of these could have passed through a 3 mm screen. Thus, although biomass differences would be negligible between the two studies due to the small size of these animals, the relatively larger numbers collected on the 1 versus 3 mm screen could influence the cluster analysis results. The biomass for SCG I was 23.1 ± 14.3 g C m^{-2} compared to 22.2 ± 6.2 g C m^{-2} for Cluster Group I in the present study.

SCG II in AC water, dominated by bivalves (Tellinidae) and sand dollars (Echinarachniidae) had a biomass of 4.4 ±1.4 g C m^{-2}. The same fauna were dominant in Cluster Groups VII (biomass=5.3 ± 2.8 g C m^{-2}) and XI (biomass=2.0 ± 1.0 g C m-^{2}). In addition, isaeid amphipods were dominant in the present study.

SCG III was located within and northeast of Anadyr Strait and in Bering Strait, was dominated by polychaetes (Pectinariidae), brittle stars (Ophiuridae), and sea urchins (Strongylocentrotidae), and had a biomass of 14.1 ± 11.3 g C m^{-2}. Cluster Group XIV in the present study, located northeast of Anadyr Strait, was dominated by similar fauna (except the polychaete family) and had a biomass of 12.5 ± 1.7 g C m^{-2}.

SCG V under AC water in the northeastern Bering Sea varied the most from stations analyzed in Cluster Group VI (present study). Whereas bivalves (Cardiidae), polychaetes (Oweniidae and Sternaspidae) and ophiuroids (Amphiuridae and Gorgonocephalidae) were dominant in SCG V, other families of bivalves (Nuculidae), polychaetes (Nephtyidae and Cirratulidae), sand dollars (Echinarachniidae) and echiurids (Echiuridae) were dominant in Cluster Group VI. SCG V had a biomass value of 7.5 ± 8.6 g C m^{-2} compared to a biomass value of 8.6 ± 1.7 g Cm^{-2} for Cluster Group VI. Small sample size in this study, along with patchiness in water mass location, may have had an influence on the variability in faunal composition seen between the two groups.

SCG VI along the Alaska coastline in the southern Chukchi Sea is composed of polychaetes (Maldanidae), sipunculids (Golfingiidae), bivalves (Astartidae), and brittle stars (Ophiuridae), and had a biomass of 11.1±7.6 g C m^{-2}. Cluster Groups V, VIII, IX, and XVI occurred in the same area under AC water and were dominated by similar polychaetes (Maldanidae), sipunculids (Golfingiidae), brittle stars (Ophiuridae), and other bivalve families (Cardiidae and Tellinidae). These cluster groups had a combined mean biomass of 8.4 ± 7.1 g C m^{-2}. This particular group included stations occurring in both the northern Bering and Chukchi Seas located at the frontal zone.

Subgroup A2 in SCG VIII is located north of Bering Strait and is composed of bivalves (Tellinidae, Nuculidae, and Nuculanidae,) and amphipods (Haustoriidae) and had a biomass of 26.6 ± 14.8 g C m^{-2}. In comparison, Cluster Group III is located in the same area and was dominated by bivalves in the families Nuculidae and Tellinidae and amphipods in the families Ampeliscidae and Isaeidae. Stoker's cluster group biomass was 26.6 ± 14.8 g C m^{-2} compared to 24.2 ± 16.9 g C m^{-2} for the present study.

No major change in faunal structure was found between this study and Stoker's work from over 10 years ago. In addition, faunal biomass for similar faunal groups is not significantly different between the two studies (Wilcoxon test, $p>0.10$). These results suggest a stable system occurs in this region, both in sediment structure, food supply, and trophic relationships. The highest biomass groups occurred in BS/A water, with the lowest in

AC water for both studies, suggesting that a high primary production produces a persistent food supply which influences benthic standing stock in the region. In addition, there was no significant difference in mean benthic biomass between years in either of the water masses for the present study (Table 3.5). This is a striking result in the context of the variance within individual cluster groups in the area, the inherent variability in benthic studies, the differences in water mass primary production, and the variability in sample size, from 2 to 15 stations in any year over the length of this study. This work concurs with Stoker's conclusion that the northern Bering and Chukchi Seas are detritus-based systems, influenced by variability in water column productivity and current regimes. Both studies suggest that sediment regimes have a qualitative influence on community structure, with the present study providing additional evidence for a quantitative influence of primary production on benthic standing stock.

Although not statistically significant, the fact that mean benthic biomass was relatively constant between years in BS/A water compared to an increasing biomass in AC water over the same three years (Table 3.5), suggests that further studies are warranted in AC water to determine if this trend in increasing biomass is real. The quality of organic carbon in the surface sediments in BS/A water is constant between years (low C/N), whereas there is a significant difference between years in surface sediment organic carbon quality in AC water (Chapter 2). Terrestrial organic matter input from local rivers varies seasonally and annually in this region and this material remains in the coastal water mass surface sediments, as suggested by combined C/N and $\delta^{13}C$ results (Parker and Scalan 1986 and 1987; Chapter 2). Assuming a relatively persistent marine food supply in both BS/A and AC waters, variations in benthic biomass in the AC system could result from interannual variations in terrestrial organic carbon inputs. A more detailed and repetitive sampling strategy is needed in the AC system to investigate this hypothesis as well as to investigate the effects of predator populations and temperature variations on benthic faunal structure and biomass.

Faunal composition for stations located in the BS/A water benthic can change with sediment grain size in both the northern Bering and Chukchi Seas (Stoker 1978 and this study). An example of the relationship between faunal composition and sediment grain size is the Combined Cluster Group A which is dominated by four benthic families, Ampeliscidae Isaeidae, Tellinidae and Nuculidae (Figure 3.5; Table 3.4). In the two major cluster groups that make up this Combined Group A, I and III (Figure 3.4; Table 3.2), the modal surface sediment grain size and dominant co-occurring fauna within all cluster group stations change from the northern Bering Sea (Cluster Group I, fine-very fine sand sediment type) to the Chukchi Sea (Cluster Group III, very fine sand and silt and clay sediment type). The amphipod families Ampeliscidae, Isaeidae and Phoxocephalidae are dominant in 100% of the stations in Cluster Group I compared to a 100% occurrence of the amphipod families Isaeidae and Haustoridae in all stations in Cluster Group III, with the amphipod family Phoxocephalidae dropping to 86% occurrence. Bivalves (Nuculidae) occur in 55% of the stations in Cluster Group I, whereas they increase to 100% occurrence in Cluster Group III in the Chukchi Sea. Similarly, amphipods (Ampeliscidae) occur in 100% of the stations in Cluster Group I and decrease to 86% of the stations in Cluster Group III. Bivalves (Tellinidae) occur in 82% of the stations in Cluster group I, decreasing to 71% of the stations in Cluster Group III. Polychaetes (Capitellidae) occur in 55% of the stations in Cluster Group I, increasing to 71% occurrence in Cluster Group III. All these fauna are primarily surface detritus feeders, yet the group that becomes dominant appears to be influenced by grain size composition.

From 1984-1986 integrated chlorophyll a was determined (Appendix B). The results show that the highest integrated chlorophyll a occurs in BS/A waters in both the northern Bering and Chukchi Seas (Figure 3.10). There is a significant positive correlation between integrated chlorophyll a and both benthic faunal abundance ($r=0.568$, $p<0.01$) and biomass ($r=0.691$, $p<0.01$) utilizing all stations data (Table 3.10). However, the relatively low correlation suggests a high variability in the data, possibly resulting from changes in water column productivity.

A significant relationship is indicated between the quality of organic matter in the sediments, characterized by C/N ratios, and benthic biomass (Figure 3.11), based on a Spearman's rho test, stated as a 1-tailed test. Benthic biomass is higher at stations where surface sediment C/N ratios are lower. The results suggest that the availability of high quality organic matter to benthic populations (low C/N ratios; Chapter 2) is correlated to high benthic biomass. The distribution in quality of labile organic matter in the surface sediments (Figure 2.7) is generally the same as the distribution of highest benthic standing stock (Figures 3.7 and 3.8). In addition, these areas coincide with regions of high integrated chlorophyll a (Figure 3.10). Benthic biomass was also positively correlated with water column depth ($r=0.405$, $p=0.05$) and negatively with surface sediment C/N ratios ($r=-0.428$, $p=0.05$; Table 3.10). Increased water column depth was correlated with lower surface sediment C/N ratios, both of which are characteristic of BS/A water (Chapter 2).

A 3-4 fold greater mean benthic biomass occurs in BS/A compared to AC water in the northern Bering and Chukchi Seas (Table 3.6). This information parallels the 5 fold greater primary production measured in BS/A compared to AC water. These combined results support the hypothesis that variation in the overlying primary productivity in the water mass influences benthic biomass. A high variability around the mean occurs for the Chukchi Sea stations (Table 3.6); this is primarily the result of data from three stations located in this water mass. These stations are: 1) 74010, biomass=58.95 g C m^{-2}, sediment type=very fine sand;

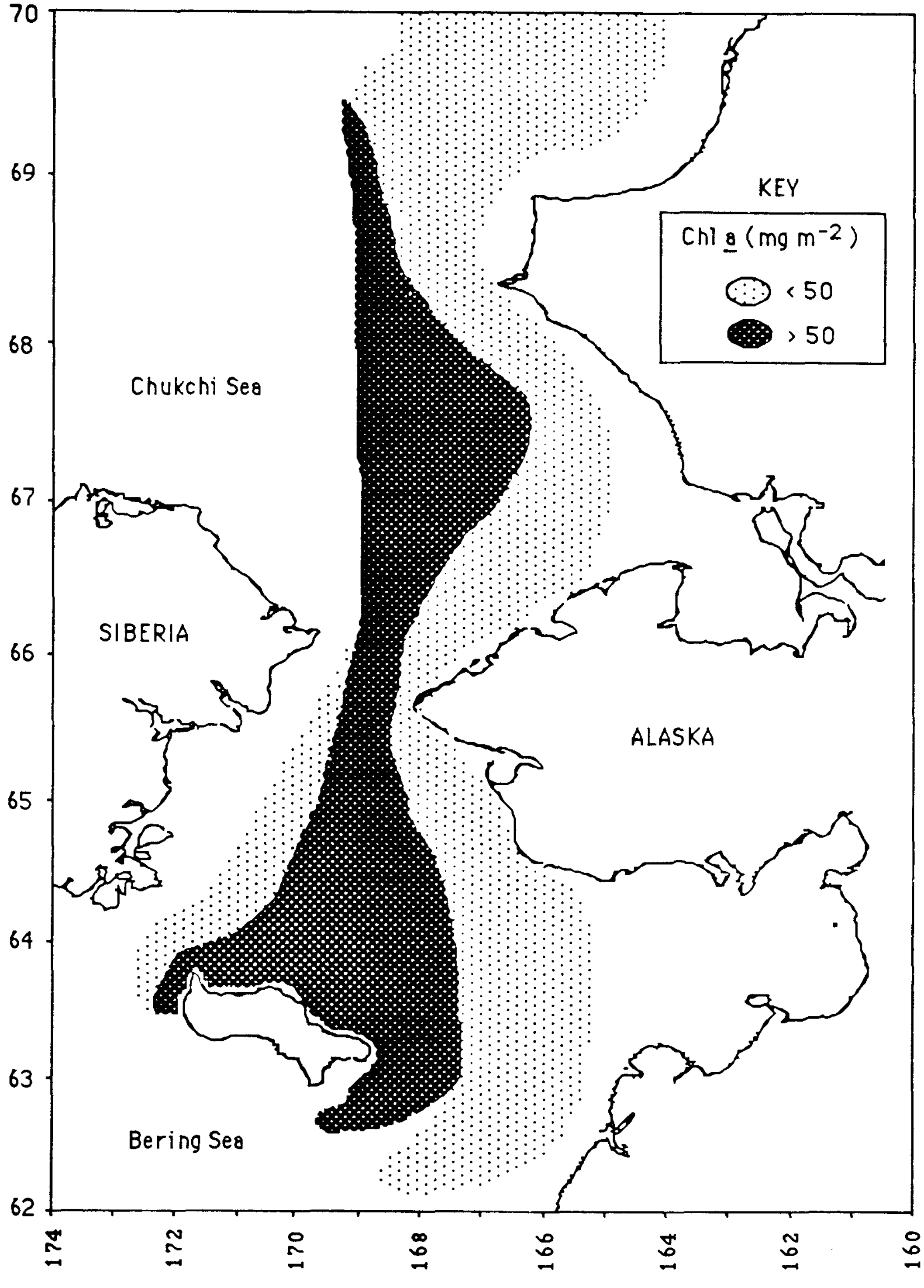


Figure 3.10. Distribution of integrated chlorophyll *a* (Chl *a*) during July through September 1985 and 1986 (ISHTAR Data Report 1986, 1987; Springer and McRoy 1986 and unpubl. data; this study).

Table 3.10. Pearson product-moment correlation matrix between environmental variables and abundance and biomass of benthic fauna in the northern Bering and Chukchi Seas. Key: n=number of stations, r=correlation coefficient, p=level of significance, ns=no significance.

	Environmental variable						
	Temperature (°C)	Salinity (‰)	Depth (m)	Bottom Chl a ($mg\ m^{-3}$)	Integrated Chl a ($mg\ m^{-2}$)	Sediment grain size (phi)	Surface sediment C/N
Abundance (no. m^{-2})	n=46 r=-0.128 p=ns	n=45 r=0.075 p=ns	n=47 r=0.116 p=ns	n=47 r=0.338 p=ns	n=34 r=0.568 p=0.01	n=33 r=-0.056 p=ns	n=38 r=-0.258 p=ns
Biomass (g C m^{-2})	n=46 r=-0.214 p=ns	n=45 r=0.075 p=0.241	n=47 r=0.405 p=0.05	n=47 r=0.505 p=0.01	n=34 r=0.691 p=0.01	n=33 r=0.007 p=ns	n=38 r=-0.428 p=0.05

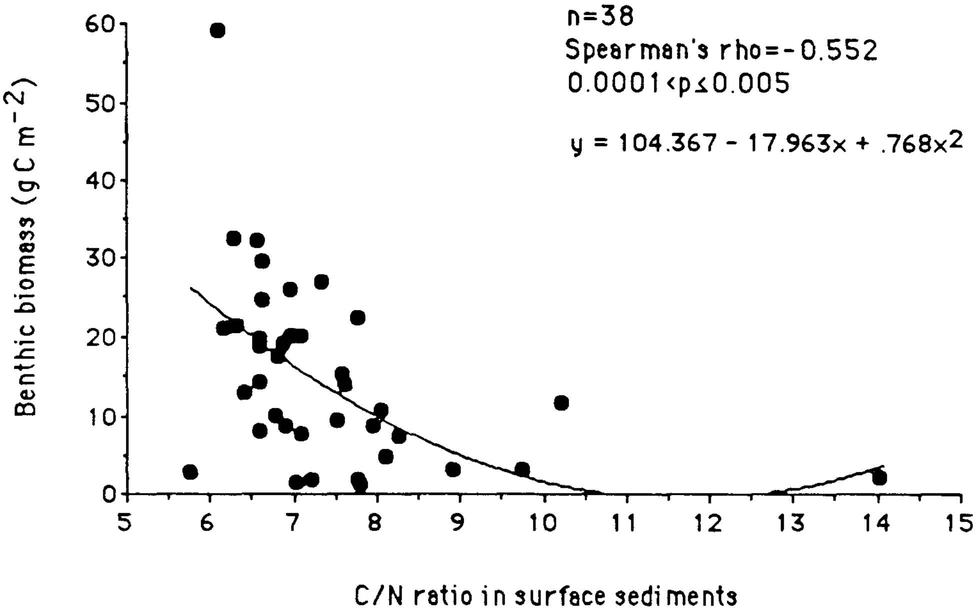


Figure 3.11. Relationship between surface sediment C/N ratios and benthic biomass.

2) 74024, biomass=7.86 g C m^{-2}, sediment type=very fine sand; 3.) 85071, biomass=8.52 g C m^{-2}, sediment type=very fine sand and silt and clay. The small sediment grain size type at these stations suggests a reduction in current and deposition of phytodetritus to the benthos. The highest biomass values occurred at Station 74010 in the Chukchi Sea over the 3 year study period, suggesting high organic matter input to the benthos in this area. Sediment porewater measurements for Stations 74024 and 85071 also show high sulfide levels in these sediments (Blackburn and Henriksen 1986 and 1987), such that chemical toxicity could have a negative impact on benthic populations at these stations.

Marine mammals are important predators on benthic fauna on the Bering/Chukchi shelf. Aprroximately 15,000 gray whales and 200,000 Pacific walrus migrate seasonally through the area (Nerini 1984; Fay et al. 1984). The major feeding areas in the study region for these benthic-feeding marine mammals are the high benthic biomass areas of the Chirikov Basin and Chukchi Sea (Fay et al. 1977 and 1984; Nelson and Johnson 1987; Nerini 1984). Walruses also feed near the Alaska coastline on deep-dwelling bivalves in regions where benthic biomass levels were low in the present study. Since Pacific walrus are known to feed under both water masses over the whole study area (B. Fay, pers. comm.), the relative difference between mean benthic biomass observed under each water mass is signficiant in itself in spite of the inability of the sampling gear to collect the deep-dwelling bivalves. The presence of large populations of benthic-feeding marine mammals emphasizes the importance of a productive and reliable invertebrate food source to maintain their populations which, in turn, is dependent on a seasonally persistent food supply.

The California gray whale feeds throughout the summer in the Chirikov Basin and Chukchi Sea and their activities could have some impact on benthic population structure. It has been suggested that gray whales influence sediment resuspension in the area through their feeding activities which may enhance secondary production by maintaining a preferable sand habitat for their amphipod food source and enhancing production by opening up space for juvenile ampeliscid amphipods to settle (Nelson and Johnson 1986).

A total of 11 dominant epifaunal species are known for the southeast and northeast Bering Sea and southeast Chukchi Sea. Of these, 7 species (the gastropod *Neptunea heros,* the sea stars *Asteria amurensis, Evasterias echinosoma, Leptasterias polaris acervata, Lethasterias nanimensis*, the sea urchin *Strongylocentrotus droebachiensis,* and the basket star *Gorgonocephalus caryi*) had their highest biomass in the northeast Bering and southeast Chukchi Sea, suggesting the presence of a major food source for these animals. Predatory sea stars (dominated by *Asterias amurensis)* comprise 45-68% of the epifaunal biomass in the northeastern Bering and southeastern Chukchi Seas (Jewett and Feder 1981). Bivalves are a major prey of sea stars, which are widely distributed in the study area (Stoker 1978 and 1981; Jewett and Feder 1981; McDonald et al. 1981; this study). The reduction of fish competitors, due to low temperatures, probably influences the high abundance of epifaunal populations in the area (Jewett and Feder 1981). The effect of sea stars on benthic community structure has yet to be determined for this area.

In summary, the high standing stock of benthic fauna in the northern Bering and Chukchi Sea is correlated with high primary production and deposition of phytodetritus, along with high quality organic matter in surface sediments in the Bering Shelf/Anadyr water. Although a major spring bloom occurs over the whole area, the low phytoplankton production in the nutrient-depleted Alaska Coastal water is correlated with decreased benthic biomass and lower quality organic carbon in surface sediments. Sediment grain size influences community structure on a small scale, with food availability having a larger scale, direct influence on overall benthic standing stock. Benthic faunal structure and biomass have not changed significantly in the area over the last 10 years, suggesting a persistent quantity and quality of phytodetrital food supply has a positive impact on stability in the system.

CHAPTER 4. BENTHIC CARBON CYCLING: III. BENTHIC METABOLISM

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 and Peterson 1979; Deuser et al. 1981; Davies and 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). The stimulation of enhanced food supply on benthic biomass and growth is well documented (Rowe 1969; Mills 1975; Parsons et al. 1977; Josefson 1985; Rudnick et al. 1985). This study addresses the hypothesis that the primary production in the overlying water masses in the northern Bering and Chukchi Seas has a major influence on benthic metabolism and carbon cycling. Sediment oxygen uptake and organic carbon mineralization rates can provide an indication of the quantity and quality of organic matter reaching the benthos and, therefore, reflect carbon flux differences in each water mass.

Sediment oxygen uptake rates provide information on aerobic utilization of organic carbon in sediments and have been shown to increase with increased carbon flux to sediments (Hargrave 1969 and 1973; Davies 1975; Pamatmat 1975; Deuser and Ross 1980; Suess 1980; Nixon 1981; Smith et al. 1983; Davies and Payne 1984). Although useful in estimating community metabolism in sediments, oxygen respiration rates underestimate total sediment metabolism since they do not measure directly anaerobic processes (Hargrave 1969; Pamatmat 1971 and 1977; Davies 1975; Patching and Raine 1983), thus requiring measurement of other oxidants, such as nitrate and sulfate. Higher temperature is known to enhance benthic metabolism (Hargrave 1969; Davies 1975; Pamatmat 1975; Smith 1978), but temperature and food supply are often correlated and, therefore, hard to separate. Davies (1975) and Wassman (1984) have shown that the amount of nutritious, labile organic material supplied to the benthos, rather than temperature, enhanced sediment oxygen uptake rates in various fjord ecosystems. Davies (1975) concluded that food supply regulated benthic community metabolism in a Scottish fjord. Pamatmat and 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 suggested that this variance was due to seasonal changes in biological activity responding to a variable organic matter supply. Data on microbial respiration in Alaskan marine waters and sediments indicate no direct cause and effect relationship with temperature or salinity (Griffiths et al. 1984). Griffiths et al. (1984) concluded that the quality of organic matter could best explain differences in microbial respiration rates.

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). Food supply, low temperatures, and hydrodynamic forces that favor food uptake and respiration are parameters determined to enhance growth and production of marine benthic bivalves in West Greenland (Petersen 1978). Work in Denmark has shown that the tube-building amphipod *Ampelisca macrocephala* (F. Ampeliscidae), which is also dominant in the northern Bering and Chukchi Seas (Chapter 3), experienced periods of growth and reproduction which were closely correlated to periods of high primary productivity, with temperature an unimportant governing factor (except at high temperatures; Kanneworff 1965). These amphipods feed primarily on bottom deposits (Thomson 1983) and an enrichment of this food source (such as phyto-and zoo-plankton detritus falling to the benthos) would increase the food value to the animals. Kanneworff

(1965) concluded that organic matter derived from phytoplankton was the essential food source for spring growth in *A. macrocephala*, and that food and feeding condition were the decisive factors regulating the life cycle of this animal. The growth of another amphipod *Pontoporeia* spp. (F. Haustoriidae, which also occurs in the study area; Chapter 3), was directly dependent on food availability in the Baltic Sea (Elmgren 1978). Elmgren (1978) concluded that food availability, not predation, limited *Pontoporeai* populations. In the middle shelf of the southeast Bering Sea high benthic biomass and sediment oxygen consumption occur under high pelagic primary production, low water temperatures, and low pelagic grazing, indicating an enhanced carbon flux to the benthos (Iverson et al. 1979; Haflinger 1981; McDonald et al. 1981; Walsh et al. 1981; Walsh and McRoy 1986).

The contribution of macrofaunal respiration to total sediment community metabolism varies with faunal abundance, species composition and season. Kemp and Boynton (1981) found macrofaunal respiration to be important in total benthic respiration measured in Chesapeake Bay, especially during the late spring and early summer months. Macrofaunal respiration can range from 20-45% of the total community respiration (Smith 1973; Pamatmat 1975; Gray 1981). There is a direct relationship between sediment oxygen respiration and nutrient regeneration (Zeitschel 1980; Smith et al. 1983; Boynton and Kemp 1985). Boynton and Kemp (1985) found high nutrient regeneration for the benthos in areas where productivity in the overlying water column was highest. Benthic nutrient regeneration can be a major source of ammonia in shallow coastal systems (Nixon et al. 1976; Zeitzschel 1980; Garber 1984).

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 and Yingst 1978; Aller 1977 and 1980; Hylleberg and Henriksen 1980). Ammonium flux can be high in coastal sediments due to polychaete or amphipod activities, either by direct ammonium excretion or stimulation of microbial processes in faunal burrow walls (Henriksen et al. 1980; Blackburn and Henriksen 1983). Various errant polychaete species, such as *Nereis spp.* and *Nephtys spp.*, can increase the rate of detritus oxidation (Hylleberg 1975; Briggs et al. 1979). Nixon et al. (1976) found that mats of the amphipod *Ampelisca spp.* can influence uptake and release of nitrate from the sediments, as well as enhancing ammonium output, depending on the overlying nutrient concentrations. In addition, bioturbation and irrigation can transport higher organic content surface sediments downwards into the sediment (Hargrave 1976; Fauchald and 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).

This chapter utilizes sediment oxygen uptake rates as indicators of variability in the quality and quantity of organic matter falling to the benthos. X-radiography of sediment cores, along with a limited data set on sediment nutrient flux rates, are used with benthic faunal abundance and biomass data to address potential bioturbation factors.

MATERIAL AND METHODS

Sediment samples were collected using either a HAPS 0.0133 m^2 benthic corer or a MK3 0.25 m^2 box corer. Subsamples were collected with 13 cm internal diameter, 26 cm long, PVC and acrylic cores (8 mm thick walls). Average sediment depth in the cores was 10-15 cm, with the remainder of the core overlain 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 without disturbing the sediments. 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 1-2 °C for an average 8-10 hours. 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 Alpha Helix Cruise 59 a YSI 49 oxygen electrode and meter were used.

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.). Sulfate reduction rates were obtained from Blackburn and Henriksen (1986). At these stations 15% of the measured sediment oxygen uptake rate was subtracted from the original value. It was assumed that this amount of oxygen was used to reoxidize sulfides and was not available for organic carbon mineralization. Organic carbon mineralization rates were estimated from the sum of known oxidants in the sediments, primarily oxygen and sulfate, since nitrate is relatively minor as an oxidant (H. Blackburn, pers. comm.). Oxygen is the major oxidant in sediments in the northern Bering Sea under all water masses (Blackburn and Henriksen 1986), 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 (Nixon et al. 1980).

Thin-section plexiglas boxes (2.5 cm x 16.0 cm x 28.0 cm) and large (13.0 cm diameter x 28.0 cm long) PVC cores were used to collect sediment at representative stations in each water mass and frozen for later laboratory analysis. Frozen sediment was extracted from the large cores and cut to 2-3 cm width slabs. Both frozen plexiglas boxes and sediment slabs were x-rayed to determine burrow structure. Minimum burrow surface area was determined for a representative core in the highly bioturbated zone of the BS/A 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 1-2 cm intervals and the fauna encountered were recorded to species level.

During Alpha Helix Cruise 85 (11-26 July 1986), six oxygen consumption cores were analyzed for ammonia and nitrate flux in collaboration with K. Henriksen (University of Aarhus, Denmark). Water samples (20-30 ml) were collected from the overlying core water with a syringe at the start and end of the 8-10 hour incubation period, frozen, and later analyzed by K. Henriksen on an autoanalyzer in the laboratory.

The parametric Pearson's product-moment correlation test was used to investigate correlations between mean oxygen uptake rates and environmental variables. A Mann-Whitney U-test was performed on the mean oxygen uptake values for stations in the BS/A and AC water masses to determine if there was a significant difference in rates between stations in the two water masses. In addition, a Kruskal-Wallis test was used to test for significant differences in oxygen uptake rates between years within each of the water masses. A statistical package, called StatView™ (Brain Power 1985), was used on a Macintosh™ computer for these analyses.

Each station designation presented in subsequent tables is composed of five numbers; the first two numbers designate the cruise, the second three numbers designate the actual station, e.g. 85-090 means Cruise 85-Station 090.

RESULTS

A total of 61 stations was occupied in the northern Bering and Chukchi Seas, 46 in Bering Shelf/Anadyr (BS/A) water and 15 in Alaska Coastal (AC) water, during 5 cruises on the R/V Alpha Helix (Figures 4.1a and b; Appendix A). The cruise dates were as follows: Cruise 59 (30 June-July 10 1984), Cruise 73 (25 July-10 August 1985), Cruise 74 (26 August-9 September 1985), Cruise 85 (11-26 July 1986) and Cruise 87 (14-24 August 1986).

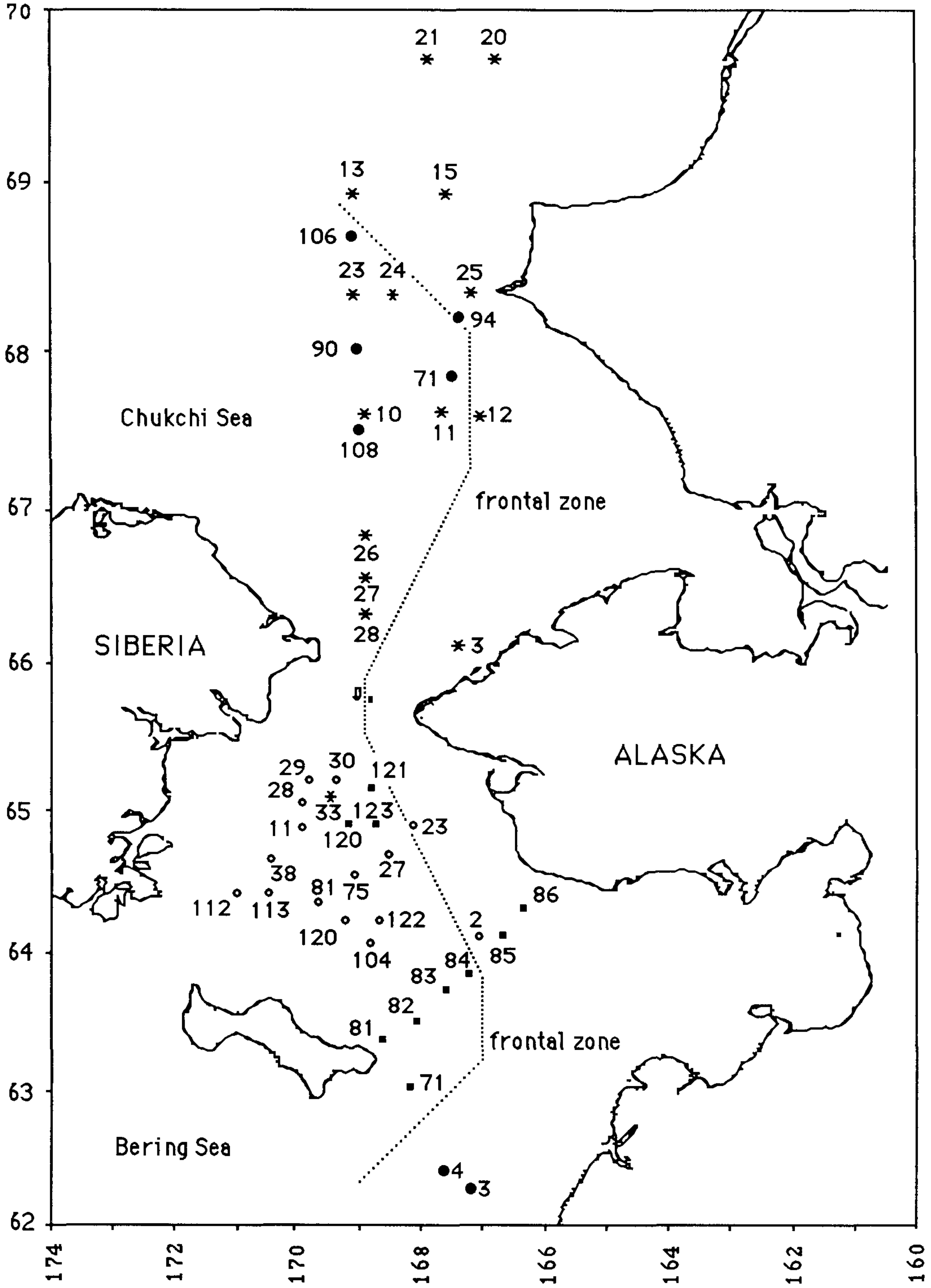


Figure 4.1a. Location of stations for benthic respiration experiments in the northern Bering and Chukchi Seas for cruises 59(▪), 73(∘), 74(∗), 85(●) and 87(+).

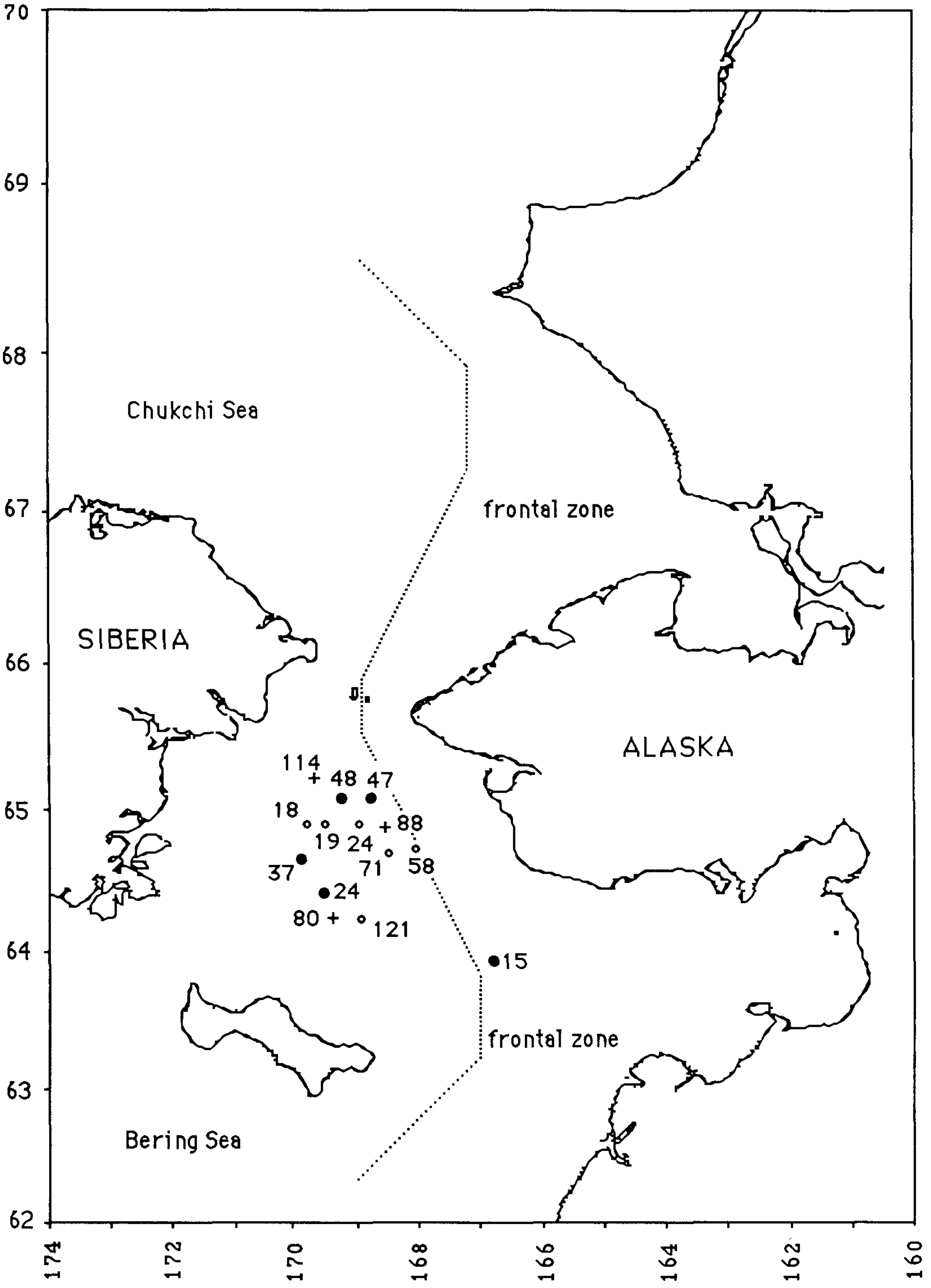


Figure 4.1b. Location of stations for benthic respiration experiments (Figure 4.1a Continued).

Oxygen uptake and carbon mineralization rates

Oxygen uptake rates were measured on duplicate sediment cores for 33 of the 46 BS/A stations and 11 of the 15 AC stations; the remainder were single core measurements (Appendix J). Before pooling average duplicate values with individual measurements, a Mann-Whitney test was performed on the data. The mean of the duplicate measurements and the single measurements for different stations in each water mass was not significantly different (BS/A: mean=19.17 mmol O_2 m^{-2} d^{-1}, ±10.63 s.d.; $p>0.25$; AC: mean=8.06 mmol O_2 m^{-2} d^{-1}, ±6.97 s.d.; $p>0.25$), thus all stations were subsequently included in the analysis.

Sediment oxygen uptake rates averaged 19.17 (n=46, ±10.63 s.d.) mmol O_2 m^{-2} d^{-1} in BS/A water and 8.06 (n=15, ±6.97 s.d.) mmol O_2 m^{-2} d^{-1} in AC water over the three year study (Table 4.1; Appendix J). There was a significant difference between values in the two water masses, based on a Mann-Whitney test, stated as a 1-tailed test, $p<0.001$. Stations under BS/A water had higher oxygen uptake rates than stations in AC water. The highest oxygen uptake rates occurred in stations in BS/A water both in the northern Bering and Chukchi Seas (Figure 4.2). In the northern Bering Sea high values (≥ 30 mmol O_2 m^{-2} d^{-1}) were measured northeast of St. Lawrence Island and in the central Chirikov Basin. Rates in the Chirikov Basin were over 40 mmol O_2 m^{-2} d^{-1} and were lowest (<10 mmol O_2 m^{-2} d^{-1}) in AC water stations and in regions of BS/A water northwest of St. Lawrence Island and north of Bering Strait. Significant interannual variability in sediment oxygen uptake rates occurred in BS/A water (Kruskal-Wallis, $p<0.005$), whereas there was no statistical difference between years in AC water (Kruskal-Wallis, $p>0.10$; Table 4.2).

Oxygen uptake rates underestimate total sediment metabolism in areas where sulfate

Table 4.1. Mean sediment oxygen uptake rates (n=number of observations, s.d.=standard deviation) in the northern Bering and Chukchi Seas according to water mass location.

	Water Mass			
	Bering Shelf/Anadyr		Alaska Coastal	
Location	Mean sediment oxygen uptake rate (mmol O_2 m^{-2} d^{-1})	s.d.	Mean sediment oxygen uptake rate (mmol O_2 m^{-2} d^{-1})	s.d.
Northern Bering Sea	19.30 (35)	10.96	10.89 (7)	6.74
Chukchi Sea	16.82 (11)	10.03	5.58 (8)	6.56
COMBINED	19.17 (46)	10.63	8.06 (15)	6.97

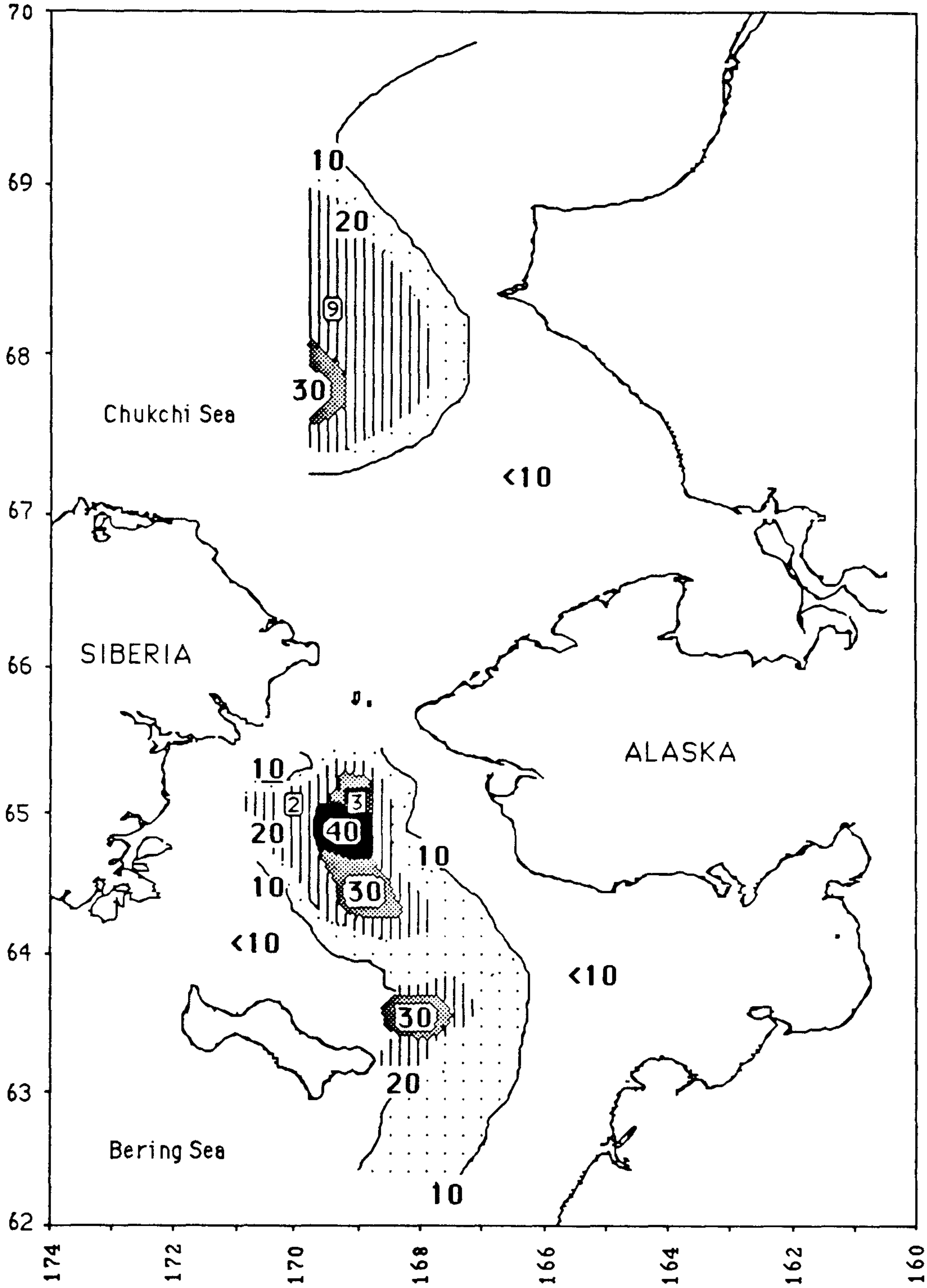


Figure 4.2. Distribution of mean sediment oxygen uptake rates (mmol $O_2 m^{-2} d^{-1}$) from July to September (1984-1986) in the northern Bering and Chukchi Seas. Boxed values indicate individual stations outside of contour interval.

Table 4.2. Mean (n) and s.d for sediment oxygen uptake rates from 1984-86 for the Bering Shelf/Anadyr (BS/A) and Alaska Coastal (AC) water masses.

		Water Mass			
		Bering Shelf/Anadyr		Alaska Coastal	
Year	Date	Mean sediment oxygen uptake rate (mmol O_2 m^{-2} d^{-1})	s.d.	Mean sediment oxygen uptake rate (mmol O_2 m^{-2} d^{-1})	s.d.
1984	30 June-July 10	24.72 (8)	10.15	9.70 (2)	0.33
1985	25 July-10 August	15.31 (18)	9.72	11.83 (3)	8.81
	26 August-9 September	9.46 (8)	5.76	3.60 (7)	3.74
	COMBINED	13.51 (26)	9.01	6.07 (10)	6.41
1986	11-26 July	26.50 (9)	5.59	13.57 (3)	9.01
	14-24 August	31.46 (3)	5.59	...	...
	COMBINED	27.54 (12)	5.78	13.57 (3)	9.01

reduction rates are high (Table 4.3). This was seen at stations (74-011 and 74-023) in the southern Chukchi Sea under BS/A water in late August and early September, where oxygen uptake rates only accounted for about 33% of the organic carbon mineralization. Only those stations (74-011 and 74-023) with high sulfate reduction rates and correspondingly high levels of free sulfide were corrected by 15% for chemical oxidation. A sulfate reduction rate was used when available for other stations (Table 4.3), but was only 1.0-2.0 mmol $SO_4^{=}$ m^{-2} d^{-1} in the northern Bering Sea, thus resulting in a 2-19% increase in organic carbon mineralization rates. Stations occupied in late August-early September (Cruise 74) under BS/A water in the southern Chukchi Sea showed a marked increase in sulfate reduction rates (3.0-8.5 mmol $SO_4^{=}$ m^{-2} d^{-1}), resulting in a 70% increase in organic carbon mineralization.

Mean organic carbon mineralization rate (Figure 4.3; Table 4.4) was 2-3 times higher in BS/A water (20.25 mmol C m^{-2} d^{-1}) compared to AC water (8.30 mmol C m^{-2} d^{-1}), which is comparable to the difference in values between mean sediment oxygen uptake rates (Table 4.1). The major difference between organic carbon mineralization and oxygen uptake rates is observed in an increase in organic carbon mineralization rates under BS/A water in the Chukchi Sea, where the mean organic carbon mineralization rate was 20.57 mmol C m^{-2} d^{-1} compared to a mean oxygen uptake rate of 16.82 mmol O_2 m^{-2} d^{-1} (which would give a carbon mineralization rate of 16.82 mmol C m^{-2} d^{-1} without including sulfate reduction). This 18% increase in organic carbon mineralization rate was due to sulfate reduction.

Using Pearson product-moment correlation coefficients, five variables, bottom salinity, temperature, density, chlorophyll a and sediment C/N ratio, have a significant relationship with oxygen uptake (Table 4.5; Appendix E). When analyzing all station data together, there

Table 4.3. Oxygen uptake, sulfate reduction and organic carbon mineralization rates (sulfate reduction rates from Blackburn and Henriksen 1986 and unpubl. data)*.

Location	Rates (mmol m^{-2} d^{-1})			
Station **	Oxygen uptake	Sulfate reduction	Organic carbon mineralization	% Aerobic respiration
74-010	14.16	3.0	20.16	70
74-011†	6.76†	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†	7.82 †	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

* Σ Organic carbon mineralized = O_2 uptake rate + 2 ($SO_4^=$ reduction rate)

** R/V Alpha Helix Cruise 74 (26 August-9 September, 1985)
R/V Alpha Helix Cruise 85 (11-26 July, 1986)

† corrected by 15% for chemical oxidation (after Blackburn and Henriksen 1986; Jørgensen 1982)

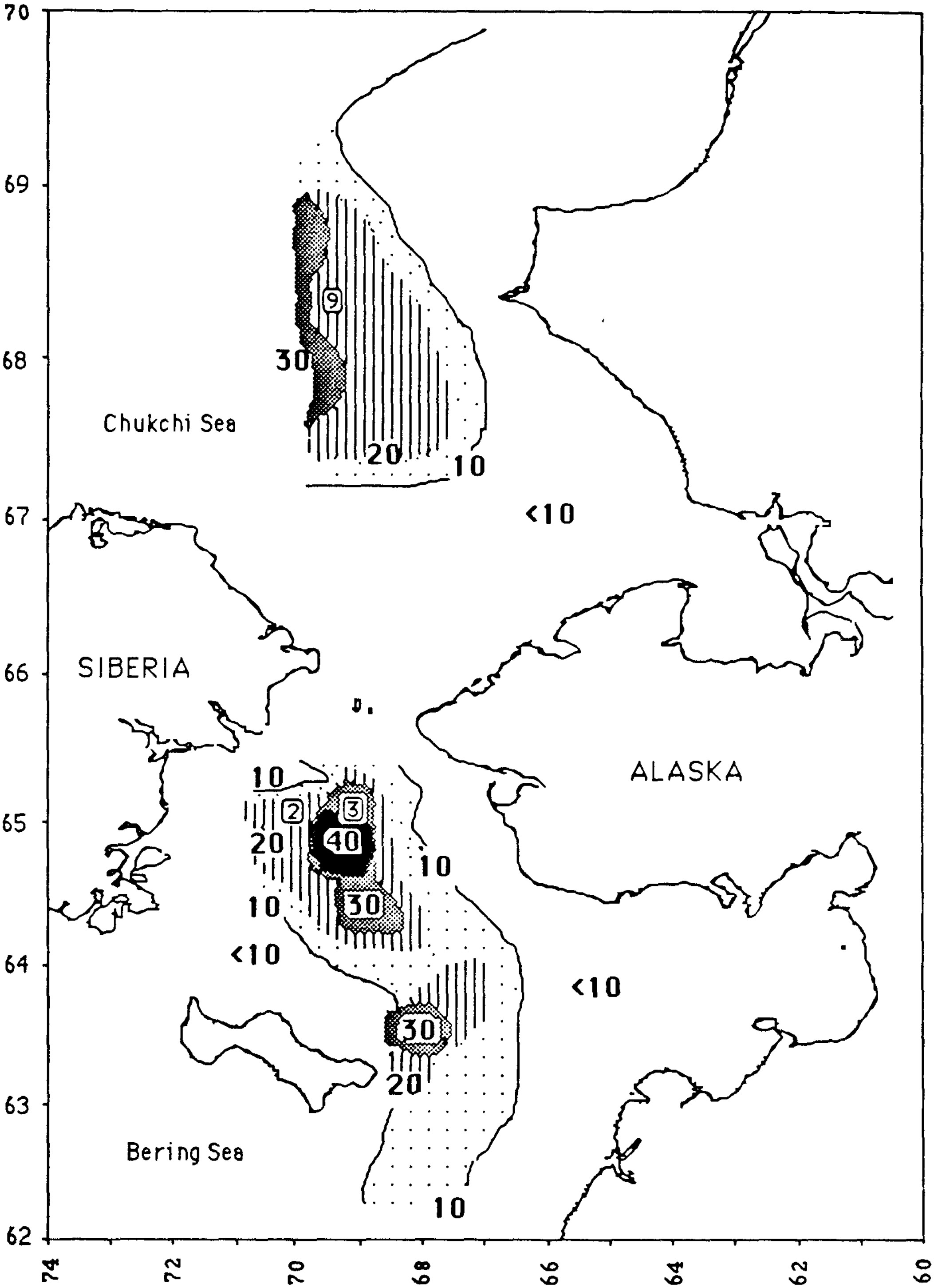


Figure 4.3 Distribution of mean benthic organic carbon mineralization rates (mmol C $m^{-2} d^{-1}$) from July to September (1984-86) in the northern Bering and Chukchi Seas. Boxed values indicate individual stations outside of contour interval.

Table 4.4. Mean (n) and s.d. for benthic organic carbon mineralization in the northern Bering and Chukchi Seas according to water mass type.

	Water Mass			
	Bering Shelf/Anadyr		Alaska Coastal	
Location	Organic carbon mineralization rate (mmol C m^{-2} d^{-1})	s.d.	Organic carbon mineralization rate (mmol C m^{-2} d^{-1})	s.d.
Northern Bering Sea	19.54 (35)	10.96	10.89 (7)	6.74
Chukchi Sea	20.57 (11)	9.74	6.03 (8)	6.95
COMBINED	20.25 (46)	10.51	8.30 (15)	7.07

Table 4.5. Correlations (Pearson product-moment) between sediment oxygen uptake and environmental parameters for all stations (see Appendix E for full correlation matrix).

Environmental parameter (number of observations)	Correlation coefficient r	Level of significance
Salinity (63)	0.263	0.05
Temperature (64)	-0.393	0.01
Density (sigma t) (62)	0.324	0.05
Bottom chlorophyll _a_ (66)	0.240	0.05
Surface sediment C/N (58)	-0.254	0.05

is a significant relationship between high oxygen uptake and low temperature, high salinity, and high sigma t (seawater density), all indicative of BS/A water. High sediment oxygen uptake correlates with high bottom chlorophyll a and low C/N ratios, which are also indicative of BS/A .

X-radiography

Cores were examined by X-radiography to investigate the vertical structure of sediments in water masses. Areas of highest bioturbation correspond to areas of high abundance and biomass in BS/A water (Figures 3.7 and 3.8). In the X-radiographs densely packed amphipod tubes of species in the F. Ampeliscidae (*Ampelisca macrocephala*) appear as thin, white vertical tubes extending 8-9 cm into the sediments at a highly bioturbated station (59-123, Figure 4.4); the large tube is an amphipod in the F. Aoridae (*Lembos arcticus*). Both amphipods are selective detritus feeders, but *A. macrocephala* is also considered a suspension feeder (Kanneworff 1968). The sediment type at this station was fine sand (Chapter 2). A minimum estimation of the increased surface area caused by the burrows is 200-300%. Another BS/A station (74-010) from the Chukchi Sea is dominated by a selective detritus/suspension-feeding bivalve in the F. Tellinidae (*Macoma calcarea*; Figure 4.5). 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, shown by the irregular clear areas at the bottom of the X-radiograph. The sediment type at this station is fine sand and silt and clay. Station 74-023 in the Chukchi Sea under BS/A water is characterized by a fine sand and silt and clay sediment (Figure 4.6). The bioturbation zone at this station extends to 6 cm and the infauna are dominated by a selective detritus-feeding bivalve in the F. Nuculidae (*Nucula belloti*).

Figure 4.4. X-radiograph of sediment core at Station 59-123 showing the infaunal bioturbation zone. KEY: Aor=F. Aoridae *(Lembos arcticus)*, Amp=F. Ampeliscidae (*Ampelisca macrocephala*).

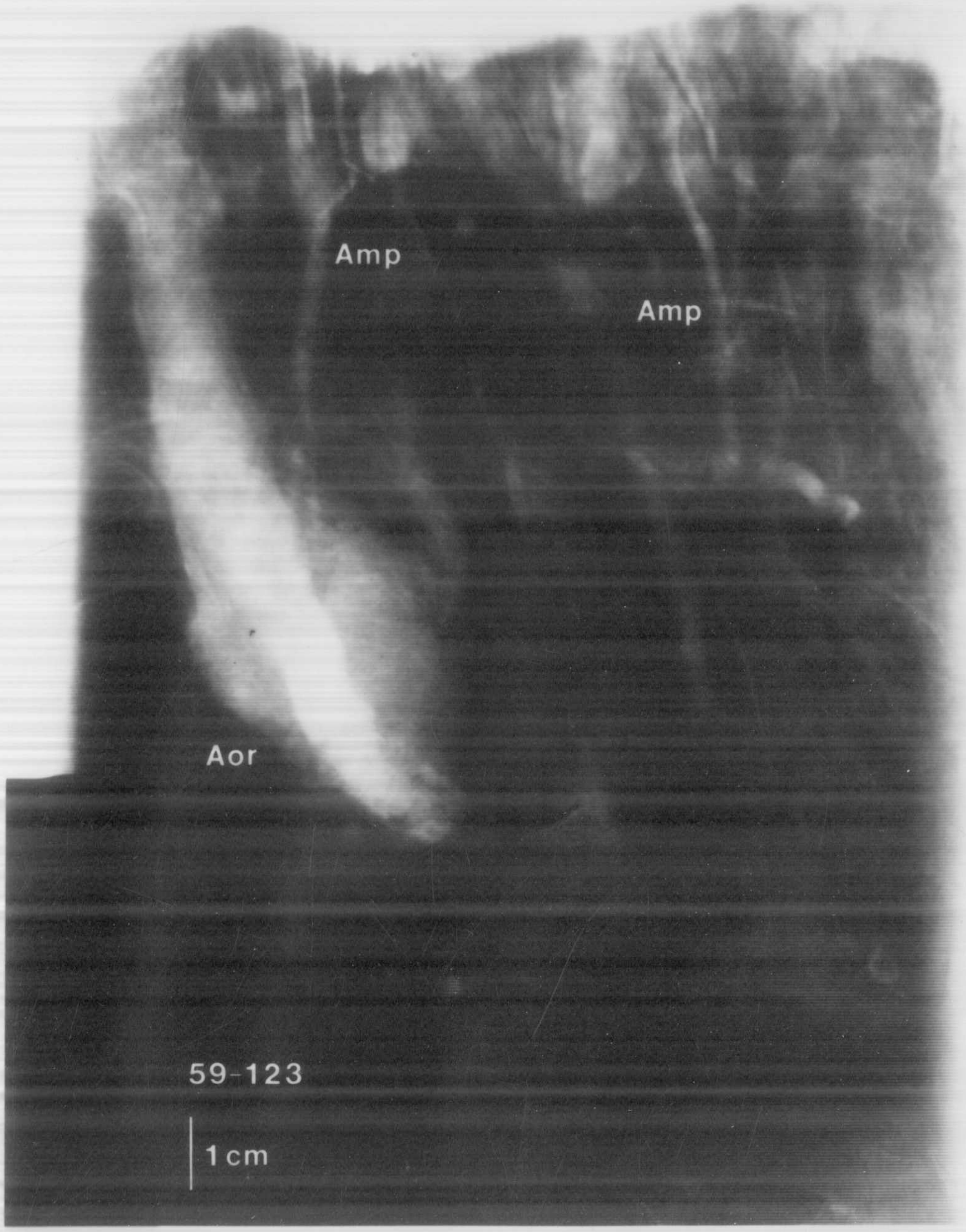

Amp
Amp
Aor
59-123
1cm

Figure 4.5. X-radiograph of sediment core at Station 74-010 showing the infaunal bioturbation zone. KEY: Amp=F. Ampeliscidae (*Byblis* sp., Tel=F. Tellinidae (*Macoma calcarea*).


Amp
Tel
Tel
74-010
1 cm
Tel
shells

Figure 4.6. X-radiograph of sediment core at Station 74-023 showing the infaunal bioturbation zone. KEY: Nuc=F. Nuculidae *(Nucula belloti)*, Tel=F. Tellinidae (*Macoma calcarea*).


Nuc
Nuc
74-023
1 cm
Tel
shells

Stations in AC water had less bioturbation than those in BS/A water. The core from Station 59-085 (Figure 4.7) had one suspension-feeding tunicate in the F. Styelidae (*Pelonaia corrugata*) and a bivalve in the F. Veneridae (*Liocyma fluctuosa*). Sediments were primarily fine sand. The core from Station 59-108 (Figure 4.8) was composed of medium sand and was dominated by sand dollars in the F. Echinarachniidae (*Echinarachnius parma*). The zone of bioturbation extended to 6 cm.

Nutrient flux

Nitrogen content in waters overlying 6 experimental oxygen uptake cores was measured in 1986 (Table 4.6). Ammonia flux out of the sediment occurred for three of the four BS/A stations measured (85-037, 85-048, and 85-071). Stations 85-037 and 85-048 are located in the northern Bering Sea ampeliscid amphipod community. These are also the only stations with a flux of nitrate into the sediments. The two AC stations (85-015 and 85-094) showed low NH_4^+ and NO_3^- flux out of the sediments. Similar patterns in NH_4^+ and NO_3^- flux in these sediments have been measured in detail by Blackburn and Henriksen (1986 and 1987).

DISCUSSION

Two factors, food supply and low temperature, have a strong limiting influence on benthic metabolism (Graf et al. 1983; Hylleburg and Vestergaard 1984). Previous studies have found one or both of these parameters to be dominant in various aquatic systems (Davies 1975; Hargrave 1973; Smith et al. 1983). In this study, the highest sediment oxygen uptake rate (mean=19 mmol O_2 m^{-2} d^{-1}) and organic carbon mineralization rate (mean=20 mmol C m^{-2} d^{-1}) occurred in sediments underlying BS/A water, characterized by low temperatures and high primary production in the summer (Walsh et al. 1987; Springer

Figure 4.7. X-radiograph of sediment core at Station 59-085 showing the infaunal bioturbation zone. KEY: Sty=F. Styelidae (*Pelonaia corrugata*), Ven=F. Veneridae (*Liocyma fluctuosa*).

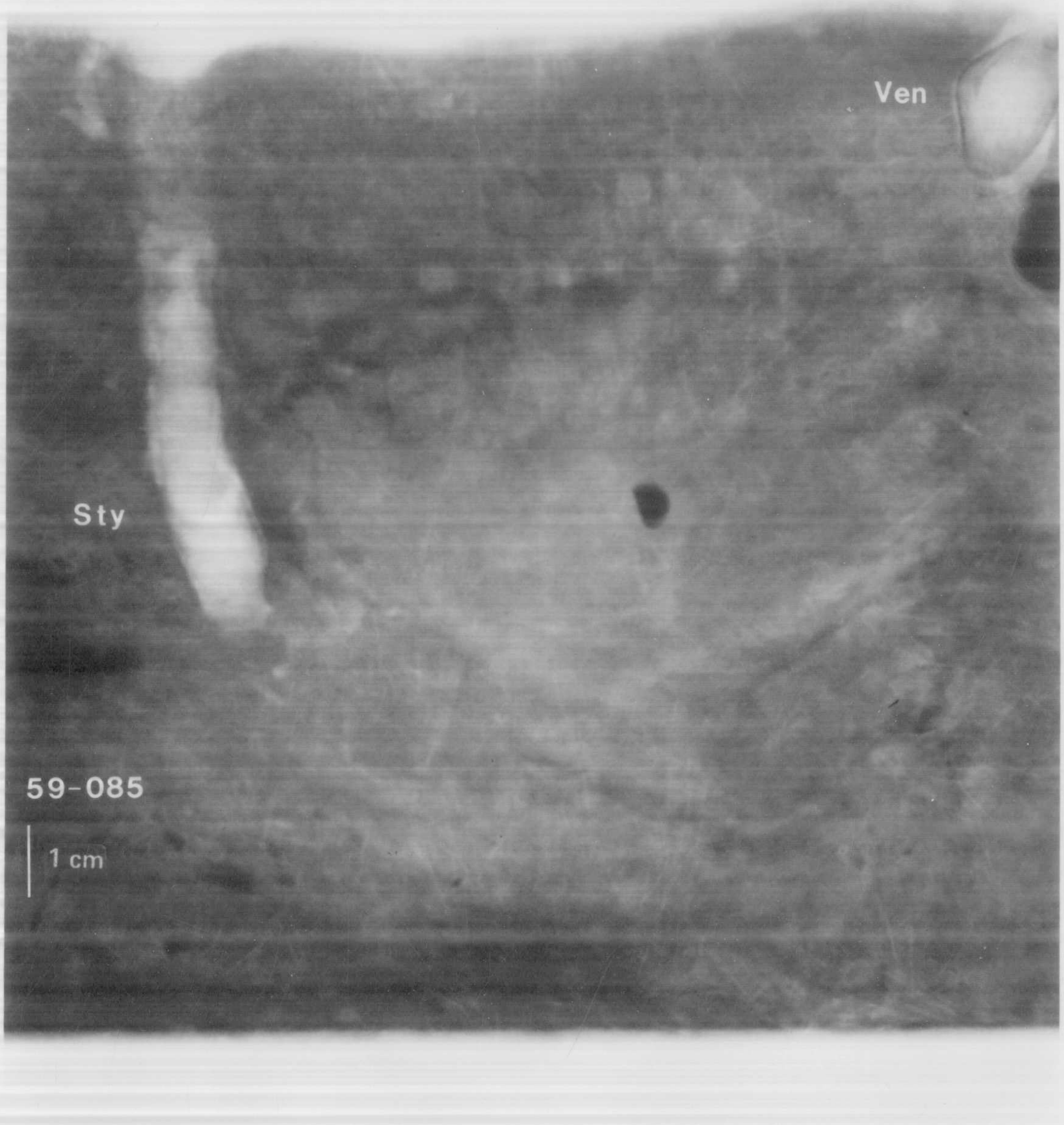
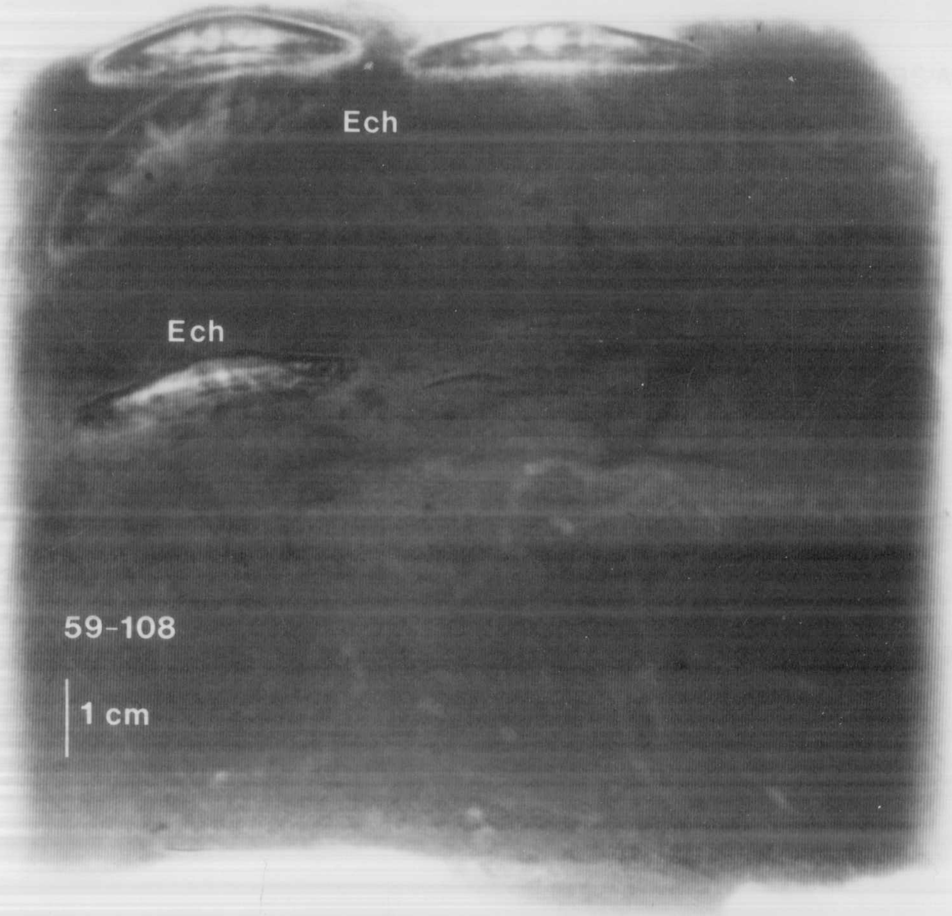

Ven
Sty
59-085
1 cm

Figure 4.8. X-radiograph of sediment core at Station 59-108 showing the infaunal bioturbation zone. KEY: Ech=F. Echinarachniidae (*Echinarachnius parma*).



Ech
Ech
59-108
1 cm

Table 4.6. Estimated nitrogen flux for sediment cores from Bering Shelf/Anadyr (BS/A) and Alaska Coastal (AC) water during Cruise 85 (11-26 July 1986).

			Nitrogen flux (mmol m^{-2} d^{-1})	
Station	Location	Water mass	NH_4^+	NO_3^-
85-015	northern Bering Sea	AC	+0.68	+0.18
85-037	northern Bering Sea	BS/A	+1.22	-0.18
85-048	northern Bering Sea	BS/A	+2.48	-0.68
85-071	Chukchi Sea	BS/A	+2.76	+0.00
85-094	Chukchi Sea	AC	+0.87	+0.71
85-106	Chukchi Sea	BS/A	+0.87	+0.02

and McRoy 1986). The measurement of higher metabolic rates in the lower temperature regime (-1 to 2° C) suggests that bacterial and benthic faunal respiration in these northern waters may not be temperature limited. Comparing the two water masses, benthic metabolism rates decreased in the warmer AC water, where average benthic populations are low, compared to high benthic metabolism and faunal populations in BS/A water. Although the data imply that the organic carbon flux to the benthos in BS/A water is 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 site in each water mass to differentiate food supply from temperature effects.

On a global basis sediment oxygen uptake in BS/A water is within the expected range for inner shelf sediments, while the AC water sediment has oxygen uptake closer to those measured in the outer shelf and upper slope regions (Table 4.7). Both inner shelf systems and BS/A water experience high water column primary production (Parsons et al. 1977; Jørgensen 1983; Springer and McRoy 1986) along with high sediment oxygen uptake, suggesting that food supply is a major regulating factor in sediment metabolism rates in these regions. In comparison, the similarity of low AC water sediment oxygen uptake to that from the less productive outer shelf and upper slope regions suggests that the reduced water column primary production in the nearshore AC water limits benthic metabolism as it does on outer shelf and slope regions.

The many factors influencing sediment oxygen uptake cumulatively influence the variability in rates between years. Although differences in sediment oxygen uptake were observed between years in BS/A water, the relative difference within each year between the BS/A and AC water masses was the same, that is, 2-3 times higher rates in BS/A water compared to AC water. The lower 1985 mean oxygen uptake may be the result of reduced

Table 4.7. Comparison of oxygen uptake rates in marine sediments from five 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 (3.6%)	20
Outer shelf	50-200	18 (5.0%)	10
Upper slope	200-1000	15 (4.2%)	3
Lower slope	1000-4000	106 (29%)	0.3
Deep sea	4000	208 (58%)	0.05

organic matter supply, although previous data indicate a seasonally reliable organic matter supply in these waters (Chapter 3). Another possibility is that samples were collected over a larger area, including stations underlying less productive BS/A waters 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 mass would enable investigation of the individual environmental parameters that influence interannual variability in sediment oxygen uptake rates.

The significant correlations between oxygen uptake and five environmental variables (bottom salinity, temperature, water density, chlorophyll a concentration, and surface sediment C/N ratios) all indicate a relationship with the quantity and quality of organic matter available. Previous data suggest that salinity and temperature do not directly influence oxygen uptake (Griffiths et al. 1984), a conclusion supported here. The significant relationship between oxygen uptake and bottom chlorophyll a concentration indicates the importance of the quantity of organic matter, and the correlation with C/N ratios in surface sediments reinforces the conclusion that the quality of organic matter can also influence oxygen uptake rates. In combination, these variables indicate that a higher quantity and quality of organic matter reaches the benthos in BS/A water than in AC water, thus resulting in higher sediment metabolism.

Total oxygen uptake is highest in the Chirikov Basin and central region of the Chukchi Sea under BS/A water (Figure 4.2). These areas correspond to regions of relatively weak current flow within each of the two main study sites (Creager and McManus 1967; Nihoul 1986; Nihoul et al. 1986) and high phytoplankton biomass and primary production (Springer and McRoy 1986) simultaneously occur, suggesting areas of high organic matter flux. In addition, the highest oxygen uptake region in the northern Bering Sea coincides with the area of highest benthic standing stock (Chapter 3). The bottom here is dominated by tube-dwelling ampeliscid amphipods (*Ampelisca macrocephala*), which bind the sediments together through tube formation, and tellinid bivalves (*Macoma calcarea*). Both animals are surface detritus and suspension feeders, which indicates a reliable, adequate food source (Stoker 1978 and 1981; this study). The high oxygen uptake region off the northeast end of St. Lawrence Island in fine-grain sediments is also dominated by these same species.

Most stations in AC water are characterized by low oxygen uptake (<10 mmol O_2 m^{-2} d^{-1}), except those occurring in the frontal zone. Low oxygen uptake rates also occur in BS/A water just north of both Anadyr and Bering Straits. This could be the result of higher current velocities 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 (Chapter 2) as well as reduced levels of bioturbation could result in reduced sediment metabolism.

Blackburn and Henriksen (1986) have measured rates of benthic carbon cycling for the northern Bering and Chukchi Seas. Aerobic respiration dominates organic carbon mineralization in AC and BS/A water in the northern Bering Sea. However, organic carbon mineralization varies under BS/A water in the Chukchi Sea depending on the amount of anaerobic respiration occurring there. They found that macrofaunal respiration accounted for 60-70% of the total aerobic mineralization in BS/A water in the northern Bering Sea but only 5-50% in the Chukchi Sea. In AC water macrofaunal respiration accounted for 10-20% 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 (pers. comm.) for amphipods and bivalves (maintained in precombusted sediments) and faunal counts made at stations in the present study, an estimate was determined for the dominant macrofaunal respiration component. The results show that dominant macrofauna accounted for 61% of the total sediment oxygen uptake rates measured in BS/A water during the present study, which falls within the 60-70% estimate for the macrofaunal respiration component of the overall aerobic mineralization determined by Blackburn and Henriksen (1986).

The dominant fauna under the highly productive regions in BS/A water have a major effect on sediment oxygen uptake and, hence, organic carbon mineralization. Aerobic respiration by the extremely high numbers of ampeliscid amphipods (~5000 individuals m^{-2}) in the high benthic biomass regions of this study play a major role in organic carbon mineralization. Bioturbation is also important in these sediments. In the Chirikov Basin, amphipods (primarily F. Ampeliscidae) result in a 200-300% increase in sediment surface area (Figure 4.4), thus enabling additional aerobic oxidation of organic material. Results (Table 4.3) show average aerobic respiration accounted for 88% of the total organic carbon mineralization for stations with high benthic biomass, which is comparable to 80% reported by Blackburn and Henriksen (1986). Ventilation of amphipod tubes by feeding currents and movement of animals allows oxygenated channels to extend 10-15 cm into the sediments (Figure 4.4). Larger surface area burrow walls and the break-up of detritus during amphipod feeding can enhance microbial respiration (Aller et al. 1983; Fenchel 1970; Henriksen et al. 1980).

The station with the highest faunal standing stock occurs in the Chukchi Sea (74-010, Figure 4.5) dominated by the tellinid bivalve *Macoma calcarea* (548 individuals m^{-2}, 35.96 g C m^{-2}, Grebmeier unpubl. data), which lives beneath the sediment surface and extends a siphon to the surface to feed on detritus. *Byblis gaimardi,* a detritus-feeding ampeliscid amphipod, is also dominant by abundance (4408 individuals m^{-2}, 7.78 g C m^{-2}, Grebmeier unpubl. data), although it builds a shallower, less permanent tubes compared to the dominant ampeliscid amphipod in the northern Bering Sea, *A. macrocephala* , and thus has less of an effect on altering sediment surface area available for aerobic respiration. Nevertheless, aerobic respiration acccunted for 70% of the total carbon mineralization at this station, which suggests that the large numbers of benthic infauna are important. The increase in anaerobic metabolism at this station corresponds to a higher sediment organic content (1.2%) and finer-grained sediments than found at stations in the Chirikov Basin (Chapter 2). Areas of high anaerobic metabolism in the southern Chukchi Sea are dominated by bivalves in the families Tellinidae and Nuculidae. Their ability 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 a chemically-adverse environment.

In the Chukchi Sea aerobic respiration accounted for only 32% of the total organic carbon mineralized at Station 74-023 under BS/A water (Figure 4.6; Table 4.3). This station also has the highest organic carbon content recorded (1.9%, Figure 2.6), consists of fine sand, silt and mud (Figure 2.4), and has a surface sediment C/N value of 7 (Figure 2.7, Appendix C). The subsurface detrital feeding bivalve *Nucula belloti* (F. Nuculidae) dominates by both abundance (680 individuals m^{-2}) and biomass (8.72 g C m^{-2}) at Station 74-023 and the animal bioturbates the top 5-6 cm of the sediment. Benthic standing stock is lower at this station and toxicity effects from high sulfide levels in these sediments may be limiting benthic populations (Gray 1981) compared to Station 74-010 (Figure 4.5).

A representative station (59-085) in AC water also has a bioturbated surface layer (6-8 cm), although absolute standing stock is lower. Styelid tunicates (*Pelonia serrugata*) and sternaspid polychaetes (*Sternaspis scutata*) occur at Station 59-085 (Figure 4.7), with the dominant fauna being sand dollars (*Echinarachnius parma,* 230 individuals m^{-2}, 4.58 g C m^{-2}). *E. parma* is also dominant (160 individuals m^{-2}) at Station 59-108 in AC water (Figure 4.8), although the bivalve family Tellinidae dominates the biomass (1.38 g C m^{-2}).

Temperatures are highest under AC water and while bioturbation occurs, low production in this water mass is likely to be the major factor limiting benthic metabolism.

Stations in the ampeliscid amphipod community (85-037 and 85-048, Table 4.6) in the northern Bering Sea show ammonia being transported out of the sediments while nitrate is transported into the sediments. Aerobic mineralization is high in these sediments and the deep tube-dwelling ampeliscid amphipods, which irrigate their burrows during feeding and respiration activities, appear to enhance the exchange of nutrients between the sediment and water column. The highest ammonia flux was in the southern Chukchi Sea in BS/A water, where aerobic respiration and organic carbon mineralization were also high.

In summary, benthic carbon cycling in the northern Bering and Chukchi Seas is influenced by the quantity and quality of organic matter available to the benthos. The sheer numbers of macrofauna under portions of BS/A water, along with the increased bioturbation levels in the sediments, enhance carbon mineralization and nutrient flux across the sediment-water interface. Highest oxygen uptake rates occurred in BS/A water in both basin regions of the northern Bering and Chukchi Sea, suggesting a high organic matter flux to the benthos. The low sediment oxygen uptake in the AC water mass suggests less organic matter supply to these sediments.

Chapter 5. BENTHIC CARBON FLOW

INTRODUCTION

Carbon flow in marine ecosystems depends on processes ranging from initial plant production to final mineralization in the sediments (Figure 5.1). Carbon to nitrogen ratios of organic matter provide an indication of nutritional quality. C/N values for marine phytoplankton average 5-7, bacteria 5.7, river particulate organic matter 8-12, land plants ≥69, surface sediments 8-12, and biochemically-resistant organic carbon buried in marine sediments >15 (Parsons et al. 1977; Meybeck 1982; Valiela 1984; see Chapter 2 for processes in the water column that influence C/N values). Organic matter entering the system can descend to the bottom unchanged, undergo various bacterial decomposition processes, as well as be repackaged in zooplankton fecal pellets or crustacean molts. Once in the sediments, consumption by macro-, meio-, and micro-fauna and bacteria occurs through aerobic and anaerobic processes.

The purpose of this chapter is to determine organic carbon flow to and within the benthos in water masses in the northern Bering and Chukchi Seas. Preliminary work by Walsh et al. (1987) suggested a dramatic difference in carbon flow within the high salinity, low temperature, and high primary production Bering Shelf/Anadyr (BS/A) water compared to the high temperature, low salinity, low primary production Alaska Coastal (AC) water (Chapter 1). Their model is used in the present paper and new information on benthic biomass and total community metabolism from the present study is included.

ASSUMPTIONS AND METHODS

Primary production, along with microplankton and zooplankton organic carbon consumption, were taken directly from Walsh et al. (1987) for inclusion in the present model (Figure 5.2). Primary production in BS/A water was 285 g C m^{-2} yr^{-1} compared to

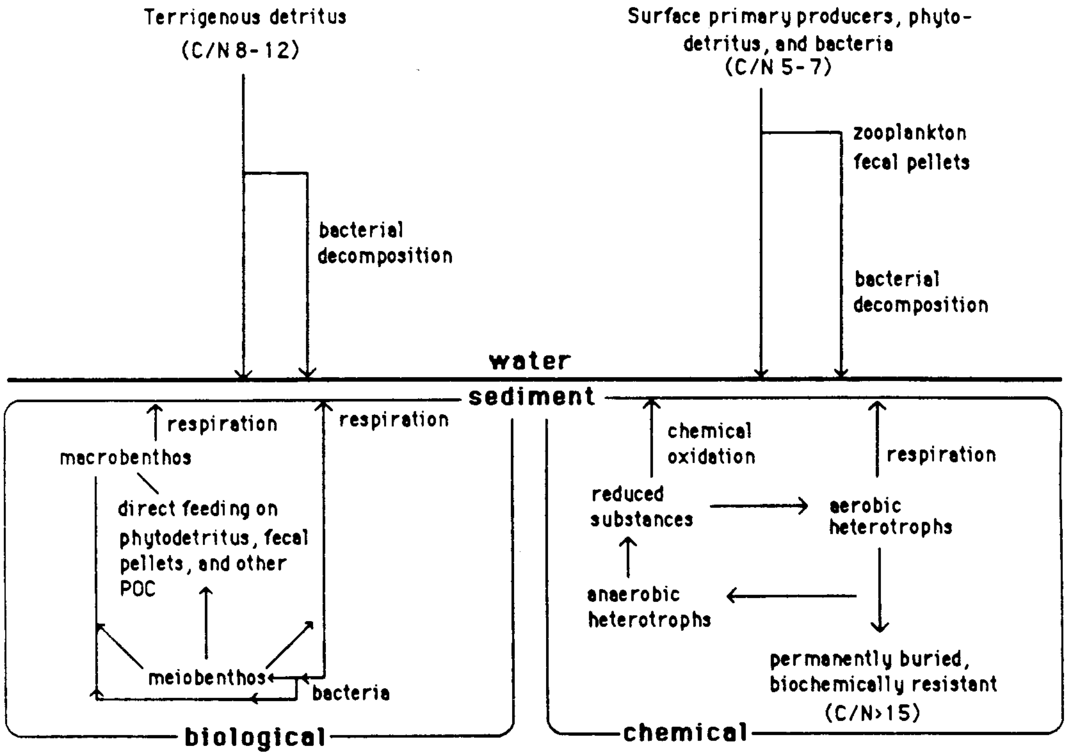


Figure 5.1. Generalized organic carbon flow in sediments (adapted from Davies 1975). C/N ratios are from Parsons et al. (1977), Meybeck (1982) and Valiela (1984).

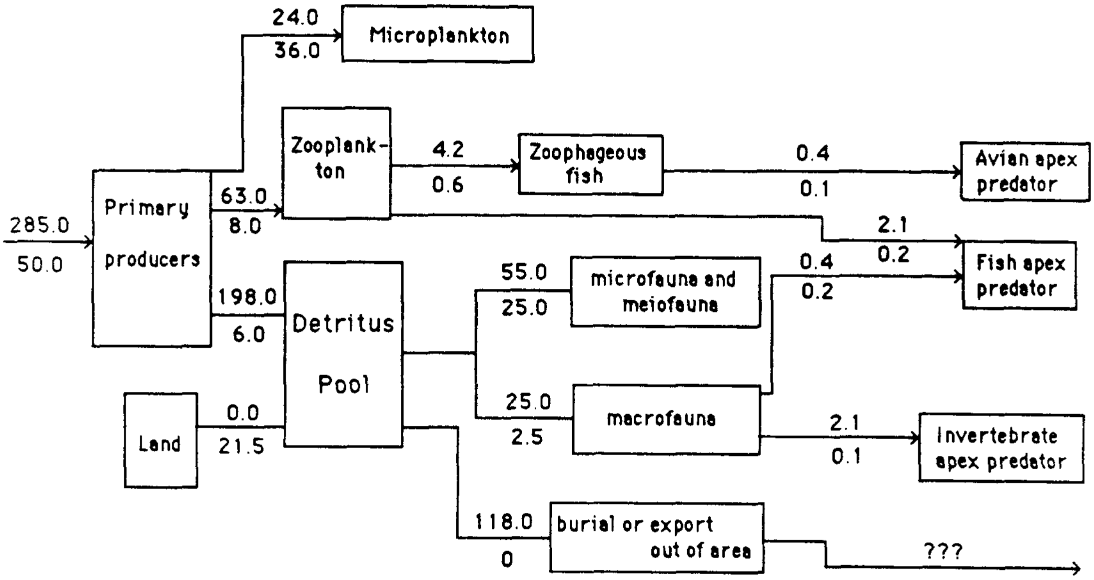


Figure 5.2. Annual carbon flow (g C m^{-2} yr^{-1}) within food webs in Bering Shelf/Anadyr water (upper value) and Alaska Coastal water (lower value) in the northern Bering and Chukchi Seas (Walsh et al. 1987).

50 g C m^{-2} yr^{-1} in AC water. They estimated microplankton carbon consumption to be at least 24.0 g C m^{-2} yr^{-1} in BS/A water compared to 36.0 g C m^{-2} yr^{-1} consumed by microplankton in AC water, assuming a 90% respiratory loss of organic carbon over a 150 day period and utilizing field data of known biomass and production. Macrozooplankton grazing rates were based on a 60% assimilation efficiency, a C/N ratio of 6, and an estimated zooplankton excretion rate of 28 mg N m^{-2} d^{-1}. Zooplankton were estimated to consume 63.0 g C m^{-2} yr^{-1} in BS/A water compared to only 8.0 g C m^{-2} yr^{-1} in AC water.

The method used to calculate annual total benthic carbon consumption was based on methods of Walsh et al. (1987). Two methods were used in the revised model to determine the annual macrofaunal carbon consumption for both the general model as well as for high benthic biomass regions. In addition, methods for calculating food chain transfer efficiencies, meiofaunal, microfaunal and microbial carbon consumption, terrestrial organic carbon input, and a marine mammal apex predator group are described.

Annual benthic carbon consumption

Annual benthic carbon consumption was based on total sediment oxygen uptake. A respiratory quotient (RQ) = 1 was assumed for conversion from oxygen uptake to carbon consumption (Nixon et al. 1980). Stations known to have high sulfate reduction were corrected for additional carbon mineralization due to this process as well as corrected for chemical oxidation (Table 4.3; Chapter 4). The mean values are 20.25 mmol C m^{-2} d^{-1} for BS/A water and 8.30 mmol C m^{-2} d^{-1} for AC water (Table 4.4). The annual benthic carbon consumption is a combination of the mean benthic carbon consumption over a 150 day primary production period during June-October and 60% of this summer mean carbon consumption rate over a 7 month winter period (November-May, based on methods of Walsh et al. (1987). The following formulas were used:

1. summer benthic carbon consumption = the mean daily benthic carbon mineralization (mmol C m^{-2} d^{-1}) for each water mass X 150 days X 12 mg C/mmol C;
2. winter benthic carbon consumption = 0.60 X the summer mean daily benthic carbon mineralization (mmol C m^{-2} d^{-1}) for each water mass X 215 days X 12 mg C/mmol C.

Method 1. Benthic macrofaunal carbon consumption based on Walsh et al. (1987)

Benthic macrofaunal carbon consumption was determined by two methods which provided a check on the assumptions and values used. The first method is based on Walsh et al. (1987). An annual production/biomass (P/B) value=0.1 and a food chain transfer efficiency=10%, along with faunal biomass data determined over three field seasons during this study, were utilized in the following formula:

mean macrofaunal carbon demand = mean benthic biomass for each water mass x (P/B)/ transfer efficiency.

The mean benthic biomass from this study for BS/A water was 20.15 g C m^{-2} and 6.31 g C m^{-2} for AC water (Table 3.6; Chapter 3).

Method 2. Benthic macrofaunal carbon consumption based on sediment metabolism experiments

The second method determines the mean macrofaunal carbon demand based on metabolism experiments (Chapter 4). The mean annual benthic carbon consumption was 67.8 g C m^{-2} yr^{-1} for BS/A water and 27.8 g C m^{-2} yr^{-1} for AC water. The average percentage of the total sediment carbon demand accounted for by the macrofaunal component was used in calculating annual macrofaunal carbon consumption. The following assumptions and modifications were included in the analysis.

Macrofauna accounted for 33% of the total benthic organic carbon mineralization in BS/A water and 13% in AC water, based on combined values for both the northern Bering and Chukchi Seas (Blackburn and Henriksen 1986). Macrofuana accounted for an average 60-70% of the 80% aerobic mineralization (as part of the total sediment carbon mineralization rate) in the northen Bering Sea. Macrofauna accounted for 5-50% of the 30-70% aerobic mineralization (as part of the total sediment carbon mineralization rate) in the Chukchi Sea. In comparison, macrofauna accounted for 10-20% of the 85% aerobic mineralization (as part of the total sediment carbon mineralization rate) in both the northern Bering and Chukchi Seas (Blackburn and Henriksen 1986).

In high benthic biomass regions in BS/A water, regional-specific percentage values for macrofaunal carbon demand as a percentage of the total sediment organic carbon mineralization rate were substituted for the general value (33%). Macrofauna accounted for 56% of the total sediment organic carbon mineralization in the northern Bering Sea, based on the highest values reported by Blackburn and Henriksen (1986), showing that macrofauna accounted for 70% of the 80% aerobic mineralization. In contrast, macrofauna are estimated to account for 35% of the total sediment organic carbon mineralization in the Chukchi Sea. This is also based on highest values reported by Blackburn and Henriksen (1986), showing that macrofauna accounted for 50% of the 30-70% aerobic mineralization. The higher percentage value of 70% was used in the latter calculation based on the conclusion that in high benthic biomass areas aerobic mineralization is a major part of the total sediment organic carbon mineralization (Blackburn and Henriksen 1986; Chapter 4).

Food chain transfer efficiency

Transfer efficiency (or ecological efficiency) is the percentage of energy consumed by a given trophic link that is available to the next link in a food web (Valiela 1984). It is the ratio of production of biomass at a given trophic link to the food consumed by that link. Food chain transfer efficiencies were determined for four stations in high benthic biomass regions dominated by amphipods and bivalves. A general invertebrate P/B of 0.1 and higher ampeliscid amphipod P/B of 1.0, based on recent data from the northern Bering Sea (R. Highsmith and K. Coyle, pers. comm.), were used in the following formula:

TE= (A + B) / C, where

TE= transfer efficiency,

A= biomass of the ampeliscid amphipods x (P/B=1.0),

B=biomass of the remaining station fauna x (P/B=0.1), and

C=annual benthic macrofaunal carbon consumption for the station determined by Method 2.

In the above formula, A + B provides an estimate of annual benthic production and C is an estimate of the annual food supply consumed by macrofauna.

Meiofaunal, microfaunal and microbial carbon consumption

The combined meiofaunal, microfaunal and microbial carbon consumption was taken as the difference between the annual benthic carbon consumption and the macrofaunal carbon consumption (Method 1).

Terrestrial carbon input

Terrestrial input into the carbon flow was determined by the difference between the size of the detrital pool (the net organic carbon available after zooplankton and microplankton deplete the primary production pool) for each water mass and the mean benthic carbon consumption for that water mass. This was taken to be the quantity to balance the detritus pool for benthic carbon consumption.

Apex predators

Apex predators in the food chain were taken from Walsh et al. (1987). In addition, a marine mammal apex predator was added. The California gray whale, *Eschrichtius robustus*, and Pacific walrus, *Odobenus rosmarus*, are dominant marine mammal predators on benthic invertebrate fauna in the region (Fay et al. 1977 and 1984; Nerini 1984; Chapter 3). The gray whale feeds primarily in BS/A water compared to walrus which feed in both BS/A and AC waters (Fay et al. 1977 and 1984; Nerini 1984; B. Fay pers. comm.). Using a mean 20 g C m^{-2} benthic standing stock in BS/A water (Chapter 3) and a 10% transfer efficiency from invertebrate biomass to all apex predators (fish, marine mammals and invertebrates) results in a combined apex predator carbon consumption value of 2 g C m^{-2} yr^{-1}. During the summer season the gray whale is estimated to consume over 9-27% of the benthic fauna annually (adjusted from a seasonal value), which converts to 1.8-5.4 g C $m^{-2}yr^{-1}$.

The Pacific walrus feeds primarily on bivalves in the total study area, which make up approximately 33% of the dominant faunal biomass in both BS/A and AC water (Grebmeier unpubl. data; Appendix I). Based on a 10% efficiency of bivalve biomass to walrus biomass alone, walrus are estimated to consume 0.7 g C $m-^{2}$ y^{-1} in BS/A water. A minimum consumption value of 1.8 g C $m-^{2}$ $yr-^{1}$ was assumed for all marine mammals in BS/A water in order to allow for a minimal carbon flow of 0.1 g C m^{-2} y^{-1} to both fish and invertebrate predators known to feed in the area.

Using a mean 6 g C m^{-2} benthic standing stock in AC water (Chapter 3) and a 10% transfer efficiency from invertebrate biomass to all apex predators (fish, marine mammals and invertebrates) results in a combined apex predator carbon consumption value of 0.6 g C m^{-2} yr^{-1}. The Pacific walrus is estimated to consume only 33% or 0.2 g C m^{-2} yr^{-1} in AC water. The remainer of the available organic carbon is divided between fish and invertebrate apex predators based on percentages determined by Walsh et al. (1987).

RESULTS AND DISCUSSION

Benthic data obtained from 1984 to 1986 in the present study were utilized to modify the Walsh et al. (1987) model of carbon flow in both BS/A and AC waters (Figure 5.3). The following discussion is focused on benthic carbon cycling in the two systems.

Annual benthic carbon demand (Table 5.1) includes macrofaunal and a combined

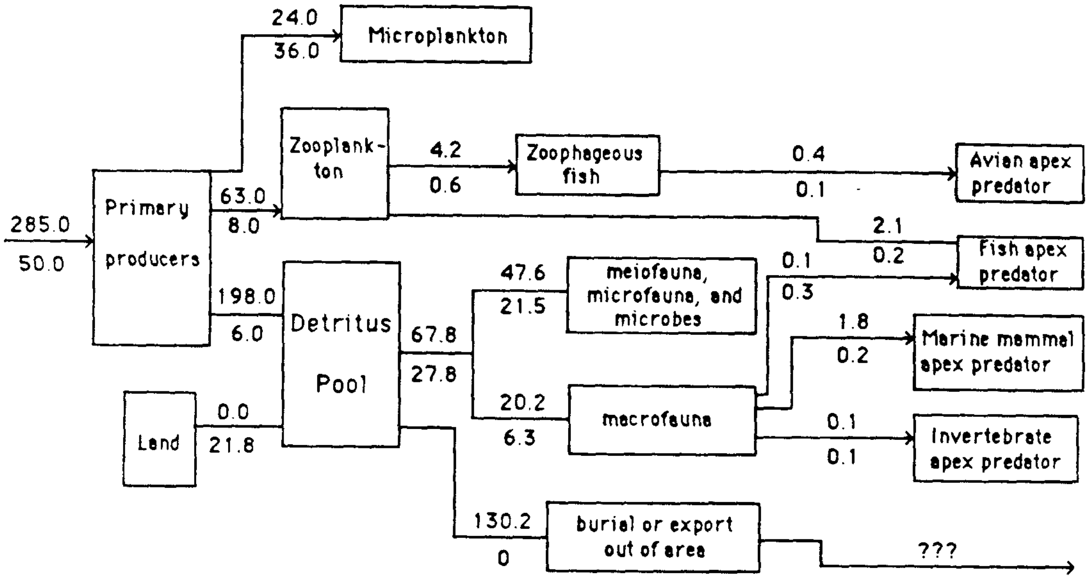


Figure 5.3. Revised annual carbon flow (g C m^{-2} yr^{-1}) in Bering Shelf/Anadyr water (upper value) and Alaska Coastal water (lower value) in the northern Bering and Chukchi Seas (from Walsh et al. 1987 and this study).

Table 5.1. Calculated annual benthic carbon consumption including macro-, meio-, and micro-faunal and microbial components in Bering Shelf/Anadyr and Alaska Coastal waters.

	Annual benthic carbon consumption ($g\,C\,m^{-2}\,yr^{-1}$)		
Water mass	Summer	Winter	Total
Bering Shelf/Anadyr	36.5	31.3	67.8
Alaska Coastal	14.9	12.9	27.8

meio- and micro-faunal and microbial component and averaged 67.8 g C m^{-2} yr^{-1} in BS/A water, a 2-3 fold increase over the average 27.8 g C m^{-2} yr^{-1} calculated for AC water. In BS/A water, a benthic consumption of 67.8, a zooplankton consumption of 63.0 and 24.0 by microplankton resulted in a net loss of 130.2 g C m^{-2} yr^{-1} either to be buried in the sediments or exported (Figure 5.3). In AC water, a 27.8 benthic carbon demand, in addition to 8.0 by zooplankton and 36.0 by microplankton, requires an additional detritus input of 21.8 g C m^{-2} yr^{-1} from the Yukon River and other external sources to balance the budget.

Benthic macrofaunal carbon consumption was calculated from both benthic biomass and annual benthic carbon consumption based on sediment metabolism experiments (Table 5.2). Both methods produced similar results, with benthic macrofaunal carbon demand ranging from 20.2-22.4 g C m^{-2} yr^{-1} in BS/A water to 3.6-6.3 g C m^{-2} yr^{-1} in AC water. Benthic macrofaunal carbon consumption was 3-6 times higher in BS/A water compared to AC water, suggesting a higher organic carbon supply to the benthos in BS/A water.

Benthic carbon demand for the BS/A system in the present model is 15% less than that estimated by Walsh et al. (1987; Figure 5.2 and 5.3). Interannual variability in sediment oxygen uptake, which occurs in this water mass (Chapter 4), as well as differences in transfer efficiences and P/B values, could account for the lower mean benthic carbon demand. The total benthic carbon demand measured for AC water is only 1% lower than the Walsh et al. (1987) estimate. This small variability in AC water may be due to a predictable spring detrital input from both phytoplankton and terrestrial sources. The detrital pool in BS/A water is regulated only by the annual marine primary production, therefore yearly variability in the quantity of available organic matter reaching the benthos may influence the variability observed in benthic carbon demand (Chapter 4).

The revised carbon flow estimates for BS/A and AC water show 69% of the detrital pool

Table 5.2. Comparison of benthic macrofaunal carbon consumption determined from benthic biomass and annual benthic carbon consumption for the two water masses in the northern Bering and Chukchi Seas.

			Benthic macrofaunal carbon consumption ($g\ C\ m^{-2}\ yr^{-1}$)	
			METHOD	
			1	2
Water mass	Mean benthic biomass ($g\ C\ m^{-2}$)	Annual benthic carbon consumption ($g\ C\ m^{-2}\ yr^{-1}$)	Based on Walsh et al. 1987	Based on metabolism experiments
Bering Shelf/ Anadyr	20.2	67.8	20.2	22.4
Alaska Coastal	6.3	27.8	6.3	3.6

is available to the benthos in BS/A water compared to only 12% in AC water (Figure 5.3). The difference between macrofaunal carbon demand (using Methods 1 and 2) and the total benthic carbon demand, which is the estimated meiofaunal, microfaunal and microbial carbon consumption, range from 45.4-47.6 g C m^{-2} yr^{-1} in BS/A water compared to a 21.5-24.2 g C m^{-2} yr^{-1} in AC water (Table 5.2). Thus, macrofauna account for 30-33% of the total benthic carbon demand in BS/A sediments in both the northern Bering and Chukchi Seas. Blackburn and Henriksen (1986) determined an average 33% for macrofaunal carbon demand for all BS/A stations. The macrofauna in AC water account for 13-23% of total benthic carbon demand, which is comparable to the previous macrofaunal carbon demand estimate of 13% (Blackburn and Henriksen 1986).

The organic carbon loss to the benthos in the northern Bering and Chukchi Sea is 69% for BS/A water compared to 12% in AC water. Recent work in St. Georges Bay, Nova Scotia, has shown organic carbon loss from the water column to the benthos of 9-65% of the particulate organic carbon produced from phytoplankton during unstratified periods (Hargrave et al. 1985; Hargrave and Phillips 1986). In that study reduced pelagic consumption and lower temperatures during high primary production resulted in sedimentation of organic matter and increased levels of benthic respiration. In addition, intermittent pulses of phytoplankton enrichment were measured in sediment traps and surficial sediments, with concurrent increases in suspended load in the bottom layer, suggesting rapid deposition of phytoplankton, but no accumulation in the sediments due to high bottom currents.

There is a 2-3 fold increase in total benthic carbon consumption in BS/A water compared to AC water, yet only 34% of the detritus available in BS/A water is utilized annually compared to an estimated 100% in AC water (Figure 5.3). Past investigators have suggested more organic carbon is produced in coastal shelf regions than consumed, resulting in carbon being exported from continental shelfs, with values ranging from 30-40% (Pace et al. 1984) to 60% (Walsh 1981; Walsh et al. 1981; Walsh and McRoy 1986). The present model projects that 46% of the primary production in BS/A water mass is exported northward through Bering Strait into the Chukchi Sea or is buried. In comparison, the model estimates little or no organic carbon from primary production or riverine sources is available in AC water for burial or export. Further studies are needed to determine if this latter conclusion is an artifact of the calculations used in the model and, thus, underestimates the available organic carbon in AC water.

The assumption of a P/B=0.1 and a transfer efficiency of 10% for calculating macrofaunal carbon demand is probably reasonable in polar benthic systems dominated by bivalves and other slow-growing fauna, which can have P/B ratios ranging from 0.1-0.3 (Stoker 1978; Peterson and Curtis 1980). In addition, the assumption is generally valid when comparing macrofaunal carbon demand determined by Method 1 and macrofaunal carbon demand calculated from the metabolism experiments (Method 2). However, the 0.1 P/B is low for individual fauna, such as polychaetes and amphipods (P/B=1-4, Robertson 1979; Peterson and Curtis 1980). Since amphipods are the dominant fauna by abundance in the high biomass areas, a higher P/B=1.0 was used for them along with individual station benthic macrofauna carbon consumption values, resulting in maximum food chain transfer efficiencies ranging from 22-53% (Table 5.4). Transfer efficiencies for invertebrates range from <10-25%, with a few cases of 40-100% (Valiela 1984). Three of the four high biomass stations in this study had maximum transfer efficiencies ranging from 22-26%, which suggest the benthic invertebrates at these stations have relatively high efficiency rates. If the aberrant 53% transfer efficiency calculated for benthic macrofauna at the highest biomass station in this study is correct, it suggests an extremely efficient benthic population in the

Table 5.3. Estimated food chain transfer efficiences for high benthic biomass areas in the northern Bering and Chukchi Seas

Station	Dominant benthic family	Benthic biomass ($g\ C\ m^{-2}$)	Total station biomass ($g\ C\ m^{-2}$)	Benthic macrofauna carbon consumption based on sediment metabolism experiments- **Method 2** ($g\ C\ m^{-2}\ yr^{-1}$)	Food chain transfer efficiency
59120	Ampeliscidae	18.2	32.2	85.5	23%
	Tellinidae	5.0			
59121	Ampeliscidae	8.7	29.5	49.4	22%
	Tellinidae	12.7			
74010	Ampeliscidae	7.8	59.0	24.4	53%
	Tellinidae	36.0			
85090	Ampeliscidae	5.8	32.4	32.9	26%
	Nuculidae	8.7			

Chukchi Sea. A larger sample size is needed in this area to address this hypothesis.

Peterson and Curtis (1980) suggest that the benthic biomass component in food webs increases in importance from the tropics northward, with highest values found in the subarctic regions. Transfer efficiences between links in the food web are higher in subarctic regions, with estimates ranging from 12-26% (Disko Bay, West Greenland) and 17-24% (North Sea) compared to tropical and temperate ranges of 3-10% (Peterson and Curtis 1980; Jones 1984). The range of transfer efficiences found in this study (22-26%) falls within ranges described above for other subarctic systems.

Zooplankton production is suggested to be more predominant than benthic production in tropical systems compared to subarctic systems, whereas zooplankton and benthic production are partitioned more equally in subarctic marine ecosystems (Peterson and Curtis 1980). Although the present study is not a latitudinal comparison, their observation of shared partitioning between zooplankton and benthic components in subarctic food webs is supported in the present study in both BS/A and AC waters. In BS/A water, zooplankton consumption accounts for 22% of the organic carbon produced compared to 24% of the organic carbon consumed by the benthos, and in AC water zooplankton consume 16% of the organic matter compared to 12% by the underlying benthos. A major difference between water masses is in microplankton consumption. They consume 8% of the organic matter in BS/A water compared to 72% in AC water.

The addition of a marine mammal apex predator group in the revised model (Figure 5.3) results in a 10-fold decrease in the amount of organic carbon available to the invertebrate apex predator group as determined in the Walsh et al. model (Figure 5.2). This data supports the conclusion that invertebrate apex predators are insignificant in the high benthic biomass regions and marine mammals are the dominant predators on benthic populations.

Peterson and Curtis (1980) suggest that a stable benthic community, with larger faunal size and longevity, favors efficient higher level consumers in polar environments. Increased benthic production in polar regions is supported by the occurrence of increased numbers of benthic-feeding marine mammals and bird populations (Peterson and Curtis 1980). The high abundance of benthic-feeding marine mammals in the northern Bering and Chukchi Seas requires a high benthic faunal production as a food supply, thus supporting part of the Peterson and Curtis (1980) observation (Fay et al. 1984; Nerini 1984). Pomeroy and Deibel (1986) suggest that in cold, high latitude ecosystems, high primary production in the water column, coupled with a reduced microbial loop, could result in deposition of high quality phytodetritus to the benthos. This process may be occurring in BS/A water, where high pelagic primary production is coupled with low microplankton consumption. Previous analyses (Chapters 2,3 and 4) support the conclusion that a high quality and quantity of organic matter settles to the sediments in BS/A water in the northern Bering and Chukchi Seas, supporting a rich and stable benthic community.

In summary, the northern Bering and Chukchi Seas are characterized by zooplankton and benthic partitioning of nearly equal proportions of the available organic matter. BS/A water supports a more productive marine food web than that in AC water. Benthic carbon demand is 2-3 times greater in BS/A water than AC water and this contrast is evident in the 3-6 fold greater macrofaunal and 2-3 fold greater meiofaunal, microfaunal and microbial production seen in the BS/A food web. Microplankton are thought to be a major consumer of organic matter in AC water while they appear only a minor component in BS/A water. Marine mammals are dominant predators over the study area, especially in BS/A water. Of the primary production in BS/A water, 46% is either buried or exported northward to the Chukchi Sea, whereas total consumption of both marine primary production and external detritus can occur in AC water.

CHAPTER 6. SUMMARY AND CONCLUSIONS

The hypothesis investigated in this thesis was whether food supplied by the variable primary production regimes of water masses in the northern Bering and Chukchi Seas is a major regulating mechanism in benthic community structure, biomass, and carbon cycling.

The results confirm that quality and quantity of organic matter reaching the benthos in both Bering Shelf/Anadyr (BS/A) and Alaska Coastal (AC) water masses influence benthic community structure and biomass. High quality marine organic matter is available annually to benthic populations in BS/A water compared to lower quality, more variable marine and terrestrial organic matter in AC water. Carbon/nitrogen ratios in BS/A water and surface sediments are low, averaging 7 (indicative of nitrogen-rich organic matter), but in AC water surface sediment C/N ratios increase to an average of 9 (indicative of nitrogen-poor organic matter). The continual settling of phytoplankton in BS/A water sustains the underlying benthos in a high quality food state annually in contrast to AC sediments, where low quality organic matter results from a combination of phytodetritus and terrestrial organic carbon. Greater variation in C/N ratios occur in AC sediments interannually, possibly due to yearly variability in terrestrial organic carbon input. Stable carbon isotope ratios suggest a marine origin for the organic carbon in BS/A sediments compared to a mixture of marine and terrrestrial organic matter in AC sediments.

Sediments under BS/A water in the northern Bering Sea are characterized by fine to very-fine sand, decreasing in grain size to very-fine sand and silt and clay in the central Chukchi Sea. Surface sediment total organic carbon averages 0.5% in the northern Bering Sea, increasing to an average 1.5% in the Chukchi Sea, suggesting an accumulation of organic matter as currents decrease in the Chukchi Sea. Sediments under AC water are more variable, with grain size ranging from gravel and medium sand to silt and clay modal size classes. Surface sediment total organic carbon ranges from 0.1-0.6% from the northern Bering to Chukchi Sea under this water mass, yet remaining at a relatively lower value compared to sediments in BS/A water in the same area.

Mean benthic biomass was 20.2 g C m^{-2} under BS/A water and decreased to a mean of 6.3 g C m^{-2} under AC water. The high benthic standing stock in BS/A water in both the northern Bering and Chukchi Seas mirrors the high water column primary production and phytoplankton biomass, leading to the conclusion that a persistent organic carbon supply to the benthos supports a rich benthic food web. The lack of high summer primary production and phytoplankton biomass in the nutrient-depleted AC water, coupled with low benthic production, suggests that a reduced food supply limits benthic biomass. In addition, there is a significant relationship between the higher quality of organic carbon in BS/A surface sediments and higher benthic biomass compared to that occurring in AC water, supporting the conclusion that food supply is a major regulating factor in benthic biomass in the region.

The composition of benthic communities in the area is influenced by food supply and sediment grain size. The BS/A water is dominated by detritus-feeding amphipods (F. Ampeliscidae and F. Isaeidae) and bivalves (F. Nuculidae and F. Tellinidae), normally living in fine to very-fine sand sediment zones. In comparison, a diverse mixture of faunal communities, including amphipods (F. Isaeidae and F. Phoxocephalidae), sand dollars (F. Echinarachniidae), and polychaetes (F. Sternaspidae and F. Maldanidae) exist under AC water in very fine to coarse-grained sediments. Comparison with benthic community structure and biomass from 10-15 years ago (Stoker 1978) shows little change in the benthos of the northern Bering and Chukchi Seas, supporting the conclusion that a consistent and reliable food supply is the major influence on stability in both BS/A and AC marine food webs. This study supports previous conclusions (Stoker 1978) that sediment regimes have a qualitative influence on community structure, while providing additional evidence that water column based primary production affects benthic standing stock.

Variations in primary production and phytoplankton biomass correlate directly with benthic standing stock and sediment metabolism. Mean sediment oxygen uptake provided an indication of the quality and quantity of organic carbon reaching the benthos. Total sediment oxygen uptake decreased from a mean 19.2 mmol O_2 m^{-2} d^{-1} in BS/A water to a mean 8.1 mmol O_2 m^{-2} d^{-1} in AC water. These rates, corrected for chemical oxidation and combined with sulfate reduction, indicated a 2-3 times higher carbon mineralization rate (20.3 mmol C m^{-2} d^{-1}) in BS/A water than in AC water (8.3 mmol C m^{-2} d^{-1}). Benthic aerobic respiration rates were variable between years in BS/A water, although consistently 2-3 times greater than rates in AC water within any one year, suggesting that interannual variability in water column primary production may have a direct influence on the availability of organic carbon to the benthos.

Bottom salinity, temperature, water density, chlorophyll a concentration, and surface sediment C/N ratios were all correlated with oxygen uptake. Nevertheless, the data, taken as a whole, suggest that salinity and temperature do not directly influence oxygen uptake. The significant relationship between oxygen uptake and bottom chlorophyll a concentrations indicate the importance of the quantity of organic matter reaching the benthos, while the correlation with C/N ratios in surface sediments supports the conclusion that quality of organic matter can also influence oxygen uptake. Higher sediment oxygen uptake occurs in BS/A water where a higher quantity and quality of organic matter reach the benthos compared to AC water.

An important conclusion from the benthic metabolism experiments is that the quality and quantity of organic carbon available to the benthos are major regulating factors in benthic metabolism, with temperature playing a less important role. Although temperature effects at an individual site were not investigated, the benthos underlying the warmer, less productive AC water had lower sediment metabolism than sites underlying the colder, more productive BS/A water. The higher carbon flux to the benthos in BS/A water appears to outweigh the colder temperature effect, with reduced organic matter to the benthos in AC water limiting benthic metabolism even at the higher temperatures. Macrofaunal respiration is an important component in carbon mineralization processes, especially in the high benthic biomass regions. Bioturbation, particularly irrigation by ampeliscid amphipods, can also enhance aerobic respiration and nutrient recycling in these high benthic biomass sediments.

The estimated annual benthic carbon consumption is 67.8 g C m^{-2} yr^{-1} in BS/A water and 27.8 g C m^{-2} yr^{-1} in AC water. Benthic macrofaunal carbon consumption was 3-6 times higher in BS/A water compared to AC water, suggesting a high organic carbon supply to the benthos in the BS/A water. The majority of food chain transfer efficiencies for benthic fauna ranged from 22-26% in high biomass regions, comparable to other transfer efficiency estimates for benthic fauna in subarctic regions. Zooplankton and benthic components consume relatively equal proportions of the available organic matter in both water masses, which is characteristic of subarctic marine ecosystems, while the microplankton community is more important in consuming organic matter in AC water. Estimates that incorporate water column primary production, zooplankton and bacterial organic matter consumption, and benthic carbon consumption indicate that 46% of the BS/A primary production is either incorporated into the sediments or exported from the study area. In comparison, the AC water system consumes all of the available primary production, requiring an external organic matter input to meet biological demands.

The results of the study support the conclusion that food supply is a major regulating mechanism in benthic community structure, biomass, and carbon cycling in the northern

Bering and Chukchi Sea. Seasonally high primary production in the water column and high food quality in surface sediments underlying BS/A water result in high benthic standing stocks and organic carbon turnover compared to lower levels observed in the less productive AC water. The seasonally reliable food source leads to stability in this benthic ecosystem.

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Appendix A. Station locations for R/V Alpha Helix cruises 59 (30 June-10 July 1984), 73 (25 July-10 August 1985), 74 (26 August-9 September 1985), 85 (11-26 July 1986), and 87 (14-24 August 1986).

Station	Latitude (N)	Longitude (W)
59070	63° 12.51	168° 27.98
59071	63° 09.07	168° 13.84
59074	63° 05.51	168° 00.02
59081	63° 29.54	168° 19.96
59082	63° 41.00	167° 57.02
59083	63° 51.04	167° 35.03
59084	64° 03.00	167° 11.00
59085	64° 12.00	166° 48.00
59086	64° 20.02	166° 32.95
59088	64° 38.03	166° 51.01
59107	64° 43.98	167° 15.52
59108	64° 52.52	167° 43.10
59120	64° 59.50	169° 08.00
59121	65° 16.53	168° 32.40
59123	64° 59.50	168° 45.00
59132	64° 12.00	170° 47.79
59134	64° 12.02	171° 45.05
59135	64° 12.02	171° 58.01
59148	63° 05.80	171° 57.10
59149	63° 51.00	167° 34.99
59150	64° 12.02	166° 47.98
73001	64° 20.01	166° 32.04
73002	64° 20.00	166° 58.00
73011	64° 58.02	169° 48.02
73012	64° 57.97	169° 30.20
73018	64° 58.00	169° 16.00
73019	64° 57.99	168° 52.09
73022	64° 58.05	167° 39.00
73023	64° 58.10	167° 51.04
73024	64° 57.95	168° 27.51
73026	64° 47.99	168° 40.00
73027	64° 48.01	168° 12.91
73028	65° 01.97	169° 23.77
73029	65° 06.00	169° 06.00
73030	65° 05.97	168° 43.98
73031	64° 58.01	168° 13.93
73038	64° 53.02	169° 45.00
73057	65° 07.01	167° 49.98

Appendix A. Continued.

Station	Latitude (N)	Longitude (W)
73058	64° 55.48	167° 45.98
73070	64° 53.03	169° 08.98
73071	64° 53.99	168° 17.95
73075	64° 40.98	169° 06.01
73076	64° 34.98	169° 25.02
73080	64° 24.46	170° 04.00
73081	64° 39.98	169° 45.96
73104	64° 10.49	169° 04.44
73112	64° 28.00	170° 49.96
73113	64° 33.04	170° 03.98
73120	64° 22.01	169° 45.97
73121	64° 22.00	169° 24.96
73122	64° 22.00	169° 24.96
74002	65° 52.00	168° 55.13
74003	66° 06.98	176° 17.92
74009	66° 48.02	168° 06.09
74010	67° 30.06	168° 55.14
74011	67° 30.02	167° 17.91
74012	68° 00.07	168° 55.40
74013	69° 00.08	168° 54.80
74015	69° 00.02	167° 27.91
74018	70° 00.00	163° 44.99
74019	70° 00.04	165° 00.06
74020	70° 00.02	166° 15.15
74021	70° 00.00	167° 35.74
74022	70° 00.00	168° 54.97
74023	68° 19.98	168° 55.07
74024	68° 20.10	168° 19.81
74025	68° 20.07	167° 09.82
74026	66° 44.93	168° 55.07
74027	66° 32.94	168° 55.05
74028	66° 20.10	168° 55.07
74030	65° 54.94	168° 54.79
74032	65° 09.98	169° 19.93
74033	65° 10.00	168° 55.97
74053	62° 49.99	168° 39.93
74055	62° 37.99	168° 04.96

Appendix A. Continued.

Station	Latitude (N)	Longitude (W)
74057	62° 25.02	167° 26.00
74060	62° 58.02	166° 28.10
85002	62° 12.96	166° 49.99
85003	62° 19.00	167° 08.85
85004	62° 25.00	167° 26.92
85015	64° 03.09	167° 10.80
85024	64° 22.93	169° 20.06
85036	64° 30.04	170° 05.96
85037	64° 26.00	169° 41.94
85043	64° 16.02	167° 34.91
85047	65° 09.00	168° 28.08
85048	65° 09.02	168° 52.06
85061	66° 45.04	167° 41.90
85064	67° 14.06	166° 12.92
85071	67° 45.98	166° 09.99
85090	67° 59.98	168° 54.97
85094	68° 16.04	167° 31.94
85106	68° 52.02	168° 55.07
85108	67° 24.30	168° 55.51
87067	64° 22.02	170° 09.02
87080	64° 10.00	169° 04.00
87086	64° 57.43	168° 03.59
87088	64° 58.05	168° 28.01
87089	64° 58.02	168° 50.02
87090	64° 58.16	169° 10.52
87092	65° 07.99	169° 30.00
87093	65° 07.98	169° 11.41
87094	65° 08.01	168° 49.95
87096	64° 47.97	168° 28.03
87097	64° 48.00	168° 50.06
87101	64° 58.00	168° 27.95
87102	64° 57.97	168° 49.96
87114	65° 08.02	169° 11.57

Appendix B. Water column measurements for stations occupied during R/V Alpha Helix cruises 59, 73, 74, 85 and 87 (cruises 74 and 85 from ISHTAR Data Report 1985, 1986 and unpubl. data.).

Station	Bottom temperature (°C)	Bottom salinity (‰)	Bottom sigma t	Depth (m)	Bottom chl a (mg m^{-3})	Integrated chl a (mg m^{-2})
59070	-0.98	33.429	26.88	26	...	...
59071	-0.24	33.229	26.69	20	0.54	...
59074	0.00	33.237	26.68	19	...	...
59081	-0.68	33.412	26.85	25	7.08	...
59082	-0.03	33.269	26.71	30	1.82	...
59083	-0.46	33.368	26.81	31	3.88	...
59084	-0.33	33.257	26.71	30	1.02	...
59085	-0.67	33.311	26.77	28	0.38	...
59086	-0.07	33.399	26.82	26	1.23	...
58088	4.19	33.179	26.32	23	1.21	...
59107	0.16	33.377	26.79	27	0.33	...
59108	-0.16	33.183	26.65	36	0.89	...
59120	-0.21	32.750	26.30	47	2.73	...
59121	0.82	32.635	26.15	50	5.48	...
59123	0.07	33.030	26.51	49	7.88	...
59132	0.90	32.309	25.89	31	3.82	...
59134	-0.72	32.677	26.26	51	3.98	...
59135	0.80	32.517	26.06	43	9.30	...
59148	-0.67	33.101	26.63	55	2.46	...
73001	1.10	32.197	25.79	24	1.03	8.995
73002	1.89	32.168	25.71	26	0.59	6.957
73011	0.31	32.656	26.20	45	0.39	60.411
73012	0.62	32.715	26.23	46	1.14	9.526
73018	0.71	32.646	26.17	42	0.43	25.835
73019	0.65	32.580	26.12	46	0.70	706.949
73022	...	...	...	...	0.72	10.104
73023	...	...	...	...	1.27	9.360
73024	...	...	...	44	4.90	223.258
73026	0.85	...	...	44	1.01	98.495
73027	1.25	...	...	40	6.71	217.520
73028	1.16	32.756	26.23	46	2.33	257.170
73029	0.16	32.604	26.16	47	0.95	236.965
73030	0.72	32.559	26.10	49	1.19	50.850
73031	1.16	32.417	25.96	40	4.80	169.410
73038	1.42	32.837	26.28	47	2.04	92.305
73057	2.62	32.313	25.77	31	1.40	26.330
73058	0.88	32.432	25.99	28	2.33	39.475
73070	1.29	32.784	26.25	44	2.46	83.130
73071	1.69	32.357	25.88	42	5.10	278.590
73075	1.12	32.779	26.25	43	3.31	205.805
73076	1.47	32.780	26.23	42	3.82	193.435

Appendix B. Continued.

Station	Bottom temperature (°C)	Bottom salinity (°/∞)	Bottom sigma t	Depth (m)	Bottom chl a (mg m^{-3})	Integrated chl a (mg m^{-2})
73080	1.47	32.774	26.23	40	3.14	104.715
73081	1.42	32.840	26.28	42	3.40	139.390
73104	1.88	32.522	26.00	34	5.70	216.770
73112	1.99	32.857	26.26	44	0.77	52.405
73113	2.19	32.795	26.19	43	1.05	83.670
73120	1.95	32.757	26.18	40	0.99	61.060
73121	2.01	32.722	26.19	40	1.36	89.230
73122	2.13	32.777	26.18	40	2.50	89.580
74002	2.56	32.428	25.87	49	1.50	50.750
74003	8.58	28.207	21.87	22	0.76	10.160
74009	4.79	32.149	25.44	32	0.80	20.155
74010	3.01	32.719	26.06	48	6.50	316.600
74011	3.27	32.591	25.94	46	5.30	112.500
74012	5.46	31.972	25.22	48	0.33	44.790
74013	2.70	32.850	26.19	51	5.30	107.715
74015	3.62	32.378	25.74	46	0.01	1.225
74018	4.82	31.092	24.60	27	1.14	17.395
74019	6.65	31.450	24.67	37	0.16	6.420
74020	4.71	32.064	24.38	42	0.70	19.540
74021	3.33	32.231	25.65	45	0.01	11.775
74022	2.28	32.515	25.96	35	0.07	2.975
74023	2.64	32.692	26.07	53	5.30	363.300
74024	2.85	32.421	25.84	49	0.54	42.600
74025	8.51	30.847	23.94	37	0.20	18.415
74026	6.03	31.940	25.13	40	1.14	46.620
74027	5.68	32.006	25.23	43	1.31	62.770
74028	2.80	32.359	...	52	0.67	50.740
74030	3.74	32.195	25.58	46	0.76	73.210
74032	2.20	32.793	26.19	47	0.63	21.440
74033	2.33	32.740	26.14	47	0.37	93.150
74053	-0.23	32.199	25.86	38	0.63	32.250
74055	1.47	31.883	25.51	30	0.63	14.670
74057	7.29	31.488	24.62	25	0.80	15.725
74060	8.28	30.848	23.98	19	1.10	23.195
85002	6.06	31.216	24.56	27	0.51	6.700
85003	1.72	31.825	25.45	19	2.09	19.065
85004	0.31	32.346	25.95	26	4.30	44.660
85015	0.53	32.426	26.00	31	0.23	8.690
85024	1.43	32.470	25.98	37	2.03	65.425
85036	2.36	32.857	26.23	43	1.40	52.140
85037	1.21	32.577	26.09	38	1.59	38.920

Appendix B. Continued.

Station	Bottom temperature (°C)	Bottom salinity (°/∞)	Bottom sigma t	Depth (m)	Bottom chl a (mg m^{-3})	Integrated chl a (mg m^{-2})
85043	0.79	32.416	25.98	30	0.35	9.575
85047	2.54	32.476	25.91	48	6.83	181.040
85048	1.86	32.845	26.26	52	1.52	794.215
85061	5.80	32.300	25.44	28	0.95	25.810
85064	3.73	32.254	25.63	35	1.14	27.900
85071	2.03	32.517	25.98	54	0.64	28.185
85075	-1.15	33.930	27.29	14	3.36	14.165
85084	0.96	32.785	26.27	23	0.29	5.705
85090	2.97	32.741	26.08	54	6.83	206.410
85094	4.71	32.135	25.44	45	0.42	14.990
85106	2.22	32.475	25.93	52	0.48	47.400
85108	3.21	32.778	26.09	48	8.25	262.725
87067	0.06	32.122	25.78	42	0.20	16.135
87080	1.93	32.173	25.71	34	0.29	18.850
87086	3.53	32.232	25.63	22	1.05	26.009
87088	1.97	32.320	25.83	47	0.42	67.135
87089	1.55	32.496	26.00	45	0.06	54.802
87090	1.12	32.433	25.98	47	0.04	37.990
87092	2.56	32.815	26.18	51	0.29	236.030
87093	2.50	32.785	26.16	51	0.23	299.525
87094	1.81	32.554	26.03	54	0.26	176.425
87096	2.10	32.287	25.79	43	0.48	84.985
87097	1.51	32.446	25.96	44	0.07	99.325
87101	1.90	32.472	25.95	47	0.23	81.490
87102	1.29	32.446	25.97	45	0.04	41.150
87114	0.58	32.385	25.97	51	0.45	45.830

Appendix C. Surface sediment measurements for stations occupied during R/V Alpha Helix cruises 59, 73,74, 85 and 87.

Station	Modal phi size (Ø)	TON (mg g^{-1})	TOC (mg g^{-1})	%TOC	C/N	$\delta^{13}C$ (‰)
59071	...	0.209	1.380	0.14	6.60	...
59074	...	0.475	2.740	0.27	5.77	...
59081	4.0	0.462	3.520	0.35	7.62	...
59082	4.0	0.546	3.960	0.40	7.32	...
59083	4.5	1.258	9.130	0.91	7.53	...
59084	3.0	1.050	7.990	0.80	7.61	...
59085	4.0	0.539	4.350	0.43	8.07	-22.45
59086	3.0	0.492	4.730	0.47	9.25	-21.68
58088	2.0	0.438	4.380	0.44	10.00	...
59108	2.0	0.104	0.930	0.09	8.92	-21.63
59120	...	0.310	2.041	0.20	6.58	...
59121	...	0.439	2.910	0.29	6.63	...
59123	3.0	0.467	3.430	0.34	7.34	...
59132	...	0.339	2.097	0.21	6.19	...
73001	5.0	1.104	9.127	0.91	8.28	...
73002	3.0	0.688	5.477	0.55	7.97	...
73011	4.0	0.455	3.005	0.30	6.60	-22.32
73018	3.0	0.558	3.524	0.35	6.32	...
73019	...	0.310	2.180	0.22	6.34	...
73022	3.0	0.078	1.091	0.11	14.05	-22.58
73023	3.0	0.537	3.876	0.39	7.79	-22.28
73024	3.0	0.551	3.946	0.40	6.99	-21.63
73026	...	0.491	3.163	0.32	6.44	...
73027	3.0	0.697	4.478	0.45	6.43	-21.27
73028	...	0.628	4.067	0.41	6.48	...
73029	...	0.382	2.442	0.24	6.40	...
73030	...	0.550	3.809	0.38	6.93	...
73031	...	0.545	3.817	0.38	7.02	...
73038	...	0.349	2.331	0.23	6.68	...
73057	3.0	0.204	1.592	0.16	7.82	-22.56
73058	2.0	0.111	1.085	0.11	9.78	-23.03
73070	...	0.402	2.620	0.26	6.52	...
73071	...	0.612	4.234	0.42	6.93	...
73075	3.0	0.325	2.161	0.22	6.65	-23.80
73076	...	0.264	1.867	0.19	7.06	...
73081	4.0	0.537	3.730	0.37	6.82	-21.72
73104	3.0	0.288	2.040	0.20	7.09	-21.31
73113	...	0.535	3.682	0.37	6.88	...
73120	...	0.343	2.489	0.25	7.26	...
73121	...	0.479	3.280	0.33	6.85	...
73122	4.0	0.645	4.266	0.43	6.62	...

Appendix C. Continued.

Station	Modal phi size (Ø)	TON (mg g^{-1})	TOC (mg g^{-1})	%TOC	C/N	$\delta^{13}C$ (‰)
74002	2.0	0.527	5.383	0.54	10.22	...
74009	4.0	0.537	4.362	0.44	8.13	...
74010	4.0	1.981	12.099	1.21	6.12	-22.83
74011	5.0	0.894	7.156	0.72	7.59	-22.47
74013	5.0	2.134	15.006	1.50	7.03	...
74015	4.0	0.686	5.344	0.53	7.79	...
74018	3.0	0.214	1.706	0.17	7.98	-23.81
74019	...	0.739	6.022	0.60	8.15	...
74020	4.0	2.070	14.088	1.41	6.81	...
74021	...	0.961	11.818	1.18	12.31	-23.41
74022	...	1.232	10.217	1.02	8.30	...
74023	4.0	2.778	19.349	1.94	6.97	...
74024	4.0	2.329	15.412	1.54	6.62	-20.98
74026	...	0.510	3.446	0.34	6.76	...
74028	...	0.675	4.303	0.43	6.38	...
74030	...	1.748	11.682	1.17	6.69	...
74032	...	0.582	3.771	0.38	6.49	...
74033	...	0.531	3.525	0.35	6.65	...
74060	4.0	0.250	2.146	0.21	8.61	-23.54
85002	3.0	0.366	2.828	0.28	7.73	...
85003	4.0	0.341	2.794	0.28	8.21	...
85004	4.0	0.397	3.034	0.30	7.65	...
85015	...	0.494	3.924	0.39	7.92	...
85024	...	0.391	2.686	0.27	6.87	...
85036	...	0.300	2.050	0.20	6.84	...
85043	...	0.149	1.013	0.10	6.83	...
85047	...	0.462	3.109	0.31	6.74	...
85048	...	0.634	4.360	0.44	6.88	...
85061	5.0	1.014	7.211	0.72	7.12	...
85064	4.0	1.380	9.962	1.00	7.23	...
85071	4.5	1.948	13.440	1.34	6.91	...
85090	5.0	2.162	13.622	1.36	6.30	...
85094	2.0	0.930	6.397	0.64	6.89	...
85106	...	2.030	14.280	1.43	7.01	...
85108	...	1.675	10.994	1.10	6.57	...
87080	...	0.293	1.929	0.19	6.58	...

Appendix D. Sediment C/N ratios with depth for stations in the Bering Shelf/Anadyr and Alaska Coastal water masses.

Bering Shelf/Anadyr water mass stations

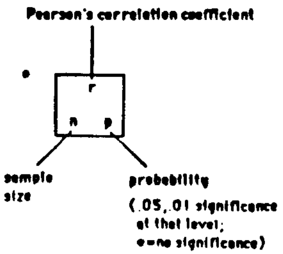
Stations	59081	59083	59120	59123	59132	74010	74024	
Depth (cm)	Sediment C/N ratios							$\bar{x}$
0	6.86	7.62	7.53	6.58	7.34	6.19	6.12	6.61
1	...	7.62	6.57	7.02	6.46	...	...	6.92
2	7.60	7.47	6.27	6.93	6.46	6.59	7.40	6.96
3	...	7.48	6.78	6.70	5.97	...	...	6.73
4	7.57	7.48	6.78	6.70	5.97	...	...	6.90
5	...	7.35	6.69	6.69	6.41	6.94	7.58	6.94
6	7.47	7.96	6.98	6.83	6.29	...	...	7.11
7	...	...	7.06	6.92	6.14	...	...	6.71
8	7.45	7.92	6.96	7.36	...	...	...	7.42
10	7.77	7.46	...	...	...	...	7.73	7.65
12	7.82	7.96	...	...	...	...	...	7.89
14	...	7.91	...	...	...	6.87	7.68	7.49

Alaska Coastal water mass stations

Stations	59085	59086	59088	59108	
Depth (cm)	Sediment C/N ratios				$\bar{x}$
0	8.07	9.49	10.00	8.92	9.12
1	7.84	8.56	8.91	7.96	8.32
2	8.00	8.47	8.89	8.42	8.45
3	7.96	8.22	8.42	8.44	8.26
4	8.06	9.07	9.40	7.99	8.63
5	7.73	9.42	9.48	7.75	8.60
6	8.13	9.72	8.60	...	8.82
8	8.19	9.44	10.06	...	9.23
10	8.07	9.02	11.08	...	9.39
12	8.04	...	10.08	...	9.06
14	7.82	9.66	10.22	...	9.23
16	...	...	8.47	...	8.47
18	...	...	10.65	...	10.65

Appendix E. Correlation matrix for all station parameters. Each box* contains r (the Pearson product-moment correlation statistic), n (the sample size) and p (the significance level). Heavy-edged boxes indicate those correlations that are significant at p=0.05 or 0.01 level.

	Temp. (°C)	Salinity (‰)	Sigma t	Depth (m)	Bot Chl a (mgm-3)	Int Chl a (mgm-2)	O_2 UR (mmol m-2 d-1)	Benthic fauna (gm-2)	Benthic fauna (gCm-2)	counts (no. m-2)	Modal phi size	TON (mgg-1)	TOC (mgg-1)	C/N
Temp. (°C)														
Salinity (‰)	-.755 84 .01													
Sigma t	-.850 83 .01	.973 83 .01												
Depth (m)	-.071 86 •	.180 84 •	.171 83 •											
Bot Chl a (mgm-3)	-.227 84 .05	.234 82 .05	.251 81 .05	.238 93 .05										
Int Chl a (mgm-2)	-.254 67 .05	.296 65 .05	.304 64 .05	.398 76 .01	.440 76 .01									
O_2 UR (mmol m-2 d-1)	-.393 64 .01	.263 63 .05	.324 62 .05	090 64 •	.240 66 .05	.133 54 •								
Benthic fauna (gm-2)	-.198 46 •	.158 45 •	.180 45 •	-.033 47 •	.221 47 •	.503 34 .01	.062 31 •							
Benthic fauna (gCm-2)	-.214 46 •	.241 45 •	.249 45 •	.405 47 .05	.505 47 .01	.691 34 .01	.268 31 •	.618** 49 .01						
counts (no. m-2)	-.128 46 •	.075 45 •	.116 45 •	.215 47 •	.338 47 •	.568 34 .01	.274 31 •	058 49 •	.507 49 .01					
Modal phi size	.114 39 •	-.044 38 •	-.078 38 •	.172 41 •	.198 43 •	.082 34 •	.007 32 •	-.001 33 •	.007 33 •	-.056 33 •				
TON (mgg-1)	.237 71 .05	-.009 69 •	-.124 68 •	.435 78 .05	.180 77 •	.083 64 •	.031 56 •	-.106 38 •	.120 38 •	-.013 38 •	.529 43 .01			
TOC (mgg-1)	.277 71 .05	-.031 69 •	-.143 68 •	.391 78 .01	.124 77 •	.034 64 •	-.017 56 •	-.149 38 •	.052 38 •	-.085 38 •	.373 43 .01	.981 78 .01		
C/N	.161 71 •	-.151 69 •	-.147 68 •	-.361 78 .01	-.240 77 .05	-.299 64 .05	-.266 56 .05	.322 38 •	-.428 38 .05	-.258 38 •	-.398 43 .05	-.186 78 •	-.046 78 •	



(.05, .01 significance at that level; • = no significance)

** without [illegible] stations, n=44, r=.948, p=.01 (see Fig. 3.6)

Appendix F. Dominant (95% cumulative density, wet weight, or organic carbon standing stock) taxa and species at benthic stations on the Bering/Chukchi shelf (after Stoker, 1981).

- Annelida
  - Polychaeta
    - Ampharetidae
      - *Ampharete acutifrons*
      - *A. reducta*
    - Capitellidae
      - *Capitella capitata*
    - Cirratulidae
      - *Chaetozone setosa*
    - Flabelligeridae
      - *Brada ochotensis*
      - *B. villosa*
      - *Flabelligera affinis*
    - Goniadidae
      - *Glycinde werini*
    - Lumbrineridae
      - *Lumbrinereis fragilis*
    - Maldanidae
      - *Axiothella catenata*
      - *Maldane sarsi*
      - *Nicomache lumbricalis*
      - *Praxillella praetermissa*
    - Nephtyidae
      - *Nepthys caeca*
      - *N. ciliata*
      - *N. longasetosa*
      - *N. rickettsi*
    - Ophelidae
      - *Travisia foresii*
    - Orbiniidae
      - *Haploscoloplos elongatus*
    - Pectinariidae
      - *Cistenides granulata*
      - *C. hyperborea*
    - Phyllodocidae
      - *Anaitides groenlandica*
    - Polynoidae
      - *Antinoella sarsi*
      - *Arcteobia anticostiensis*
      - *Harmothoe imbricata*
      - *Polynoe canadensis*

Appendix F. Continued.

- Sabellidae
  - *Chone duneri*
  - *C. infundibuliformis*
  - *Potamilla neglecta*
- Scalibregmidae
  - *Scalibregma inflatum*
- Sigalionidae
  - *Phloe minuta*
- Spionidae
  - *Spiophanes bombyx*
- Sternaspidae
  - *Sternaspis scutata*
- Terebellidae
  - *Artacama proboscidea*
  - *Nicolea venustula*
  - *Proclea emmi*
  - *Terebellides stroemi*

- Anthropoda
  - Amphipoda
    - Ampeliscidae
      - *Ampelisca burilai*
      - *A. macrocephala*
      - *Byblis gaimardi***
      - *Haploops laevis*
    - Aoridae
      - *Lembos arcticus*
    - Corophiidae
      - *Corophium crassicorne*
      - *Ericthonius tolli*
    - Gammaridae
      - *Melita dentata*
      - *M. formosa*
      - *M. quadrispinosa*
    - Haustoriidae
      - *Haustorius eous*
      - *Pontoporeia femorata*
    - Isaeidae
      - *Protomedeia fascata*
      - *P. grandimana*
      - *Photis spasskii*
    - Lysianassidae
      - *Anonyx nugax pacifica*
      - *Orchomene lepidula*

Appendix F. Continued.

- Oediceratidae
    - *Aceroides latipes*
    - *Bathymedon nanseni*
- Phoxocephalidae
    - *Harpinia gurjanovae*
    - *Paraphoxus milleri*
    - *P. simplex*

Cumacea

- Leuconidae
    - *Eudorella emarginata*
    - *E. pacifica*
    - *Eudorellopsis deformis*
    - *Leucon nasica*
    - *Leucon #2*

Mollusca

- Bivalvia
    - Astartidae
        - *A. borealis*
        - *A. montegui*
    - Cardiidae
        - *Clinocardium ciliatum*
        - *Cyclocardia crebricostata*
        - *Serripes groenlandicus*
    - Kellidae
        - *Pseudophthina rugifera*
    - Mytilidae
        - *Musculus niger*
    - Nuculidae
        - *Nucula tenuis**
    - Nuculanidae
        - *Nuculana minuta*
        - *N. radiata*
        - *Yolida hyperborea*
        - *Y. scissurata*
    - Tellinidae
        - *Macoma brota*
        - *M. calcarea*
        - *M. lama*
        - *M. loveni*
        - *Tellina lutea*

Appendix F. Continued.

- Thyassiridae
  - *Thyasira fluxuosa*
- Veneridae
  - *Liocyma fluctuosa*

Gastropoda
- Cylichnidae
  - *Cylichna nucleola*
- Turritellidae
  - *Tachyrhynchus erosus*

Echinodermata
- Echinoidea
  - Echinarachniidae
    - *Echinarachnius parma*
  - Strongylocentrotidae
    - *Strongylocentrotus droebachiensis*

- Holothuroidea
  - Synaptidae
    - *Cucumaria calcigera*

- Ophiuroidea
  - Amphiuridae
    - *Diamphiodia craterodmeta*
  - Gorgonocephalidae
    - *Gorgonocephalus caryi*
  - Ophiuridae
    - *Ophiura flagellata*
    - *O. maculata*
    - *O. sarsi*

Sipunculida
- Golfingiidae
  - *Golfingia margaritacea*

Priapulida
- Priapulidae
  - *Priapulus caudatus*

Echiurida
- Echiuridae
  - *Echiurus echiurus*

Appendix F. Continued.

- Chordata
  - Ascidiacea
    - Molgulidae
      - *Molgula siphonalis*
    - Styelidae
      - *Pelonaia corrugata*
      - *Styela rustica*
    - Rhodosomatidae
      - *Chelyosoma inaequale*

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* In the northern Bering and Chukchi Seas the bivalve *Nucula tenuis* recorded by Stoker (1978) is probably the species *Nucula belloti*, based on revised taxonomic descriptions. *N. tenuis* occurs in the southeastern Bering Sea, being replaced by *N. belloti* in the northern Bering and Chukchi Seas (N. Foster, pers. comm., University of Alaska Museum, Fairbanks).

** A new species of *Byblis* has been found by Highsmith and Coyle (unpubl. data), which may be combined with *B. gaimardi* in Stoker's data.

Appendix G. Carbon conversion values for dominant benthic fauna based on formalin-preseved wet weight biomass. Familial values were obtained directly from individual values for lowest taxa level available based on data from Stoker (1978). When two species per familial level were present (only 3 cases occurred) the mean value was used.

Taxa	Organic carbon as percent of total wet weight
Foraminifera	1.0
Cnidaria	
Anthozoa	6.1
Rhynchocoela	9.3
Annelida	
Polychaeta	6.9
F. Ampharetidae	6.9
F. Capitellidae	6.8
F. Cirratulidae	6.9
F. Flabelligeridae	4.4
F. Goniadidae	6.9
F. Lumbrineridae	9.3
F. Maldanidae	7.0
F. Magelonidae	6.9
F. Nephtyidae	7.2
F. Ophelidae	9.5
F. Orbiniidae	6.1
F. Oweniidae	6.9
F. Pectinariidae	4.5
F. Phyllodocidae	8.7
F. Polynoidae	7.3
F. Sabellidae	7.5
F. Sigalionidae	6.9
F. Spionidae	6.9
F. Sternaspidae	4.1
F. Syllidae	6.9
F. Terebellidae	6.1
Arthropoda	
Crustacea	
Amphipoda	7.4
F. Ampeliscidae	6.8
F. Corophiidae	6.6
F. Gammaridae	7.5
F. Haustoriidae	9.2
F. Isaeidae	6.8

Appendix G. Continued.

Taxa	Organic carbon as percent of total wet weight
F. Lysianassidae	8.1
F. Oediceratidae	7.4
F. Phoxocephalidae	7.4
F. Pleustidae	7.4
Cumacea	7.4
F. Diastylidae	7.4
F. Lampropidae	7.4
F. Leuconidae	7.4
Isopoda	
F. Anthuridae	7.4
Mollusca	
Bivalvia	2.8
F. Astartidae	1.5
F. Cardiidae	3.3
F. Montacutidae	2.8
F. Myidae	2.8
F. Nuculidae	3.9
F. Nuculanidae	4.7
F. Tellinidae	3.5
F. Thyasiridae	2.8
F. Veneridae	2.8
Gastropoda	6.2
F. Cylichnidae	6.2
F. Muricidae	6.2
F. Trochidae	3.0
F. Turridae	6.2
Polyplacophora	6.2
Ectoprocta	2.1
F. Alyconidiidae	2.1
Ectoprocta sp.	2.1
Echinodermata	1.8
Echinoidea	1.8
F. Echinarachniidae	0.8
F. Strongylocentrotidae	1.1
Holothuroidea	1.8
F. Synaptidae	1.8
Ophiuroidea	1.4
F. Amphiuridae	1.4
F. Ophiactidae	1.4

Appendix G. Continued.

Taxa	Organic carbon as percent of total wet weight
F. Ophiuridae	1.4
Priapulida	1.4
Sipunculida	4.5
F. Golfingiidae	4.5
Echiurida	
F. Echiuridae	5.1
Chordata	
Ascidiacea	4.1
F. Mogulidae	4.1
F. Pyuridae	4.1
F. Styelidae	1.4

Appendix H. Mean (and s.d.) abundance and biomass for benthic fauna in individual cluster groups.

Cluster Group	Station	x Abundance (no. m^{-2})	Biomass	
			y (g m^{-2})	z (g C m^{-2})
I	73075	8908	505.85	24.50
	73122	5555	241.97	13.99
	73018	7628	520.22	21.29
	73011	5845	405.20	19.65
	73024	6398	706.67	25.91
	73104	14,365	342.17	20.05
	73081	3245	308.18	17.43
	73027	8605	289.30	12.84
	59120	7383	725.42	32.24
	59123	5548	685.47	26.82
	59121	2865	739.49	29.52
Mean n=11		$\bar{x}$= 6940 s.d.= 3131	$\bar{y}$=497.27 s.d.= 191.65	$\bar{z}$=22.20 s.d.= 6.20
II	59148	2293	405.14	13.30
	74003	2765	86.29	3.23
Mean n=2		$\bar{x}$= 2529 s.d.= 338	$\bar{y}$= 245.72 s.d.=225.46	$\bar{z}$= 8.27 s.d.= 7.12
III	74010	9188	1593.22	58.95
	85090	12,115	629.60	32.36
	74011	2548	330.84	15.11
	85071	2048	118.01	8.52
	74023	2068	484.31	20.14
	73080	1668	493.14	17.70
	74053	7923	485.53	16.67
Mean n=7		$\bar{x}$=5365 s.d.=4286	$\bar{y}$=590.66 s.d.= 470.71	$\bar{z}$=24.21 s.d.= 16.92
IV	59081	900	388.84	13.65
	59149	3195	180.03	9.02
Mean n=2		$\bar{x}$=2048 s.d.=1623	$\bar{y}$=284.4 s.d.= 147.65	$\bar{z}$=11.3 s.d.= 3.27

Appendix H. Continued.

Cluster Group	Stations	x Abundance (no.m^{-2})	Biomass y (g m^{-2})	 z (gC m^{-2})
V	74009	2623	196.52	4.61
	85061	2433	411.99	7.44
	85094	785	34.97	1.69
Mean		$\bar{x}$=1947	$\bar{y}$=214.49	$\bar{z}$=4.58
n= 3		s.d.= 1011	s.d.= 189.15	s.d.= 2.88
VI	59150	1190	699.30	10.44
	73001	1418	257.43	7.36
	74024	2178	190.06	7.86
Mean		$\bar{x}$=1595	$\bar{y}$= 382.26	$\bar{z}$= 8.55
n= 3		s.d.= 517	s.d.= 276.62	s.d.= 1.65
VII	74055	4423	160.94	4.53
	74057	2370	883.76	8.34
	73058	5785	97.22	2.89
Mean		$\bar{x}$=4193	$\bar{y}$=380.64	$\bar{z}$=5.25
n=3		s.d.=1719	s.d.=436.88	s.d.=2.80
VIII	73002	1190	290.97	8.49
	73023	2510	894.40	22.33
	74002	1080	318.94	11.58
	85094	687	423.29	19.15
Mean		$\bar{x}$= 1367	$\bar{y}$=481.90	$\bar{z}$= 15.39
n= 4		s.d.=792	s.d.= 290.97	s.d.= 6.44
IX	74013	488	51.65	1.33
	74015	890	29.69	1.73
	74020	545	170.43	9.91
Mean		$\bar{x}$= 641	$\bar{y}$= 83.92	$\bar{z}$= 4.32
n=3		s.d.=218	s.d.= 75.72	s.d.= 4.84
X	59107	7770	35.32	1.95

Appendix H. Continued.

Cluster Group	Stations	x Abundance (no. m^{-2})	Biomass y (g m^{-2})	 z (g C m^{-2})
XI	59180 73057 73122	315 305 1535	108.61 17.58 39.00	3.04 1.03 1.82
Mean n= 3		$\bar{x}$= 718 s.d.= 707	$\bar{y}$= 55.063 s.d.= 47.59	$\bar{z}$=1.96 s.d.=1.013
XII	59074	140	42.00	2.01
XIII	59071	463	2143.76	18.57
XIV	59134 59135	1558 1810	744.84 517.48	11.27 13.67
Mean n= 2		$\bar{x}$= 1684 s.d.= 178	$\bar{y}$= 631.16 s.d.= 160.77	$\bar{z}$=12. 47 s.d.= 1.70
XV	59070	313	549.60	22.90
XVI	74025	193	71.28	3.86
XVII	59132	188	2376.97	20.92

Appendix I. Dominant faunal families by abundance and biomass for benthic stations within each individual cluster group in the northern Bering and Chukchi Seas.

Cluster Group	Station	Family	Abundance (no. m^{-2})	Family	Biomass (g C m^{-2})
I	73075	Ampeliscidae	6410	Ampeliscidae	15.15
		Isaeidae	958	Astartidae	2.22
		Capitellidae	220	Lysianassidae	1.30
	73122	Ampeliscidae	4063	Ampeliscidae	7.92
		Isaeidae	418	Nuculanidae	1.81
		Phoxocephalidae	203	Rhynchocoela sp.	1.19
	73018	Ampeliscida	5948	Ampeliscidae	12.72
		Isaeidae	658	Astartidae	3.39
		Lysianassidae	210	Tellinidae	1.45
	73011	Ampeliscidae	4558	Ampeliscidae	10.05
		Isaeidae	508	Tellinidae	2.85
		Lysianassidae	198	Nephtyidae	2.57
	73024	Ampeliscidae	4060	Ampeliscidae	10.12
		Isaeidae	863	*Alcyonidiidae	7.71
		Phoxocephalidae	263	Tellinidae	2.55
	73104	Ampeliscidae	9298	Ampeliscidae	13.69
		Isaeidae	1213	Nuculanidae	2.06
		Phoxocephalidae	900	Cardiidae	0.79
	73081	Ampeliscidae	1573	Ampeliscidae	11.03
		Tellinidae	73	Tellinidae	1.89
		Nuculidae	70	Nuculidae	1.28
	73027	Ampeliscidae	3230	Ampeliscidae	7.23
		Isaeidae	3085	*Alcyonidiidae	1.16
		Phoxocephalidae	420	Astartidae	1.15
	59120	Ampeliscidae	5990	Ampeliscidae	18.20
		Lysianassidae	373	Tellinidae	5.03
		Isaeidae	195	Cardiidae	2.72
	59123	Ampeliscidae	4695	Ampeliscidae	10.65
		Lysianassidae	175	Tellinidae	8.63
		Tellinidae	85	Astartidae	1.58
	59121	Ampeliscidae	2065	Tellinidae	12.66
		Tellinidae	243	Ampeliscidae	8.65
		Phoxocephalidae	65	Veneridae	1.49

Appendix I. Continued.

Cluster Group	Station	Family	Abundance (no. m^{-2})	Family	Biomass (g C m^{-2})
II	59148	Leuconidae	495	Tellinidae	8.24
		Ampeliscidae	383	Sternaspidae	1.01
		Orbiniidae	238	Ampeliscidae	0.68
	74003	Oweniidae	1480	Tellinidae	1.22
		Alcyonidiidae	340	Oweniidae	0.77
		Isaeidae	208	Alcyonidiidae	0.50
III	74010	Ampeliscidae	4408	Tellinidae	35.96
		Phoxocephalidae	940	Ampeliscidae	7.78
		Isaeidae	598	Nuculidae	4.51
	85090	Ampeliscidae	2715	Nuculidae	8.72
		Nuculidae	1713	Ampeliscidae	5.75
		Haustoriidae	1405	Anthozoa sp.	3.60
	74011	Synaptidae	658	Nuculidae	5.35
		Nuculidae	373	Nephtyidae	2.81
		Gammaridae	353	Rhynchocoela sp.	1.64
	85071	Ampeliscidae	383	Nephtyidae	3.97
		Haustoriidae	313	Maldanidae	1.40
		Capitellidae	270	Haustoriidae	1.14
	74023	Nuculidae	680	Nuculidae	13.24
		Ampeliscidae	335	Sternaspidae	2.26
		Capitellidae	303	Anthozoa sp.	1.98
	73080	Phoxocephalidae	678	Nuculidae	6.60
		Nuculidae	250	Tellinidae	5.41
		Isaeidae	125	Cardiidae	2.88
	74053	Isaeidae	3783	Tellinidae	5.26
		Nuculidae	1218	Nuculidae	3.59
		Leuconidae	1053	Nephtyidae	1.91
IV	59081	Nuculidae	273	Tellinidae	6.32
		Tellinidae	140	Nuculidae	3.85
		Isaeidae	113	Anthozoa sp.	2.57
	59149	Nuculidae	1840	Ampeliscidae	2.09
		Ampeliscidae	408	Nephtyidae	1.76
		Tellinidae	363	Golfingiidae	1.35

Appendix I. Continued.

Cluster Group	Station	Family	Abundance (no. m^{-2})	Family	Biomass (g C m^{-2})
V	74009	Tellinidae	565	Cardiidae	1.64
		Phoxocephalidae	378	Styelidae	1.52
		Nuculidae	328	Nuculidae	0.54
	85061	Thyasiridae	380	Styelidae	5.13
		Styelidae	360	Nuculidae	0.79
		Oediceratidae	238	Nephtyidae	0.76
	85064	Sternaspidae	90	Sternaspidae	0.87
		Phoxocephalidae	85	Nephtyidae	0.57
		Oediceratidae	75	Nuculanidae	0.07
VI	59150	Echinarachniidae	230	Echinarachniidae	4.58
		Maldanidae	130	Nephtyidae	2.82
		Isaeidae	125	Tellinidae	1.22
	73001	Cirratulidae	250	Nephtyidae	2.16
		Capitellidae	195	Holothuroidea sp.	1.23
		Amphiuridae	135	Styelidae	1.21
	74024	Echiuridae	545	Nuculidae	3.45
		Nuculidae	520	Tellinidae	1.17
		Phoxocephalidae	213	Nephtyidae	0.83
VII	74055	Echiuridae	880	Cardiidae	1.36
		Oediceratidae	808	Oediceratidae	0.66
		Ampharetidae	688	Echinarachniidae	0.55
	74057	Foraminifera sp.	780	Echinarachniidae	6.64
		Haustoriidae	230	Cardiidae	0.89
		Nuculidae	225	Nephtyidae	0.23
	73058	Isaeidae	4905	Isaeidae	0.85
		Phoxocephalidae	218	Nephtyidae	0.63
		Echinarachniidae	190	Echinarachniidae	0.40
VIII	73002	Corophiidae	273	Tellinidae	1.82
		Capitellidae	165	Molgulidae	1.40
		Gammaridae	98	Maldanidae	1.13
	73023	Ampeliscidae	365	Molgulidae	8.41
		Isaeidae	358	Cardiidae	4.28
		Phoxocephalidae	315	Ampharetidae	2.23

Appendix I. Continued.

Cluster Group	Station	Family	Abundance (no. m^{-2})	Family	Biomass (g C m^{-2})
	74002	Orbiniidae	125	Cardiidae	1.77
		Pectinariidae	125	Pectinariidae	1.54
		Gammaridae	80	Ampharetidae	1.53
	85094	Maldanidae	80	Nephtyidae	5.50
		Polynoidae	67	Maldanidae	4.10
		Golfingiidae	50	Golfingiidae	2.47
IX	74013	Nuculidae	163	Ophiuridae	0.44
		Nuculanidae	60	Nuculanidae	0.28
		Ophiuridae	45	Nuculidae	0.23
	74015	Ophiuridae	215	Maldanidae	0.84
		Maldanidae	183	Nephtyidae	0.30
		Leuconidae	138	Trochidae	0.13
	74020	Ampeliscidae	143	Golfingiidae	3.17
		Maldanidae	88	Nephtyidae	2.43
		Capitellidae	83	Maldanidae	1.25
X	59107	Isaeidae	6710	Isaeidae	1.12
		Ampeliscidae	450	Ampeliscidae	0.34
		Phoxocephalidae	198	Golfingiidae	0.12
XI	59108	Echinarachniidae	160	Tellinidae	1.38
		Orbiniidae	30	Veneridae	0.56
		Oediceratidae	28	Nephtyidae	0.29
	73057	Nuculidae	78	Nephtyidae	0.37
		Oediceratidae	38	Lumbrinereidae	0.22
		Hautoriidae	33	Cardiidae	0.11
	73022	Isaeidae	1160	Ophelidae	0.50
		Echinarachniidae	185	Nephtyidae	0.48
		Cardiidae	25	Isaeidae	0.24
XII	59074	Maldanidae	35	Nephtyidae	1.34
		Nuculidae	20	Phyllodocidae	0.33
		Nephtyidae	15	Syllidae	0.15
XIII	59071	Echinarachniidae	335	Echinarachniidae	16.26
		Alcyonidiidae	18	Alcyonidiidae	1.04
		Trochidae	15	Nephtyidae	0.40

Appendix I. Continued.

Cluster Group	Station	Family	Abundance (no. m^{-2})	Family	Biomass (g C m^{-2})
XIV	59134	Ophiuridae	1128	Strongylocentrotidae	6.58
		Ophiactidae	178	Cardiidae	1.23
		Strongylocentrotidae	58	Anthozoa sp.	1.16
	59135	Ophiuridae	1270	Alcyonacea Neptheidae	4.75
		Ophiactidae	140	Nephtyidae	3.19
		Strongylocentrotidae	58	Stronglylocentrotidae	1.90
XV	59070	Terebellidae	80	Pyuridae	12.10
		Sabellidae	80	Sabellidae	3.05
		Nephtyidae	28	Nephtyidae	2.64
XVI	74025	Golfingiidae	28	Cardiidae	2.78
		Maldanidae	25	Anthozoa sp.	0.34
		Syllidae	15	Maldanidae	0.30
XVII	59132	Echinarachniidae	118	Echinarachniidae	16.76
		Nephtyidae	23	Strongylocentrotidae	1.87
		Strongylocentrotidae	10	Cardiidae	1.38

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*The dominant species, *Alyconidiidae vermiliforma*, is a filamentous, gelatinous bryozoan. Values presented are minimum for stations in 73024 and 73027 where extremely large amounts were collected and originally misinterpreted at sea.

Appendix J. Sediment oxygen uptake and water mass for stations in the northern Bering and Chukchi Seas. Rates are for duplicate experiments except where standard deviation is blank, indicating only one sediment core was measured.

Station	Average oxygen uptake rate (mmol O_2 m^{-2} d^{-1})	Standard deviation	Water mass	
			Bering Shelf/ Anadyr	Alaska Coastal
59071	12.62	...	x	
59081	22.12	4.46	x	
59082	31.07	16.89	x	
59083	23.86	1.85	x	
59084	17.62	0.74	x	
59085	9.46	0.00		x
59086	9.93	1.27		x
59120	45.62	3.71	x	
59121	26.25	9.54	x	
59123	18.62	4.82	x	
73002	15.74	...		x
73011	23.76	6.29	x	
73018	28.56	...	x	
73019	2.04	...	x	
73023	1.75	0.93		x
73024	15.91	7.67	x	
73027	21.08	...	x	
73028	15.38	0.27	x	
73029	8.42	...	x	
73030	19.31	11.82	x	
73038	16.63	...	x	
73058	18.01	...		x
73071	41.60	...	x	
73075	16.23	0.37	x	
73081	11.18	0.64	x	
73104	7.88	0.74	x	
73112	1.82	1.01	x	
73113	5.53	...	x	
73120	10.49	7.52	x	
73121	17.96	9.85	x	
73122	11.72	...	x	
74003	3.63	...		x
74010	14.16	11.50	x	
74011	7.95	6.32	x	

Appendix J. Continued.

Station	Average oxygen uptake rate (mmol O_2 m^{-2} d^{-1})	Standard deviation	Water mass	
			Bering Shelf/ Anadyr	Alaska Coastal
74012	1.07	0.64		x
74013	11.66	1.33		x
74015	3.65	0.10		x
74020	1.93	0.50		x
74021	2.63	0.83		x
74023	9.20	7.15	x	
74024	21.38	0.59	x	
74025	0.65	0.37		x
74026	6.41	1.19	x	
74027	6.79	...	x	
74028	6.76	0.59	x	
74033	2.99	0.45	x	
85003	3.19	...		x
85004	18.15	6.19	x	
85015	18.15	4.00		x
85024	28.94	...	x	
85037	16.66	6.00	x	
85047	31.62	...	x	
85048	30.80	0.11	x	
85071	28.19	3.12	x	
85090	24.34	4.21	x	
85094	19.37	6.63		x
85106	29.02	1.51	x	
85108	30.82	3.60	x	
87080	37.92	...	x	
87088	28.28	8.63	x	
87114	28.19	5.54	x	