WINTER STUDIES OF UNDER-ICE BENTHOS ON THE

CONTINENTAL SHELF OF THE NORTHEASTERN BERING SEA

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Dean of College
of Mathematics, Physical Sciences,
and Engineering

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and Advanced Study

WINTER STUDIES OF UNDER-ICE BENTHOS ON THE CONTINENTAL SHELF OF THE NORTHEASTERN BERING SEA

A
THESIS

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University of Alaska in Partial Fulfillment
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MASTER OF SCIENCE

By

Samuel Whiteford Stoker
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ABSTRACT

A total of 76 samples from 16 benthic stations over the eastern Bering Sea shelf were taken between 31 January and 17 February, 1970 for purposes of assessing the quantity and distribution of benthic macrofauna. A total of 129 species or taxa were found, with an average density of 1,133 indiv/m^2 and average biomass of 127 g wet/m^2. Species were subjected to elemental analysis for determination of organic carbon and nitrogen content, yielding average values of 5.1% carbon and 1.1% nitrogen expressed as percentage wet weight, which translated into biomass values of 6.5 g C/m^2 and 1.4 g N/m^2 averaged over all stations. Correlation studies yielded 9 species affinity groups, and regression analysis indicated that about 40% of the variability of distribution and density of the major species could be accounted for by salinity, sediment mode particle size, depth, temperature, or dissolved oxygen, with no one factor assuming dominance. Of the 129 species or taxa, 35 account for about 80% of total numbers, wet weight biomass, or carbon biomass, with 8 species making up over 50% of the totals in all categories. Of these 35 major species, 8 are known to be food species of the Pacific walrus. These 8 comprise only 10% of the total number of individual organisms encountered, but make up 60% of the wet weight biomass and 49% of the carbon biomass over the region sampled.

ACKNOWLEDGMENTS

I wish to express my gratitude and appreciation to Dr. C. Peter McRoy, under whose supervision this study was undertaken, and to the U. S. Coast Guard and in particular the officers and men of the U.S.C.G.C. Northwind, without whose cooperation the study would not have been possible.

In addition I would like to thank Dr. Howard Feder and Dr. John Goering for their advice and assistance, Mr. George Mueller for his help in identifying the organisms found, and Dr. Daniel Hawkins and Mr. Ivan Frohne for their advice and assistance in statistical analysis and data reduction.

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INTRODUCTION

Considering our present level of knowledge concerning the sublittoral benthos of the world ocean, that of the continental shelf of the Bering Sea is relatively well known and thoroughly investigated, though even here huge areas are very poorly known, and our understanding of processes and controlling factors is severely limited. Based on currently available literature (e.g. reviews by Filatova and Barsanova, 1964; Kuznetsov, 1964; Neyman, 1960), there seem to be no samples or data available for Norton Sound, for instance, nor for that vast area between St. Lawrence Island and Bering Strait known as the Chirikof Basin. There is also as yet a complete lack of information regarding growth, turnover, and productivity rates for the Bering Sea benthos, and only scanty data upon which to evaluate controlling ecological factors. In addition, all previous studies have been seasonal in nature, confined to the ice-free summer months, with nothing known about the effects of winter ice cover upon the benthos.

The present study was initiated in January, 1970, with a 17 day sampling program conducted by the University of Alaska along the cruise track of the U. S. Coast Guard Icebreaker Northwind through the ice-locked northeast Bering Sea (Fig. 1).

The objectives of this study were: (1) to investigate benthic distribution and standing stock beneath the winter ice pack; (2) to compare results with estimates by Soviet investigations during the summer; (3) to evaluate the effect of ice cover upon the benthos;

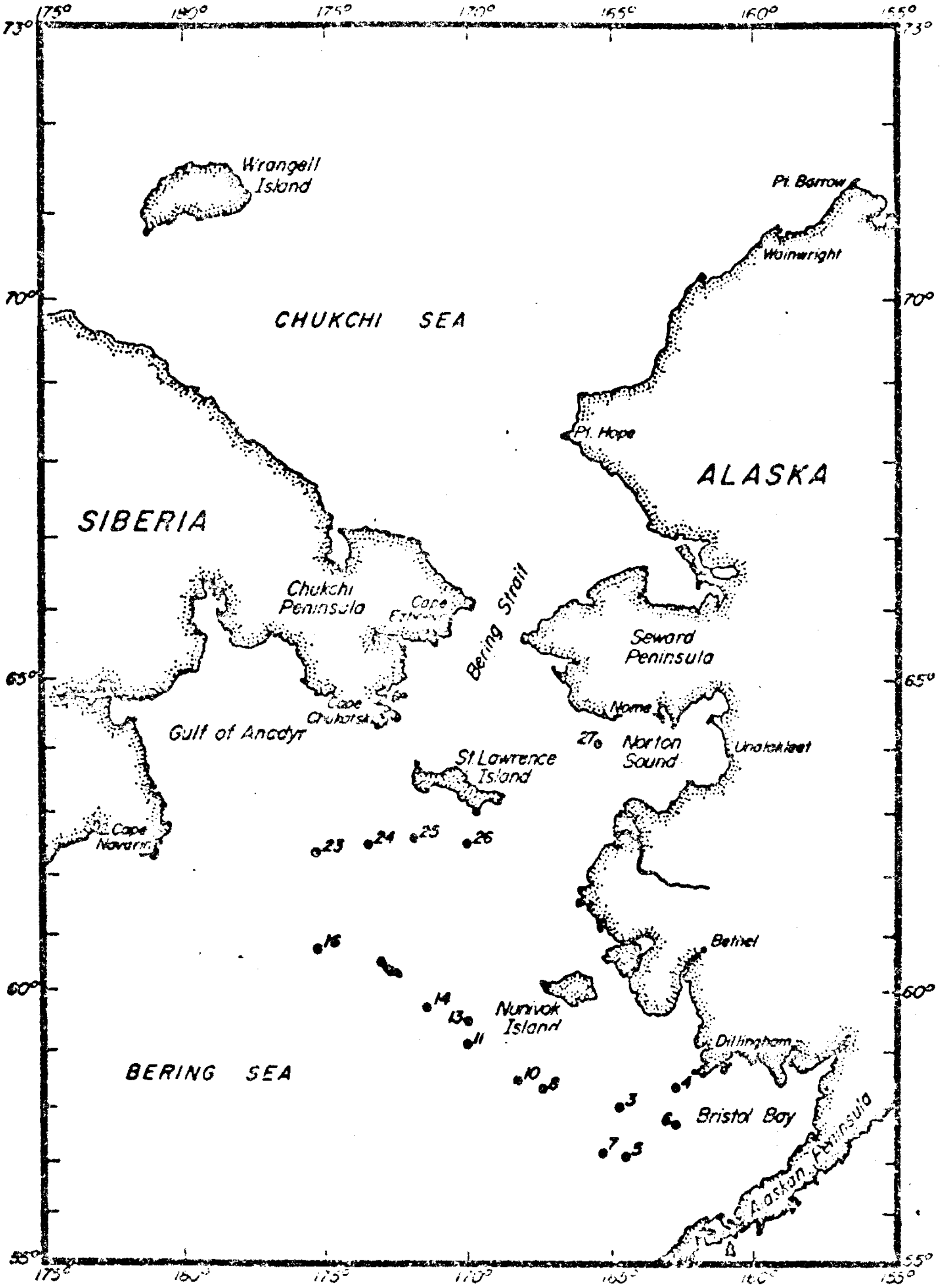

Figure 1. Benthic stations on the Bering Sea shelf, 31 Jan–17 Feb, 1970.

(4) to correlate distribution and abundance with observed environmental factors; and (5) to assess the proportion of benthic standing stock available as winter food for the Pacific walrus population. In addition, it was hoped that this study would lay the groundwork for future investigations of benthic productivity over the northeast Bering Sea shelf, particularly for those species essential to food webs of benthic feeding marine mammals. The major species encountered were submitted to elemental analysis to determine organic carbon and nitrogen content. It is felt these data provide more precise information regarding standing stock, particularly for food web and energy flow studies, and would be more applicable to productivity studies than the conventional wet weight or dry weight values.

Description of Study Area

The continental shelf of the Bering Sea is one of the largest in the world ocean, comprising 45% of the Bering Sea proper, with an area of 1,015,438 km^2 (Lisitsyn, 1969). This shelf area includes Bristol Bay, Norton Sound, the Gulf of Anadyr, and all the region lying north and east of the Pribilof Islands (Fig. 1).

The Bering Sea is essentially an embayment of the North Pacific, separated from it only by the Aleutian-Komandorsky Island systems and the Alaska Peninsula. The sills between these islands are often of great depth, sometimes exceeding 4,000 meters (Filatova and Barsanova, 1964), permitting virtually unrestricted exchange. The greater part of this exchange seems to take place through the Komandorsky passes on the western side, where the straits are more numerous and broader, and the sill depths greater. By contrast, the exchange with the Chukchi Sea and Arctic Ocean is limited to Bering Strait, 92 km wide and less than 50 meters deep, and is a one-way exchange, from south to north. Thus the fauna of the Bering is predominantly of Pacific origin, the Arctic forms limited to those few shallow water species which have penetrated south through Bering Strait in opposition to the normal current flow.

The circulation of the Bering forms a huge counter-clockwise gyre moving north along the eastern side, thus endowing the eastern Bering with warmer bottom temperatures (Filatova and Barsanova, 1964). The main body of this flow swings westwardly below St. Lawrence Island and back south along the western margin, with a portion continuing north past St. Lawrence and through Bering Strait (Lisitsyn, 1969).

There are only 3 major rivers emptying into the Bering - the Anadyr on the western side and the Yukon and Kuskokwim on the eastern. These three rivers account for 67% of the total runoff of 403.4 km^3/yr received by the Bering, with the Yukon providing 46% of this total (Lisitsyn, 1969). The importance of the Yukon-Kuskokwim outflow into the Bering may be misleading, however, in terms of present sediment deposition. Surface sediments from Norton Sound, in the path of the Yukon plume, indicate that the bulk of Yukon sediments are not being deposited upon entering the Bering, but are carried north into the Chukchi (D. M. Hopkins U.S.G.S., Menlo Park, personal communication).

The Anadyr, on the western side, appears to plume south and out over the abyssal Commander Basin (Filatova and Barsanova, 1964). These observations have been limited to summer, and may not reflect winter conditions when the Bering Sea shelf is largely ice-bound. During a recent winter submarine survey beneath the ice pack we observed a heavy turbid layer extending from about 35 meters to the bottom over the shelf between St. Matthew and St. Lawrence Islands, indicating a heavy suspended sediment load and possible winter deposition, of unknown type or origin (Stoker, unpublished data from U.S.C.G.C. Burton Island Cruise, 1972).

The Bering Sea shelf is extremely flat, with an average slope of 4 to 6 cm/km, exhibiting only scattered minor relief in the form of gently sloping depressions and low mounds and ridges, thought to be sediment-buried relics of sub-aerial erosion and glaciation during the Pleistocene (Scholl *et al.*, 1968). The sediments of the shelf are generally very well-sorted terrigenous materials, steadily decreasing in particle size with depth from medium sand in the shallow zones to silt-clay at 100 meters.

The primary productivity of the Bering Sea is quite high, averaging 1.46 mgC/m^3-hr for Bristol Bay and 1.71 mgC/m^3-hr over the major part of the northeast shelf in summer (Taniguchi, 1969). Summer productivity in the Chirikof Basin, north of St. Lawrence Island, is even higher, 18.2 mgC/m^3-hr at the one station sampled (McRoy *et al.*, 1972). This productivity rate compares favorably with the highest values encountered in the world ocean. Recent investigations also indicate that productivity may be maintained at fairly high rates during the ice-covered months, at least during late winter and early spring, by diatoms utilizing the under surface of the pack ice as a substrate (McRoy *et al.*, 1972), though the productivity of the water column beneath the ice is negligible during this period. The degree to which primary productivity rates and patterns are reflected in the benthos is uncertain, though it has been shown in other areas that correlations do exist (Rowe, 1969).

Past Benthic Investigations in the Bering Sea

The benthic fauna of the Bering shelf has been observed to be abundant and diverse, and is important as a vital link in the food webs of epifaunal invertebrates, commercially valuable fishes, and marine mammals. Past investigations of the Bering shelf benthos have been primarily Soviet, with major emphasis on the western shelf and the Gulf of Anadyr. These studies have been rather extensive and complete in defining distribution and wet weight standing stock during summer months, but contain no winter observations and include inadequate analysis of productivity, energy flow, or controlling physical and biological factors.

Soviet studies have described the benthic faunal assemblages in two ways, by feeding type (Kuznetsov, 1964), and by dominant species (Filatova and Barsanova, 1964; Neyman, 1960). By feeding type the shelf benthos is composed of five trophic groups: sessile seston feeders, mobile and partly mobile seston feeders, selective detritus feeders, nonselective detritus feeders, and carnivores (Kuznetsov, 1964). Kuznetsov's trophic classification are retained throughout the present study. In all descriptions of faunal assemblages by dominant species, major elements of more than one trophic group are found, though generally one trophic group does dominate, at least numerically.

From a review of available literature it appears that at least seven physical factors influence the qualitative and quantitative distribution of Bering Sea benthic fauna. These factors are sediment particle size, bottom temperature, salinity, depth, sedimentation rates, circulation intensity, and suspended particulate content. Several of these conditions are closely interdependent. There seems to be a close correlation between sediment particle size, depth, and circulation intensity, with particle size decreasing with depth and increasing with intensified circulation. Though it is difficult or impossible, given the data available, to define just what the controlling factors are, or what their influence is, it does appear possible to predict in a general sense the faunal types and abundance to be found in a given area from descriptions of sediment particle size, bottom temperature, and depth (Neyman, 1960). Thus for the eastern Bering shelf in summer, with a mean biomass of 74 g/m^2, wet weight, the maximum average standing stock, 211 g/m^2, is attained on mud, muddy sand, and sandy mud at depths of 50-150 meters. At less than 50 meters the bottom is sand, with a biomass of 8-50 g/m^2, and at depths greater than 150 meters, where fine, soft mud prevails, the biomass decreases to 20-30 g/m^2. The highest local biomass occurs just south of St. Lawrence Island on muddy sand, reaching 500 g/m^2 (Neyman, 1960). Neyman (1960) conjectures that this high biomass is an indirect reflection of the low bottom temperatures of this region, which exclude benthic feeding fishes.

The maximum bivalve mollusc biomass, 300 g/m^2, occurs on the northwestern shelf on muddy sand bottom, dominated by the species *Macoma calcarea*, *Leda pernula*, *Nucula tenuis*, and *Serripes groenlandicus* (Neyman, 1960). In deeper water, on muddy bottom, *Yoldia hyperborea* and *Yoldia thraciaeformis* seem to predominate, while on the shallower southeastern shelf, with fine sand bottom, *Cyclocardium crebricostata* and *Clinocardium ciliatum*, with maximum biomass of 90 and 160 g/m^2 respectively, are the leading bivalves. This distribution likely reflects both sediment type and bottom temperature as well as circulation patterns and suspended particulate content (Neyman, 1960). The main concentrations of *Macoma calcarea*, *Nucula tenuis*, *Leda pernula*, and *Yoldia hyperborea* are described at bottom temperatures below 3°C, with *Macoma calcarea* seeming to prefer the -1°C to +1°C range and *Yoldia hyperborea* the 2-3°C range. *Yoldia thraciaeformis* is described as preferring temperatures around 2°C, while *Cyclocardium crebricostata* is found at temperatures exceeding 3°C (Neyman, 1960). These descriptions were all based on summer studies.

The maximum biomass of the echinoid *Echinarachnius parma*, 494 g/m^2, is found south of St. Lawrence on muddy sand with bottom temperature between 2°C and 11°C. The asteroid *Ctenodiscus crispatus* is found at depths exceeding 100 meters on mud bottom with temperatures in the 2-5°C range, where it reaches 200 g/m^2, while the holothurian *Chiridota* sp., attaining a biomass of 70 g/m^2, is found at the 100-200 meter depth on sand-gravel bottom just north of the Pribilofs. The most common echnioderm seems to be the ophiuroid *Ophiura sarsi*, which occurs on muddy sand south of St. Lawrence. At temperatures under 2°C this species attains a biomass of 140 g/m^2, falling to 82 g/m^2 at temperatures between 2°C and 3°C, and decreasing further, to 42 g/m^2, in the 3-4°C range, indicating a strong temperature preference (Neyman, 1960).

The maximum polychaete biomass, between 50 and 100 g/m^2, occurs on muddy sand at temperatures greater than 2°C, while maximum amphipod biomass, 30 g/m^2, is found on muddy sand at the 0-1°C range (Neyman, 1960).

METHODS

Benthic sampling during the Northwind cruise of 31 Jan-17 Feb, 1970, was begun in Bristol Bay, continued as conditions and opportunity permitted from there northwest to the International Date Line, recommenced upon recrossing the date line southwest of St. Lawrence Island, and continued east to beyond St. Lawrence and then north to Nome (Fig. 1). Five replicates were taken at each station for faunal collection and a sixth for sediment analysis, using a 0.1 m^2 surface area van Veen grab or modified Petersen grab. Stations 3 through 13 were collected with a van Veen, after which the grab was lost. The remaining stations, 14 through 27, were collected with a Petersen grab. The Petersen was modified by weighting with 5 kg lead, by removing the chain-drive closing mechanism and replacing it with one using 3/8 inch stainless steel cable, and by adjusting the tripping lever. Such modifications were necessary due to freezing conditions. After modification the grab functioned as efficiently as the van Veen and achieved about the same depth of penetration (Table 1). In using either grab a maximum descent velocity of about 125 m/min could be achieved without preliminary tripping.

Upon retrieval of the grab the sediment volume was measured to estimate the depth of grab penetration. Samples were sieved through 3 mm and 1 mm stainless steel screens, the retained organisms separated from debris and preserved in 6% formalin buffered with sodium borate, labeled, and retained for sorting and analysis at the University of Alaska campus in Fairbanks.

A sediment sample was also taken, frozen, and returned to Fairbanks for sediment particle size analysis using standard determination techniques (Krumbein and Pettijohn, 1938).

At each station benthic sampling was conducted in conjunction with a coexisting program of the University of Alaska that provided data on temperature, salinity, dissolved oxygen and inorganic nutrients.

Table 1. Environmental data from benthic sampling stations on the Bering Sea shelf, 31 Jan–16 Feb, 1970 (see Fig. 1 for station locations).

				Bottom Water		
Station	Depth m	Sediment Mode Phi Units	Grab Penetration cm	Temp. °C	Oxygen ml/liter	Salinity °/oo
3	59	3.75	1.7	0.74	7.23	32.24
4	24	2.75	3.4	-1.72	7.74	31.60
5	69	4.00	3.0	0.64	7.17	32.16
6	45	2.75	4.0	-1.71	7.61	31.66
7	63	3.75	3.0	0.65	7.57	31.90
8	63	3.75	3.8	-0.08	7.34	32.03
10	62	3.75/2.75	5.5	-1.22	7.51	31.79
11	63	3.75	5.1	0.18	7.30	32.02
13	54	--	5.0	-0.29	7.39	31.92
14	99	5.00	4.2	-0.23	7.46	32.29
16	103	4.00	10.5	0.72	7.30	32.50
23	90	6.00/3.75	7.8	-0.71	7.30	32.27
24	70	3.75	8.5	-1.75	7.56	31.70
25	54	3.75	3.5	-1.74	7.50	31.58
26	45	2.75	1.6	-1.70	7.46	31.68
27	20	4.00	2.0	-1.73	8.13	32.14
Averages	61	3.80	4.5	-0.62	7.47	31.97

measurement of primary productivity, and observations of marine mammals and birds (McRoy, unpublished data; McRoy *et al.*, 1972, McRoy, Stoker *et al.*, 1971).

Over the following year, at Fairbanks, the samples were sorted into phyla and subsequently identified, when possible, to genus, species, and feeding type. The number of individuals of each species was recorded for each sample, and the total wet weight of each species in each sample obtained.

Prior to weighing, specimens were allowed to blot on absorbent paper for about 10 minutes. Representative specimens of each species were dried at 90°C for 8 hours in a vacuum oven and weighed again to obtain dry/wet weight ratios. For the determination of mollusk dry/wet weight ratios the shells were removed when possible and shell weight ratios calculated. These dried specimens were then pulverized, acidified with 10% HCl solution to replace carbonates, dried for 8 hours at 90°C, and analyzed for organic carbon and nitrogen content using a Perkin-Elmer model 240 CHN Microanalyzer. At least two replicates were run for each sample.

The data were processed by an IBM-360/40 computer using a program written by Ivan Frohne and Sam Stoker for determination of sample and station means in terms of number of individuals, wet weight biomass, dry weight biomass, organic carbon and nitrogen values, and average weight per individual in terms of carbon and nitrogen. Means were determined for each species, genera, class, and phyla at each sample and station, and totals accumulated for each sample and station.

RESULTS

Seventy-seven samples were collected from 16 benthic stations on the ice-covered shelf of the northeast Bering Sea between 31 January and 17 February, 1970. These stations represent a transect from Bristol Bay northwest to the International Date Line, and from the Date Line back north and east to the vicinity of Nome (Fig. 1).

Physical Description of the Stations

The Bering Sea shelf over the area sampled is very flat and uniform in physical structure and configuration. This area was exposed to subaerial erosion and leveling during the Pleistocene, and represents a flooded peneplain of primarily relic, well-sorted, terrigenous sediments (Scholl *et al.*, 1968). The average depth over the 16 stations sampled was 61 meters, with a range of from 20 meters at Station 27, in Norton Sound, to 103 meters at Station 16, west of St. Matthew Island.

The sediment particle size over this transect ranged from a phi size of 2.75, in the medium sand category, to 6.00, representing coarse to medium silt. The mean phi size encountered was 3.80, in the medium sand range. With the exception of Station 14, with mode size of 5.0, and Station 23, with mode size 6.0, all stations fall in the 2.75 to 4.0 range, representing fine to medium sand. The general trend is for the finer sediment modes to be found at the deeper stations (Table 1). This leaves the relatively coarse phi mode size of 4.00 described at Station 16 open to doubt. Likewise, the phi size of 4.00 found at

Station 27 is considered doubtful considering the shallow depth, though in this case it may be due to a very local abberation. Quantities of eelgrass (*Zostera marina*) detritus were found in the samples at Station 27. It is presumed that this detritus and associated sediments originated in the eelgrass beds along the southern margin of the Seward Peninsula and were carried to the vicinity of Station 27 by ice-rafting or some other mechanism, which possibly accounts for the fine sediment size. In general, the sediments were found to be unimodal and well sorted, with only Stations 10 and 23 yielding bimodal samples (Table 1). At almost all stations quantities of dead mollusc shells and shell fragments were found, and at Stations 16 and 23 numerous polished pebbles, of basaltic composition, from 1 to 2 cm in diameter were encountered. These pebbles may be the result of ice-rafting from St. Lawrence and St. Matthew Islands, or may be the result of benthic-feeding walrus. Walrus are known to ingest quantities of stones and pebbles when feeding, which are subsequently defecated upon the moving ice and thus transported to remote areas (J. Burns, Alaska Dept. Fish and Game, personal communication). The vicinities of Stations 16 and 23 are known to be areas of heavy winter concentrations of feeding walrus (Burns, 1965).

Salinities at the stations sampled proved to be fairly uniform, ranging from 31.58 °/₀₀ to 32.50 °/₀₀ with an average value of 31.97 (McRoy, unpublished data). Dissolved oxygen values were also rather uniform, and always near saturation, ranging from 7.17 to 8.13 ml/liter, with mean value of 7.47 (Table 1). With the exception of Station 27, all oxygen values fell in the range of from 7.17 to 7.74. The bottom temperatures over the transect averaged -0.62°C, with a range of from -1.75 to 0.74°C, the warmer temperatures generally being encountered at the deeper stations. All salinity, oxygen, and temperature values noted above and listed in Table 1 are for near-bottom water between 31 January and 17 February, 1970.

At this time of year the pack ice in the Bering is at about its maximum extent in terms of both coverage and thickness. The southern ice edge at that time of year normally extends about to the limits of the continental shelf, with a thickness of from 1 to 2 meters (McRoy *et al.*, 1972). This ice is subject to considerable wind stress, and is constantly breaking up, shifting, and reforming, creating numerous pressure ridges and open leads.

The water column at this time of year is generally well-mixed from top to bottom, probably due both to vertical convection and wind-caused turbulence. During the sample period the wind velocity averaged 19 knots, with an average air temperature of -28.3°C. The theoretical freezing point of seawater of the salinities encountered is from -1.71°C to -1.80°C. The bottom water over most of the area sampled is thus very near the freezing point, and may in fact be supercooled at Stations 4, 24, and 25 (Table 1). It is assumed that the freezing point of the benthic invertebrates encountered is very close to that of the bottom water in which they are found as their body fluids are generally isotonic with it.

Biological Results

From the 16 stations sampled, a total of 98 species representing 85 genera were identified, sorted for counting, weighing, and elemental analysis, and coded for statistical processing. Six other organisms were identified to genera but not to species, and 1 anthozoan, 1 nemertean, 1 sipunculid, 11 groups of amphipods, 5 groups of cumaceans, and 1 ascidian remain unidentified, though all were sorted and coded as species for purposes of distribution and correlation studies. The latter groupings or taxa are based upon features of gross morphology and may ultimately be found to be composed of more than one species, particularly where the amphipod groups are concerned. Of the 98 organisms identified to species, there is 1 nemertean, 1 priapulid, 1 echiuroid, 7 echinoderms, 54 polychaetous annelids, and 33 molluscs (Table 2).

By phyla, the crustacean arthropods, primarily amphipoda, comprised 48% of the individuals over the study area, though they contributed only 7.1% of the wet weight biomass and 9.7% of the organic carbon biomass (Fig. 2, Table 3). The average crustacean density over the area was 635 indiv/m^2 and the average biomass was 5.42 g wet/m^2. Molluscs, primarily pelecypods, averaged 122 indiv/m^2, accounting for only 10.5% of the individuals present, but had a mean biomass of 82.8 g wet/m^2, 44.8% of the total. They also contributed 43.3% of the total organic carbon (Fig. 2, Table 4). Annelid density was estimated at 297 indiv/m^2, 33.6% of the total, with a biomass of 23.2 g wet/m^2, 27.7% of the total. Annelid contrbution to organic carbon biomass was estimated at 30.9% of the total (Fig. 2, Table 5). The echinoderms represented the lesser of the four major phyla in all categories, averaging 62 indiv/m^2, 6.4% of the total, 11.4 g wet/m^2, 12.5% of the total, and 8.2% of total organic carbon biomass (Fig. 2, Table 6). These four phyla comprised, on the average, 98.4% of the individuals over the study area (Table 7), 91.6% of the wet weight biomass (Table 8), 90.5% of the organic carbon (Table 9), and 92.1% of the organic nitrogen (Table 10). These values varied considerably from station to station.

The mean density encountered over the study area was 1,133 indiv/m^2, including all species and taxa. This number varied from 330 indiv/m^2 at Station 13 to 4,414 indiv/m^2 at Station 24 (Table 11). As Station 13 was represented by only one sample rather than the normal five, the low values attributed to it may not be entirely valid.

The number of species encountered per station ranged from 10, again at Station 13, to 42 at Station 27, with a mean value of 27. These estimates include groups of amphipods and cumaceans coded and dealt with as species as well as those organisms positively identified to species level.

Table 2. Average organic carbon and nitrogen content of benthic species from the Bering Sea shelf, 31 Jan-16 Feb, 1970.

Phylum and Species	C_{org} % wet wt	N_{org} % wet wt	Dry wt % wet wt	C_{org} % dry wt	N_{org} % dry wt
Annelida					
Ammotrypane aulogaster	5.9	1.6	25.8	22.8	6.2
Ampharete acutifrons	4.9	1.1	13.3	37.0	8.0
Ampharete goesi	5.6	1.3	21.7	26.0	6.1
Ampharete longopaliolata	5.6	1.3	21.7	26.0	6.1
Amphitrite cirrata	4.4	1.0	20.7	21.1	5.0
Antinoella badia	5.2	1.4	14.3	36.5	9.7
Artacama proboscidea	4.7	1.1	22.2	21.3	5.0
Audouinia tentaculata	5.6	1.3	21.7	26.0	6.1
Axiothella catenata	5.6	1.3	21.7	26.0	6.1
Brada villosa	3.6	0.9	20.0	17.9	4.6
Capitella capitata	5.6	1.3	21.7	26.0	6.1
Chaetozone setosa	6.9	1.4	19.4	35.4	7.2
Chone dunneri	6.6	1.9	19.2	34.6	9.7
Chone gracilis	5.6	1.3	21.7	26.0	6.1
Eteone barbata	5.6	1.3	21.7	26.0	6.1
Eteone longa	5.6	1.4	16.6	33.5	8.4
Eunoe nodosa	6.1	1.4	16.2	37.4	8.8
Gattyana ciliata	5.6	1.3	21.7	26.0	6.1
Glycera capitata	6.4	1.5	19.2	33.2	7.8
Glycera sp.	5.6	1.3	21.7	26.0	6.1
Glycinde armigera	5.6	1.3	21.7	26.0	6.1
Jasmineira pacifica	5.6	1.3	21.7	26.0	6.1
Lumbrinereis heterapoda	5.6	1.3	21.7	26.0	6.1
Lumbrinereis l. japonica	7.3	1.8	20.1	36.5	9.0
Lumbrinereis sp.	5.6	1.3	21.7	26.0	6.1
Magelona japonica	5.6	1.3	21.7	26.0	6.1
Maldane sarsi	4.9	1.1	19.1	25.6	5.8
Nephtys ciliata	4.4	1.2	19.7	22.4	5.9

Table 2 Con't.

Phylum and Species	C_{org} % wet wt	N_{org} % wet wt	Dry wt % wet wt	C_{org} % dry wt	N_{org} % dry wt
Annelida					
Nephtys longosetosa	5.8	1.4	20.0	29.1	7.0
Neoamphitrite groenlandica	3.7	0.8	17.2	21.6	4.8
Nicolea zastericola	5.6	1.3	21.7	26.0	6.1
Onuphis parva-striata	4.9	1.1	13.6	35.8	8.4
Ophelia limacina	3.9	1.0	28.0	13.9	3.7
Pectinaria hyperborea	3.5	0.7	17.8	18.9	4.1
Pholoe minuta	5.6	1.3	21.7	26.0	6.1
Phyllodoce groenlandica	3.5	0.8	16.2	21.6	4.8
Phyllodoce maculata	5.6	1.3	21.7	26.0	6.1
Phyllodoce sp.	5.6	1.3	21.7	26.0	6.1
Pista cristata	4.8	1.0	21.5	22.4	4.8
Polycirrus medusa	4.2	0.9	30.7	13.8	2.9
Polynoe canadensis	5.6	1.3	21.7	26.0	6.1
Potamilla neglecta	5.6	1.3	21.7	26.0	6.1
Praxillella praetermissa	6.2	1.5	20.2	30.8	7.4
Prionospio malgreni	5.6	1.3	21.7	26.0	6.1
Scalibregma inflatum	5.8	1.2	18.1	30.8	6.8
Scolelepis fuliginosa	5.6	1.3	21.7	26.0	6.1
Scoloplos armiger	6.3	1.5	20.6	30.5	7.4
Spio filicornis	5.6	1.3	21.7	26.0	6.1
Spiophanes bombyx	5.3	1.3	23.8	22.4	5.3
Spiophanes kroyeri	5.6	1.3	21.7	26.0	6.1
Sternapsus fossor	2.3	0.6	20.9	11.1	3.0
Sternapsus scutata	3.8	1.0	22.7	16.7	4.4
Stylaroides plumosa	5.6	1.3	21.7	26.0	6.1
Syllis fasciata	6.2	1.5	17.7	34.9	8.3
Terrebelides stroemi	4.7	1.0	24.9	18.9	4.2
Timarete japonica	12.6	2.3	38.5	32.8	5.9
Travisia brevis	5.9	1.3	55.6	10.6	2.3

Table 2 Con't.

Phylum and Species	C_{org} % wet wt	N_{org} % wet wt	Dry wt % wet wt	C_{org} % dry wt	N_{org} % dry wt
Annelida					
Averages	5.6	1.3	21.7	26.0	6.1
Mollusca					
Admete couthouyi	3.1	.7	64.0	4.1	1.1
Assiminea sp.	5.5	1.3	48.0	11.5	2.7
Astarte borealis	3.1	0.6	45.5	6.9	1.2
Clinocardium ciliatum (lg.)	2.0 (avg.)	.5 (avg.)	32.8	7.2	1.7
Clinocardium ciliatum (sm.)			52.3	2.4	0.5
Cyclocardia ventricosa	3.1	0.6	45.5	6.9	1.2
Cylichna nucleola	12.6	3.6	49.8	25.8	6.1
Cylicha occulta	7.9	1.9	63.8	12.4	2.9
Diplodonta aleutica	15.5	3.0	71.5	21.7	5.0
Hiatella arctica	3.1	0.6	45.5	6.9	1.2
Liocyma fluctuosa	3.1	0.6	45.5	6.9	1.2
Lyonsia norvegica	3.1	0.6	45.5	6.9	1.2
Macoma calcarea (lg.)	3.2 (avg.)	.6 (avg.)	48.0	7.1	1.4
Macoma calcarea (sm.)			43.7	6.7	1.4
Mohnia sp.	7.9	1.9	63.8	12.4	2.9
Musculus niger	3.1	0.6	45.5	6.9	1.2
Mya truncata	3.1	0.6	45.5	6.9	1.2
Mysella tumida	3.1	0.6	45.5	6.9	1.2
Natica clausa	3.1	0.6	45.5	6.9	1.2
Neptunea heros	7.9	1.9	63.8	12.4	2.9
Nucula tenuis	4.2	.8	43.6	9.6	1.8
Nuculana radiata	2.8	.6	51.7	5.32	1.1
Odostoma cassandra	7.9	1.9	63.8	12.4	2.9
Polinices caurinus	7.9	1.9	63.8	12.4	2.9
Retusa semon	7.9	1.9	63.8	12.4	2.9

Table 2 Con't.

Phylum and Species	C_{org} % wet wt
Mollusca	
Serripes groenlandicus (sm.)	1.9
Siliqua alta	4.1
Solariella obscura	8.3
Spisula alaskana	3.1
Sulcoretusa sp.	7.9
Thyasira gouldi	3.1
Trophonopsis beringi	3.1
Turitellopsis reticulata	4.8
Turitellopsis sp.	4.8
Cyclocardium crebricostata	1.3
Yoldia hyperborea	4.3
Yoldia intermedia	3.1
Yoldia thraciaeformis	3.1
Yoldia sp.	3.1
Unident. gastro. foot	---
Averages overall	5.1
Bivalve	3.1
Gastropod	7.9

N_{org} % wet wt	Dry wt % wet wt	C_{org} % dry wt	N_{org} % dry wt
.4	46.2	4.0	0.9
1.0	32.5	12.6	3.1
1.9	64.9	12.7	2.9
0.6	45.5	6.9	1.2
1.9	63.8	12.4	2.9
0.6	45.5	6.9	1.2
.8	62.1	4.9	1.2
1.0	70.5	6.2	1.5
1.0	70.5	6.2	1.5
.3	64.9	2.1	0.5
1.0	36.9	11.9	2.8
0.6	45.5	6.9	1.2
0.6	45.5	6.9	1.2
0.6	45.5	6.9	1.2
---	25.2	38.7	9.8
1.2			
.6	45.5	6.9	1.2
1.9	63.8	12.4	2.9

Table 2 Con't.

Phylum and Species	C_{org} % wet wt
Unident. Foraminifera	--
Unident. Nemertean	5.4
Linneus torquatus	6.5
Unident. Tunicate	2.0
Pelonaia corrugata	4.1
Unident. Anemone	5.3
Unident. Sipunculida	5.1
Priapulus humanus	3.9
Echiurus echiurus	1.7
Echinodermata	
Amphipholis squamatma	2.2
Amphiura craterodmeta	2.7
Ophiopus arcticus	5.6
Ophiura flagellata	1.6
Ophiura sarsi	1.4
Ophiuroid Average	2.7
Cucumaria populifera	5.8
Echinarachnius parma	1.6
Leptosynapta sp.	3.2

N_{org} % wet wt	Dry wt % wet wt	C_{org} % dry wt	N_{org} % dry wt
—	—	2.0	0.3
1.5	16.7	32.6	9.1
1.6	19.1	34.0	8.1
1.0	10.7	18.7	9.5
0.8	22.2	18.5	3.7
1.3	15.3	34.9	8.5
1.3	14.3	35.5	8.7
1.0	12.7	30.4	7.9
0.4	24.7	7.0	1.7
0.4	45.1	4.9	1.0
0.5	50.8	5.3	1.0
1.1	52.9	10.6	2.1
0.3	56.0	2.9	0.5
0.3	49.3	2.9	0.6
0.5	50.8	5.3	1.0
0.9	23.5	24.8	3.8
0.3	52.0	3.2	0.6
0.9	43.4	7.3	2.0

Table 2 Con't.

Phylum and Species	C_{org} % wet wt	N_{org} % wet wt	Dry wt % wet wt	C_{org} % dry wt	N_{org} % dry wt
Amphipoda					
Species A	7.4	1.5	19.7	37.7	7.7
Species B	7.0	1.4	19.2	36.6	7.0
Species C	6.7	1.6	17.8	37.9	8.9
Species D	6.3	1.3	18.7	33.8	7.2
Species H	4.9	1.1	17.1	28.5	6.3
Species I	6.3	1.3	18.7	33.8	7.2
Species J	6.7	1.3	19.8	33.9	6.7
Species K	6.3	1.3	18.7	33.9	7.2
Species L	6.3	1.3	18.7	33.9	7.2
Species M	6.3	1.3	18.7	33.9	7.2
Species P	6.3	1.3	18.7	33.9	7.2
Amphipod Average	6.3	1.3	18.7	33.8	7.2
Cumacea					
Species A	4.9	1.0	18.6	24.6	5.5
Species C	———	———	————	————	———
Species D	———	———	————	————	———
Species E	———	———	————	————	———
Species G	———	———	————	————	———
Balanus sp.	———	———	————	————	———
Pagurus sp.	———	———	————	————	———

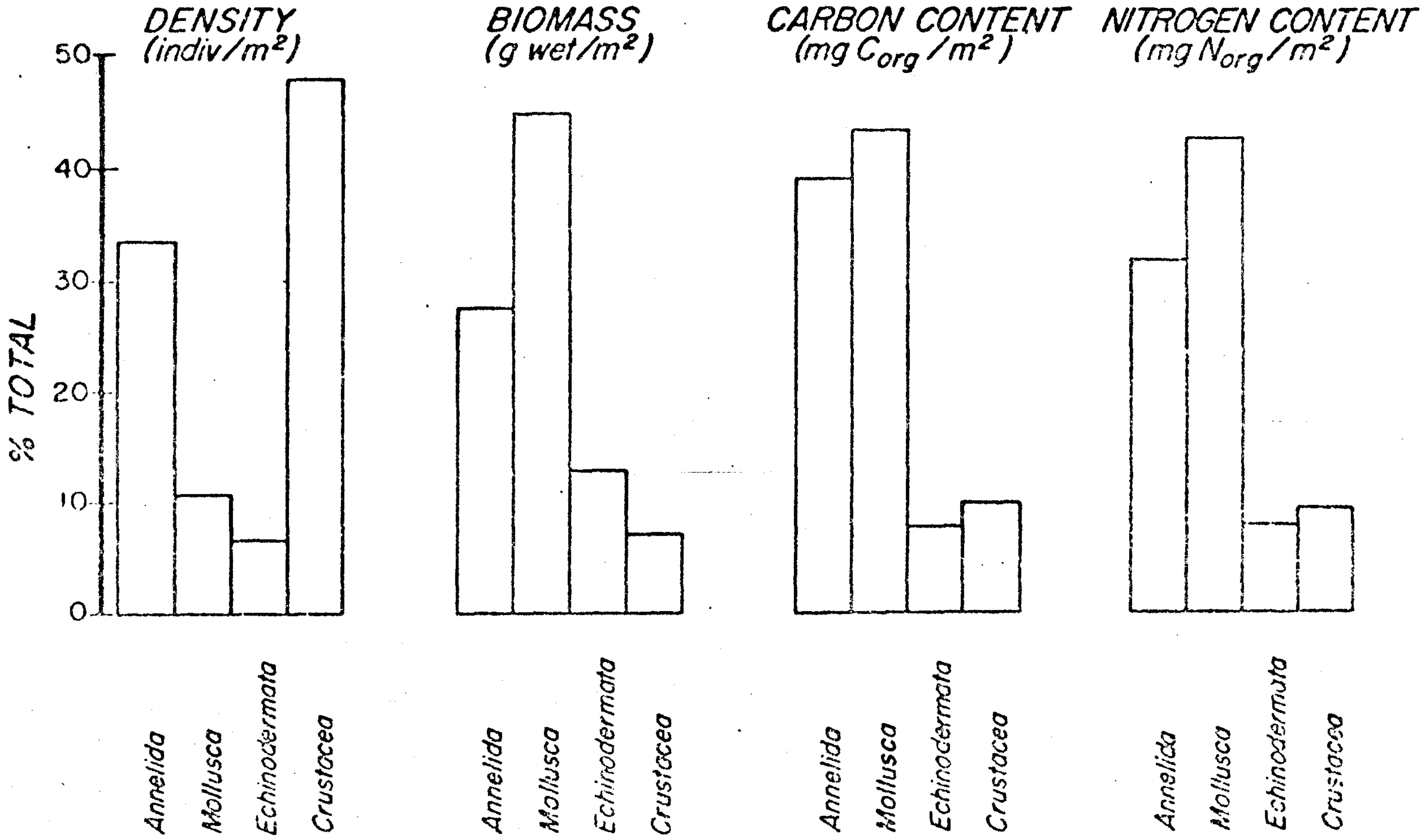

Figure 2. Relative contributions of the major benthic phyla to density, biomass, organic carbon, and organic nitrogen at stations on the Bering Sea shelf.

Table 3. Quantitative characteristics of crustaceans at benthic station on the Bering Sea Shelf, 31 Jan-16 Feb, 1970.

Station	No. Species	Density Indiv./m^2	Crustacean Density % of Total	Biomass g wet/m^2	Crustacean Biomass % of Total	Organic Carbon mg/m^2	Crustacean Organic Carbon % of Total	Organic Nitrogen mg/m^2	Crustacean Organic Nitrogen % of Total
3	4	462	70.4	1.3	2.5	74	2.7	16	3.6
4	4	212	22.3	1.2	4.2	61	3.8	13	3.8
5	6	370	59.5	22.7	21.1	817	18.9	398	30.3
6	6	280	38.0	10.8	7.9	738	12.9	154	12.0
7	5	214	51.9	1.4	0.2	96	0.5	20	0.4
8	4	212	49.1	0.7	2.0	47	3.3	10	3.1
10	3	236	43.9	0.3	0.4	19	0.4	4	0.4
11	3	14	2.6	0.1	0.1	3	0.1	1	0.1
13	0	0	0	0	0	0	0	0	0
14	2	556	79.7	5.5	19.1	372	26.5	73	23.7
16	3	62	6.2	0.3	0.2	16	0.4	4	0.4
23	7	1598	43.2	11.7	4.2	782	7.5	155	7.0
24	2	3564	80.7	18.4	11.7	1237	20.4	245	19.0
25	7	680	79.8	6.5	17.3	451	25.5	90	24.6
26	8	1308	92.6	3.6	15.8	255	19.9	52	16.8
27	10	404	50.8	2.4	7.3	151	12.2	31	10.5
	Average	636	48.0	5.4	7.1	320	9.7	79	9.7

Table 4. Quantitative characteristics of molluscs at benthic stations on the Bering Sea Shelf, 31 Jan-16 Feb, 1970.

Station	No. Species	Density Indiv./m^2	Mollusc Density % of Total	Biomass g wet/m^2	Mollusc Biomass % of Total	Organic Carbon mg/m^2	Mollusc Organic Carbon % of Total	Organic Nitrogen mg/m^2	Mollusc Organic Nitrogen % of Total
3	5	30	4.6	3.8	7.3	114	4.2	24	5.5
4	3	62	6.5	5.0	7.2	310	19.7	74	20.9
5	5	13	2.9	3.0	2.8	115	2.7	24	1.8
6	5	42	5.7	47.8	35.0	1,959	34.0	479	37.1
7	2	52	12.6	745.8	94.9	17,494	94.6	4263	94.9
8	5	10	2.2	26.1	74.0	867	61.9	187	59.7
10	4	24	4.5	48.0	74.6	3,733	81.3	876	81.0
11	4	24	4.5	32.3	61.4	1,384	59.8	320	58.3
13	3	80	24.2	25.3	38.6	1,057	38.8	226	35.9
14	3	20	2.9	14.2	49.2	595	42.3	133	42.9
16	8	504	50.1	118.3	85.5	3,257	77.6	717	76.8
23	8	732	19.8	168.5	60.0	5,623	53.7	1123	50.8
24	7	132	3.0	63.5	40.4	2.189	36.1	437	34.0
25	5	48	5.6	8.7	23.2	437	24.6	100	27.4
26	8	36	2.6	6.1	27.2	451	35.1	104	33.4
27	14	128	16.1	8.3	25.3	325	26.3	73	24.3
	Average	121	10.5	82.8	44.8	2,494	43.3	572	42.8

Table 5. Quantitative characteristics of annelids at benthic stations on the Bering Sea Shelf, 31 Jan-16 Feb, 1970.

Station	No. Species	Density Indiv./m^2	Annelid Density % of Total	Biomass g wet/m^2	Annelid Biomass % of Total	Organic Carbon mg/m^2	Annelid Organic Carbon % of Total	Organic Nitrogen mg/m^2	Annelid Organic Nitrogen % of Total
3	12	114	17.4	2.2	4.3	110	4.0	28	6.5
4	16	272	28.6	12.3	42.6	983	62.4	218	61.5
5	18	226	36.3	64.5	60.1	2480	57.5	615	46.8
6	12	346	47.0	41.1	30.0	2450	42.6	537	41.8
7	14	138	33.5	12.9	1.6	541	2.9	138	3.1
8	8	228	49.6	8.4	23.9	486	34.7	117	37.3
10	14	258	48.0	14.6	23.0	798	17.4	191	17.7
11	14	470	87.7	20.2	38.3	919	39.7	226	41.3
13	7	250	75.8	40.3	61.4	1663	61.1	403	64.1
14	9	122	17.5	9.2	31.7	442	31.4	104	33.5
16	9	96	9.5	13.3	9.6	647	15.4	150	16.1
23	13	1256	33.9	66.4	23.7	3205	30.6	729	33.0
24	19	654	14.8	43.5	27.7	2102	34.7	492	38.3
25	13	96	11.4	5.4	14.3	328	18.5	83	22.6
26	8	46	3.4	0.3	1.4	18	1.4	4	1.4
27	14	182	23.0	16.3	49.9	501	40.6	131	44.2
Average		297	33.6	23.2	27.7	1105	30.9	260	31.8

Table 6. Quantitative characteristics of echinoderms at benthic stations on the Bering Sea Shelf, 31 Jan-16 Feb, 1970.

Station	No. Species	Density Indiv./m^2	Echinoderm Density % of Total	Biomass g wet/m^2	Echinoderm Biomass % of Total	Organic Carbon mg/m^2	Echinoderm Organic Carbon % of Total	Organic Nitrogen mg/m^2	Echinoderm Organic Nitrogen % of Total
3	4	42	6.4	44.3	86.0	2415	89.1	365	84.4
4	1	400	42.0	9.1	31.4	149	9.5	29	8.1
5	1	4	0.6	1.2	1.1	32	0.8	6	0.5
6	1	68	9.2	37.0	27.1	609	10.6	118	9.2
7	1	8	1.9	25.7	3.3	363	2.0	71	1.6
8	0	0	0	0	0	0	0	0	0
10	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0
16	1	304	30.2	2.8	2.1	46	1.1	8	0.3
23	2	74	2.0	24.0	8.6	369	3.5	72	5.6
24	2	26	0.6	30.2	19.2	455	7.5	89	6.9
25	1	2	0.2	6.1	16.3	87	4.9	17	5.4
26	0	0	0	0	0	0	0	0	0
27	1	66	8.3	1.5	4.6	33	2.7	7	2.2
Average		62	6.4	11.4	12.5	285	8.2	49	7.8

The wet weight biomass ranged from 22.5 g wet/m^2 at Station 26 to 786 g wet/m^2 at Station 7, with mean value of 127 g wet/m^2. The extreme biomass at Station 7 was largely composed of one species, *Clinocardium ciliatum*, represented by one size class of rather large individuals. If this station is excluded, the mean biomass is 82.7 g wet/m^2. Wet weight biomass values by sample and station were submitted to analysis of variance which yielded an F ratio of 4.25 for 75 samples at 15 stations (Station 13 excluded), indicating significant difference between stations in terms of biomass at the 99% confidence level.

Carbon and nitrogen content, averaged over all major species, was determined as 5.1% carbon and 1.1% nitrogen, percentage formalin wet weight. The amphipod crustaceans led in carbon and nitrogen values with percentages of 6.3 and 1.3 respectively, and the ophiuroid echinoderms presented the lowest values, 2.7% carbon and 0.9% nitrogen. The gastropod molluscs were determined to have values of 7.9% carbon and 1.9% nitrogen. However, due to the small number of gastropods available for analysis, and due to the broad spectrum of results observed when dealing with gastropods, such an average is considered uncertain. Most of the major species, with the exception of some of the molluscs, fall close to the average values for carbon and nitrogen content (Table 2). The wide range of values exhibited by the molluscs is largely due to variable shell weights, which are included in the percentage

Table 7. Total number of individuals (%) contributed by major benthic phyla at stations on the Bering Sea shelf, 31 Jan-16 Feb, 1970.

Station	Annelida	Mollusca	Echinodermata	Crustacea	Cumulative Total
3	17.4	4.6	6.4	70.4	98.8
4	28.6	6.5	42.0	22.3	99.4
5	36.3	2.9	0.6	59.5	99.4
6	47.0	5.7	9.2	38.0	100.0
7	33.5	12.6	1.9	51.9	100.0
8	49.6	2.2	0	46.1	97.8
10	48.0	4.5	0	43.9	96.3
11	87.7	4.5	0	2.6	94.8
13	75.8	24.2	0	0	100.0
14	17.5	2.9	0	79.7	100.0
16	9.5	50.1	30.2	6.2	96.0
23	33.9	19.8	2.0	43.2	98.9
24	14.8	3.0	0.6	80.7	99.1
25	11.3	5.6	0.2	79.8	96.9
26	3.36	2.6	0	92.6	98.4
27	22.9	16.1	8.3	50.8	98.0
Average	33.6	10.5	6.4	48.0	98.4

Table 8. Total wet weight biomass (%) contributed by major benthic phyla at stations on the Bering Sea shelf, 31 Jan-16 Feb, 1970.

Station	Annelida	Mollusca	Echinodermata	Crustacea	Cumulative Total
3	4.3	7.3	86.0	2.5	100.0
4	42.6	17.2	31.4	4.2	95.4
5	60.1	2.8	1.1	21.1	85.1
6	30.0	35.0	27.1	7.9	100.0
7	1.6	94.9	3.3	0.2	100.0
8	23.9	74.0	0	2.0	99.9
10	23.0	74.6	0	0.4	98.1
11	38.3	61.4	0	0.1	99.7
13	61.4	38.6	0	0	100.0
14	31.7	49.2	0	19.1	100.0
16	9.6	85.5	2.1	0.2	97.4
23	23.7	60.0	8.6	4.2	96.4
24	27.7	40.4	19.2	11.7	98.9
25	14.3	23.2	16.3	17.3	71.1
26	1.4	27.2	0	15.8	44.4
27	49.9	25.3	4.6	7.3	87.1
Average	27.7	44.8	12.5	7.1	91.6

Table 9. Total organic carbon (%) contributed by major benthic phyla at stations on the Bering Sea shelf, 31 Jan-16 Feb, 1970.

Station	Annelida	Mollusca	Echinodermata	Crustacea	Cumulative Total
3	4.0	4.2	89.1	2.7	100.0
4	62.4	19.7	9.5	3.8	95.4
5	57.5	2.7	0.8	18.9	79.8
6	42.6	34.0	10.6	12.8	100.0
7	2.9	94.6	2.0	0.5	100.0
8	34.7	61.9	0	3.3	99.9
10	17.4	81.3	0	0.4	99.2
11	39.7	59.8	0	0.1	99.7
13	61.1	38.8	0	0	100.0
14	31.4	42.3	0	26.4	100.0
16	15.4	77.6	1.1	0.4	94.4
23	30.6	53.7	3.5	7.5	95.3
24	34.7	36.1	7.5	20.4	98.7
25	18.5	24.6	4.9	25.4	73.4
26	1.4	35.1	0	19.9	56.4
27	40.6	26.3	2.7	12.2	81.7
Average	30.9	43.3	8.2	9.7	90.5

Table 10. Total organic nitrogen (%) contributed by major benthic phyla at stations on the Bering Sea shelf, 31 Jan-16 Feb, 1970.

Station	Annelida	Mollusca	Echinodermata	Crustacea	Cumulative Total
3	6.5	5.5	84.4	3.6	100.0
4	61.5	20.9	8.1	3.8	94.2
5	46.8	1.8	0.4	30.3	79.3
6	41.8	37.1	9.2	12.0	100.0
7	3.1	94.9	1.6	0.4	100.0
8	37.3	59.7	0	3.1	100.0
10	17.7	81.0	0	0.4	99.1
11	41.3	58.3	0	0.1	99.7
13	64.1	35.9	0	0	100.0
14	33.5	42.9	0	23.7	100.0
16	16.1	76.8	0.3	0.4	93.6
23	33.0	50.8	5.6	7.0	96.4
24	38.3	34.0	6.9	19.0	98.3
25	22.6	27.4	5.4	24.6	80.0
26	1.4	33.4	0	16.8	51.6
27	44.2	24.3	2.2	10.5	81.2
Average	31.8	42.8	7.8	9.7	92.1

Table 11. Summary of means of biological characteristics of benthos at stations on the Bering Sea shelf, 31 Jan-16 Feb, 1970.

			Standing Stock			Elemental Composition		
Station	Total No. Species	Density Indiv./m^2	Biomass g wet/m^2	Organic Carbon mg/m^2	Organic Nitrogen mg/m^2	Organic Carbon % wet	Organic Nitrogen % wet	C/N Atomic Ratio
3	24	656	51.5	2,712	433	5.3	0.8	7.3
4	30	952	28.9	1,575	355	5.4	1.2	5.2
5	30	622	107.3	4,315	1,313	4.0	1.2	3.8
6	26	736	136.7	5,756	1,284	4.2	0.9	5.2
7	27	412	785.8	18,494	4,491	2.4	0.6	4.8
8	30	460	35.2	1,401	314	4.0	0.9	5.2
10	28	538	64.3	4,589	1,081	7.1	1.7	5.0
11	22	536	52.7	2,314	548	4.4	1.0	4.9
13	10	330	65.6	2,720	629	4.1	1.0	5.1
14	15	698	28.9	1,407	309	4.9	1.1	5.3
16	21	1,006	138.3	4,198	933	3.0	0.7	5.3
23	32	3,702	280.7	10,464	2,212	3.7	0.8	5.5
24	33	4,414	157.3	6,062	1,285	4.3	0.9	5.5
25	30	852	37.8	1,774	367	4.7	1.0	5.6
26	28	1,412	22.5	1,285	311	5.7	1.4	4.8
27	42	796	32.7	1,236	298	3.8	0.9	4.8
Average	27	1,133	126.6	4,390	1,010	4.5	1.0	5.2

ratios. For species not found in sufficient numbers for analysis, average values for the closest taxonomic category for which there are values were applied to them.

The atomic ratio of carbon to nitrogen is 5.2 to 1 for all species at all stations. The range of this carbon/nitrogen ratio is from 3.8/1 to 7.3/1 (Table 11). Only two stations (3 and 5) represent such extreme values, however, the remainder falling in the range of 4.8/1 to 5.6/1.

The organic carbon biomass over the study area ranged from 1.24 g/m^2 at Station 27 to 18.5 g/m^2 at Station 7. It should be noted that the lower carbon value occurred at a different station than did the lower wet weight biomass. The mean organic carbon biomass was estimated at 4.4 g/m^2 with Station 7 included, or 3.5 g/m^2 excluding Station 7.

Organic nitrogen values ranged from 0.30 g/m^2 at Station 27 to 4.5 g/m^2 at Station 7, with mean value of 1.0 g/m^2. If Station 7 is excluded from the average, this mean drops to 0.78 g/m^2.

Of the 129 species or taxa, only one, the ubiquitous polychaete *Scoloplos armiger*, was encountered at every station, while 56 species occurred at only one station (Table 12). In terms of either density, wet weight biomass, or organic carbon biomass, there were only 35 species which contributed individually 0.5% or more of the total value of any category. These 35 species, however, constitute a total of 88% of the density, 89% of the wet weight biomass, and 78% of the total organic carbon over the transect (Table 13). Even more startling is the fact that only 8 of these species contribute 5% or better, by species, of any one of the above values, yet these 8 species make up a total of 68% of the density, 69% of the total wet weight biomass, and 53% of the total organic carbon biomass (Table 13).

Of these 35 species mentioned above, 10 are recognized as walrus food species (J. Burns, personal communication; personal observation). These 10 species constitute only 10% of the total benthic density encountered, but make up 61% of the wet weight biomass and 49% of the total organic carbon biomass (Table 14).

By feeder type, the majority of the species encountered are selective detritus feeders (Fig. 3), though the majority of the individuals, and the greatest biomass, is contributed by mobile and partly mobile seston feeders. Of the 35 species referred to above and in Table 14, and considered as major species for purposes of this study, 14 are classified as selective detritus feeders, 9 as carnivores or scavengers, 6 as non-selective detritus feeders, 5 as mobile or partly mobile seston feeders, and one as a sessile seston feeder (Kuznetsov, 1964). As the amphipod groups comprise most of the mobile and partly mobile seston feeders, this trophic category very likely will assume dominance by number of species as well as by density and biomass when the amphipod groups are broken down to

Table 12. Benthic species from the Bering Sea shelf ranked by frequency of occurrence, with means for stations where species occurs.

Species	No. Stations Where Present	Density Indiv./m^2	Biomass g wet/m^2	Weight mg wet/indiv.	Organic Carbon mg/m^2	Organic Nitrogen mg/m^2
Scoloplos armiger	16	92	1.64	18	103.2	25.1
Amphipod A	15	155	.94	6	70.8	14.2
Nucula tenuis	13	13	1.95	149	81.1	15.6
Amphipod H	12	64	0.2	4	13.3	2.9
Pholoe minuta	12	7	0.0	4	2.7	0.4
Macoma calcarea	11	74	18.6	149	81.1	15.6
Praxillella praetermissa	10	23	2.4	107	155.8	37.2
Yoldia hyperborea	10	15	9.7	639	417.1	96.7
Nemertinea (unident.)	10	11	1.2	116	69.2	19.3
Nephtys ciliata	10	10	1.81	183	80.9	21.2
Amphipod J	9	653	4.81	7	323.5	63.7
Tinarete japonica	9	7	0.06	9	8.1	1.5
Cumacea D	8	64	0.66	10	30.1	6.8
Chaetozone setosa	8	11	0.19	17	13.8	2.6
Cylichna nucleola	8	4	0.19	52	24.3	5.7
Glycera capitata	8	2	0.07	33	5.7	1.1
Phyllodoce maculata	8	2	0.02	13	1.4	0.3
Cumacea A	7	24	0.12	5	6.5	1.2
Starnapsus fossor	7	16	2.76	175	64.1	6.4
Prionospio malgreni	7	6	0.03	4	1.4	0.3
Lumbrinereis l. japonica	6	22	1.06	49	78.6	19.2
Pectinaria hyperborea	6	10	3.92	392	132.8	29.0
Gattyana ciliata	6	8	0.09	11	5.3	1.2
Magelona japonica	6	7	0.06	8	3.3	0.8
Eteone longa	6	4	0.05	11	3.5	0.6
Admete couthouyi	6	3	2.38	893	75.8	16.7
Ophiura sarsi	5	21	32.67	157	461.7	91.5
Cumacea C	5	20	0.03	2	1.4	0.3

Table 12 Con't.

Species	No. Stations Where Present
Serripes groenlandicus	5
Priapulus humanus	4
Amphipod C	4
Amphipod B	4
Artacama proboscidea	4
Ammotrypane aulogaster	4
Phyllodoce groenlandica	4
Lumbrinereis heteropoda	4
Scalibregma inflatum	3
Axiothella catenata	3
Polinices caurinus	3
Brada villosa	3
Anthozoa (unident.)	3
Terebellides stroemi	3
Trophonopsus beringi	3
Echinarachnius parma	2
Clinocardium ciliatum	2
Nephtys longosetosa	2
Ophelia limacina	2
Turitellopsis reticulata	2
Nuculana radiata	2
Cylichna occulta	2
Pelonia corrugata	2
Onuphis parva-striata	2
Diplodonta aleutica	2
Spio filicornis	2
Solariella obscura	2
Polycirrus medusa	2
Ophiopus arcticus	2

Density Indiv./m^2	Biomass g wet/m^2	Weight mg wet/indiv.	Organic Carbon mg/m^2	Organic Nitrogen mg/m^2
14	0.26	19	5.8	1.0
11	1.15	104	44.3	11.5
11	0.72	65	48.2	11.3
8	0.02	2	1.2	0.2
5	6.02	1338	285.7	66.2
4	0.55	138	32.3	8.7
4	0.04	11	2.5	0.3
4	1.17	334	66.8	15.5
22	0.73	33	41.9	9.0
13	0.67	50	38.8	8.9
11	0.30	27	24.0	5.6
7	0.12	16	4.2	1.1
7	4.37	656	233.1	56.9
5	1.56	335	74.5	16.33
2	0.51	217	15.4	3.8
234	10.29	44	168.9	32.9
220	401.62	1826	8112.7	1927.8
28	0.83	30	48.0	11.6
22	0.18	8	7.0	1.8
13	12.80	985	559.4	133.1
13	6.56	505	180.6	37.3
13	0.17	13	21.8	5.2
11	4.72	429	193.8	38.7
9	2.16	240	105.2	24.6
9	0.21	33	32.3	7.4
8	0.07	9	3.7	0.9
7	1.61	230	133.0	29.8
5	1.34	267	56.5	11.7
5	0.71	142	39.8	7.7

Table 12 Con't.

Species	No. Stations Where Present	Density Indiv./m^2	Biomass g wet/m^2	Weight mg wet/indiv.	Organic Carbon mg/m^2	Organic Nitrogen mg/m^2
Travisia brevis	2	5	4.85	1078	287.1	60.6
Chone dunneri	2	4	0.16	40	10.6	3.0
Assiminea sp.	2	3	4.07	1357	224.7	53.7
Echiurus echiurus	2	3	0.37	122	6.4	1.5
Odostoma cassandra	2	3	0.16	53	12.7	3.0
Polynoe canadensis	2	3	0.20	67	11.3	2.7
Ampharete acutifrons	2	2	0.46	228	22.4	4.8
Eunoe nodosa	2	2	0.33	165	20.0	4.7
Maldane sarsi	1	1094	54.89	50	2685.8	609.3
Ophiura flagellata	1	344	3.10	9	50.5	8.1
Amphipholis squamatma	1	66	1.50	23	33.0	6.6
Spiophanes bombyx	1	62	0.36	6	19.2	4.5
Lineus torquatus	1	40	3.56	89	231.4	55.2
Amphipod I	1	32	0.12	4	7.3	1.6
Leptosynapta sp.	1	20	1.46	73	46.0	12.8
Cucumaria populifera	1	18	37.42	2079	2181.6	336.8
Cyclacardium crebricostata	1	18	1.72	96	22.9	5.3
Hiatella arctica	1	12	2.23	186	69.8	12.5
Cumacea E	1	12	0.11	10	5.4	1.2
Yoldia intermedia	1	10	1.84	184	57.6	10.3
Musculus niger	1	10	0.51	51	16.0	2.9
Syllis fasciata	1	8	0.19	24	11.7	2.8
Amphipod D	1	8	0.05	6	2.9	0.6
Capitella capitata	1	6	0.01	2	0.6	0.1
Astarte borealis	1	5	0.57	114	17.8	3.2
Neptunea heros	1	4	43.70	10,925	3461.0	812.8
Ascidacea (unident.)	1	4	2.98	745	59.9	30.4
Neoamphitrite groenlandica	1	4	0.93	233	34.6	7.7
Antinoella badia	1	4	0.42	105	22.0	5.8

Table 12 Con't.

Species	No. Stations Where Present	Density Indiv./m^2	Biomass g wet/m^2	Weight mg wet/indiv.	Organic Carbon mg/m^2	Organic Nitrogen mg/m^2
Amphiura craterodmeta	1	4	0.12	30	3.2	0.6
Amphipod L	1	4	0.09	22	5.4	1.2
Amphipod K	1	4	0.07	17	4.2	0.9
Lyonsia norvegica	1	4	0.02	5	0.6	0.1
Eteone barbata	1	4	0.02	5	1.1	0.3
Glycinde armigera	1	4	0.02	5	1.1	0.3
Siliqua alta	1	3	0.83	415	34.1	8.3
Ampharete longopaleolata	1	3	0.07	23	3.9	0.9
Ampharete goesi	1	3	0.03	10	1.6	0.4
Yoldia thraciaeformis	1	2	28.88	14,440	903.9	161.7
Pista cristata	1	2	7.08	3540	341.3	73.1
Liocyma fluctuosa	1	2	3.10	1550	97.0	17.4
Cyclocardia ventricosa	1	2	1.16	580	36.3	6.5
Sternapsus scutata	1	2	0.44	220	16.6	4.4
Sipunculida (unident.)	1	2	0.42	210	21.3	5.3
Amphipod M	1	2	0.37	183	23.1	4.9
Amphitrite cirrata	1	2	0.29	145	12.7	3.0
Thyasira gouldi	1	2	0.24	120	7.5	1.3
Potamilla neglecta	1	2	0.09	45	5.1	1.2
Nicolea zostericola	1	2	0.08	40	4.5	1.1
Mya truncata	1	2	0.04	20	1.3	0.2
Jasmineira pacifica	1	2	0.03	15	1.7	0.4
Cumacea G	1	2	0.02	10	0.9	0.2
Retusa semen	1	2	0.01	5	0.8	0.2
Sulcoretusa sp.	1	2	0.01	5	0.3	0.2
Turitellopsis sp.	1	2	0.01	5	0.8	0.2
Scolelepis fuligenosa	1	2	0.01	5	0.6	0.1
Spiophanes kroyeri	1	2	0.01	5	0.6	0.1

Table 12 Con't.

Species	No. Stations Where Present
Balanus sp.	1
Pagurus sp.	1
Amphipod P	1
Stylaroides plumosa	1
Audouria tentaculata	1
Chone gracilis	1

Density Indiv./m^2	Biomass g wet/m^2	Weight mg wet/indiv.	Organic Carbon mg/m^2	Organic Nitrogen mg/m^2
2	0.01	5	--	--
2	--	--	--	--
2	0.01	4	0.5	0.1
<1	<0.01	3	0.2	--
<1	<0.01	3	--	--
<1	<0.01	5	--	--

Table 13. Benthic species contributing greater than 0.5%, greater than 1% (*), greater than 2% (**), or greater than 5% (***) of total number of individuals, biomass, or organic carbon over the region samples. Feeding types: SD = selective detritus; NSD = nonselective detritus; SS = sessile seston; MPS = mobile or partly mobile seston; c = carnivore.

Species	Total No. Indiv.	% Total No. of All Species	Total Biomass g wet/m^2	% Total Biomass of All Species	Total Organic Carbon mg/m^2	% Total Organic Carbon of All Species	Feeder Type	C/N Weight Ratio
***Amphipod J	5,878	32.4	43.3	2.1	2,903	4.1	MPS	5.1
***Amphipod A	2,332	12.9	14.1	0.7	1,047	1.5	MPS	4.9
****Scoloplos armiger*	1,475	8.1	26.3	1.3	1,651	2.4	NSD	4.1
****Maldane sarsi*	1,094	6.0	54.9	2.7	2,686	3.8	NSD	4.4
****Macoma calcarea*	814	4.5	205.3	10.1	6,502	9.3	SD	4.9
**Amphipod H	773	4.3	3.3	0.2	160	0.2	MPS	4.5
**Cumacea D	512	2.8	5.3	0.3	241	0.3	SD	---
***Echinarachnius parma*	468	2.6	20.6	1.0	338	0.5	MPS	5.3
***Clinocardium ciliatum*	440	2.4	803.2	39.6	16,225	23.1	MPS	4.5
**Ophiura flagellata*	344	1.9	3.1	0.2	51	0.1	SD	5.8
***Praxillella praetermissa*	231	1.3	24.8	1.2	1,548	2.2	NSD	4.2
**Nucula tenuis*	170	0.9	25.3	1.3	1,054	1.5	SD	5.3
Cumacea A	166	0.9	0.9	<0.1	39	0.1	SD	4.5
****Yoldia hyperborea*	152	0.8	97.1	4.8	4,171	5.9	SD	4.3
Lumbrinereis l. japonica	130	0.7	6.3	0.3	466	0.7	C	4.1
Sternapus fossor	110	0.6	19.3	1.0	499	0.6	NSD	3.7
Nemertinea (unident.)	110	0.6	12.7	0.6	692	1.0	C	3.6
****Ophiura sarsi*	104	0.6	163.4	8.1	2,304	3.3	SD	4.8
**Nephtys ciliata*	99	0.6	18.1	0.9	799	1.1	C	3.8
Cumacea C	98	0.5	0.2	<0.1	7	<0.1	SD	---
Chaetozone setosa	89	0.5	1.5	0.1	102	0.2	SD	4.9
Pholoe minuta	89	0.5	0.4	<0.1	20	<0.1	C	---
**Pectinaria hyperborea*	60	0.3	25.5	1.2	790	1.1	SD	4.6
**Turitellopsis reticulata*	26	0.1	25.6	1.3	1,119	1.6	C	4.1
Nuculana radiata	26	0.1	13.1	0.7	361	0.5	SD	4.8

Table 13 Con't.

Species	Total No. Indiv.	% Total No. of All Species	Total Biomass g wet/m^2	% Total Biomass of All Species	Total Organic Carbon mg/m^2	% Total Organic Carbon of All Species	Feeder Type	C/N Weight Ratio
Pelonia corrugata	22	0.1	9.4	0.5	388	0.6	SS	5.0
Anthozoa (unident.)	20	0.1	13.1	0.7	699	1.0	C	4.1
***Cucumaria populifera*	18	0.1	37.4	1.9	2,182	3.1	SD	6.5
**Artacama proboscidea*	18	0.1	24.1	1.2	1,139	1.6	NSD	4.3
Admete couthouyi	16	0.1	14.3	0.7	449	0.6	C	3.7
Travisia brevis	9	0.1	9.7	0.5	574	0.8	NSD	4.6
Assiminea sp.	6	<0.1	8.1	0.4	449	0.6	C	4.3
***Neptunea heros*	4	<0.1	43.7	2.2	3,461	4.9	C	---
**Yoldia thraciaeformis*	2	<0.1	28.9	1.4	904	1.3	SD	---
Pista cristata	2	<0.1	7.1	0.4	3,413	0.5	SD	4.7
sum>0.5%<1		87.8		88.9		78.2		
sum>1.0%<2		82.8		83.1		71.0		
sum>2.0%<5		78.9		75.8		64.1		
sum>5.0%		67.8		69.1		52.8		

Table 14. Contribution of known walrus food species to benthic density, biomass, and organic carbon on the Bering Sea shelf, 31 Jan-16 Feb, 1970.

Species	avg density indiv./m^2	avg biomass g wet/m^2	avg organic carbon mg/m^2
Macoma calcarea	51	12.8	406
Clinocardium ciliatum	28	50.2	1,014
Nucula tenuis	11	11.6	66
Yoldia hyperborea	10	6.1	261
Pectinaria hyperborea	4	1.6	49
Nephtys ciliata	6	1.1	50
Nuculana radiata	2	.8	23
Pelonia corrugata	1	.6	24
Neptunea heros	<1	2.7	216
Yoldia thraciaeformis	≤1	1.8	57
total	114	79.3	2,166
% total benthos	9.9	61.4	49.3

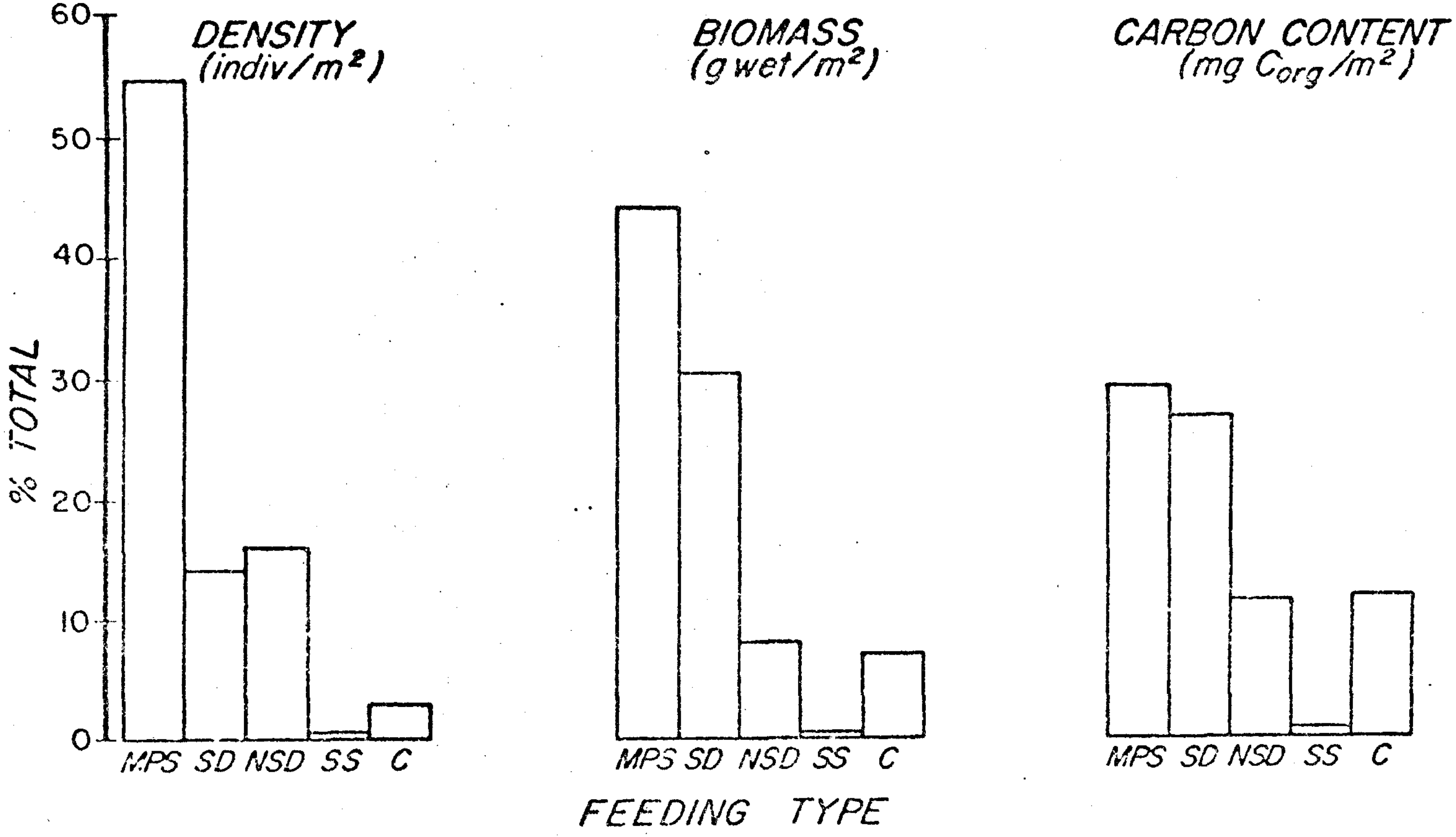

Figure 3. Relative contributions by feeder type to benthic density, biomass, and organic carbon at stations on the Bering Sea shelf.

species. Of the 35 major species, the mobile or partly mobile seston feeders constitute 55% of the density, 44% of the wet weight biomass, and 29% of the organic carbon (Fig. 3).

The 35 major species were subjected to a stepwise regression analysis (BMD02R) based upon occurrence or non-occurrence and density at each station in order to assess correlation affinities between species. At the 95% confidence level 9 groups of species were established as having affinities in terms of distribution and density, these groups ranging in size from 10 species to 2 (Table 15). It will be seen that several species are repeated in more than one affinity group, in which case they are considered ubiquitous within the groups where listed. Several of the 35 species showed no positive correlation with any other species.

These same 35 species were then submitted to stepwise regression analysis (BMD02R) with environmental values (temperature, depth, salinity, oxygen, sediment particle mode size) read in as parameters in order to assess the influence of environmental factors upon distribution and density. The results were not entirely satisfactory, due largely to the small number of stations, though for each of the major phyla about 40% of the variability in distribution and density could be accounted for by the 5 environmental factors mentioned. The remaining variability may be due to biological factors, or to physical factors

Table 15. Benthic species from the Bering Sea shelf which show affinity correlation values exceeding 0.50 (95% confidence that correlation exceeds 0), based on distribution and density, with major environmental factors influencing distribution and density, and feeder type (see Table 3) indicated for each species.

Species	Environmental Influences	Feeder Type
	Group 1	
Ophiura flagellata	sal/depth/sed	SD
Yoldia thraciaeformis	sal/depth/sed	SD
Clinocardium ciliatum	sal/depth/sed	MPS
Pista cristata	sal/depth/sed	SD
Yoldia hyperborea	sal	SD
Lumbrinereis l. japonica	depth	C
	Group 2	
Maldani sarsi	sed	NSD
Macoma calcarea	sed	SD
Ophiura sarsi	sed/sal	SD
Assiminea sp.	sal/sed	C
Nemertinea	sed/sal	C
Amphipod J	sal/sed	MPS
Nucula tenuis	sed	SD
Pelonia corrugata	sal	SS
Lumbrinereis l. japonica	depth	C
	Group 3	
Nuculana radiata	no correlation	SD
Artacama proboscidea	depth	NSD
Scoloplos armiger	sal/depth	NSD
Pectinaria hyperborea	no correlation	SD
Amphipod J	sal/sed	MPS
Praxillella praetermissa	no correlation	NSD
Nucula tenuis	sed	SD
Chaetozone setosa	no correlation	SD
Lumbrinereis l. japonica	depth	C
Neptunea heros	no correlation	C
	Group 4	
Nephtys ciliata	sal/temp/sed/oxy	C
Pholoe minuta	no correlation	C
	Group 5	
Sternapsus fossor	oxy/sal/depth	NSD
Cumacea A	oxy/sal	SD

Table 15 Con't.

Species	Environmental Influences	Feeder Type
	Group 6	
Travisia brevis	sed	NSD
Echinarachnius parma	depth	MPS
Amphipod H	depth/oxy	MPS
	Group 7	
Admete couyouthi	oxy	C
Turitellopsis reticulata	sed	C
	Group 8	
Amphipod A	sed	MPS
Cumacea C	sal	SD
Anthozoa	temp	C
	Group 9	
Cucumaria populifera	temp	SD
Cumacea D	temp/oxy	SD

as yet unassessed. In the case of each major phylum, no one factor emerged as dominant (Fig. 4). In considering the various affinity groups, however, there does appear to be some correlation between the species representing the group and the physical factors influencing their distribution, at least for groups 1 and 2, where the same factors exert the dominant influence over the majority of species within the groups.

DISCUSSION

As previously stated, the primary objectives of the present study were to assess distribution of benthos beneath the winter ice pack of the Bering Sea shelf, to compare such distribution and standing stock with Soviet estimates from summer months, to evaluate the influence of environmental factors upon this distribution and abundance, and to evaluate the distribution and abundance of walrus food species and lay the groundwork for productivity studies directed at these food species.

The choice of sampling instruments and methods used to attain these ends was dictated partly by the limitations imposed by the ship and by the weather and ice conditions, which limited samplers to small grabs of less than 75 kg loaded weight. Within this limitation

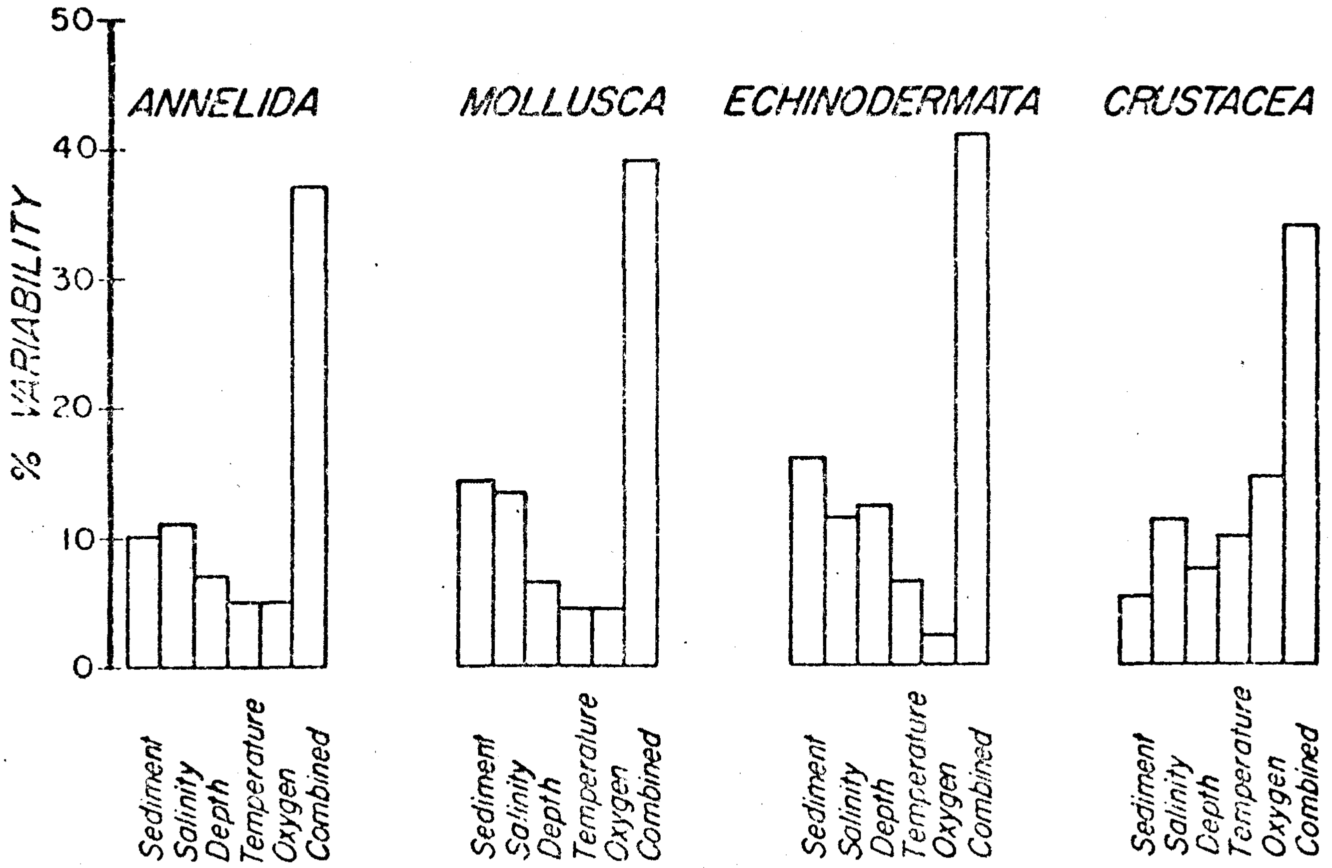

Figure 4. Percent of variability of distribution and density of major benthic phyla accounted for by observed environmental factors on the Bering Sea Shelf.

the choice of samplers was made on the basis of Ulf Lie's 1963-64 investigation of the benthic infauna of Puget Sound (Lie, 1965). Lie found that five replicates with the 0.1 m^2 van Veen grab obtained 75-80% of the species found in ten replicates, and while the number of species was still increasing at the tenth sample, the increment of increase was only 3%. It was also estimated that 5 samples would estimated 95% of the individuals estimated from 10 grabs. Lie further determined that a 1 mm screen would retain 95% of the standing crop in terms of wet weight biomass, and 86% of the number of species, though only 25% of the total number of individuals. It was found, however, that a smaller screen size was not practical for Bering Sea work due to the general coarseness of sediments.

This same sediment coarseness, combined with strong bottom currents in some regions, results in a hard-packed substrate difficult to penetrate with existing grabs. In some areas, such as northeast of St. Lawrence Island, the grab penetrated only a few centimeters (Table 1), probably insufficient to capture some of the deep-burrowing forms, particularly bivalve molluscs. It is felt, however, that this is a problem not unique to this particular study. The large bivalve, *Mya truncata*, is known to be a major contributor to the diet of the Pacific walrus in the northern Bering Sea (personal observation), yet this deep-burrowing species appears on none of the distributional studies.

A second sampling problem encountered in winter studies in ice-covered seas is that of maintaining station position. Due to ice conditions it was not possible to anchor or otherwise hold the ship in constant position during sampling, and as the drift rate of the pack ice was sometimes as high as 3 to 6 knots, a 30 minute series of six grabs often represented, in effect, a close-spaced transect over 1 to 3 miles.

Quantitative Features of the Fauna

The wet weight biomass of 127 g wet/m^2 averaged over the stations occupied by this study is considerably greater than the average of 74.4 g/m^2 observed by Neyman for the same region in the summer (Neyman, 1960). Due to the extreme patchiness of the fauna, however, and the extreme variability of samples, such an increase cannot be considered statistically valid.

It has been proposed (Neyman, 1960) that one of the reasons for the relatively low benthic biomass encountered on the eastern shelf, and particularly in the Bristol Bay region, is due not to low productivity but to high predation by benthic feeding fishes, which generally vacate the shelf during winter. The relatively large numbers and species of invertebrate carnivores found, particularly species which prey upon bivalve molluscs (Table 12) may also be an indication of high benthic productivity on the eastern shelf. In analyzing walrus stomach samples from the north Bering Sea very large numbers of opercula from predatory gastropods such as *Neptunea* sp. have been found (personal observation), indicating that the abundance of such predators may be considerably higher than even the present sampling would indicate.

No quantitative figures are presently available but if, as seems the case, such gastropods contribute a considerable part of the walrus diet then this raises the walrus itself to the third or fourth trophic level, a situation demanding high benthic productivity for maintenance of the population.

It is estimated that the present population of the Pacific walrus herd is about 120,000 animals composed of approximately 1/3 adult males, 1/3 adult females, and 1/3 subadults (F. Fay, Institute of Arctic Health, Fairbanks, personal communication). Given an average estimated weight of 900 kg for females and subadults and 1,400 kg for adult males, this yields a walrus biomass of approximately 127,350 metric tons. This population is in residence in the Bering Sea for about 270 days a year, from October through June. From captive animals it is estimated that adult and subadult walrus consume between 5 and 7% of their body weight daily, perhaps as much as 10% in the wild (Fay, personal communication). The walrus herd might consume then, between 1,700,000 and 3,440,000 metric tons of benthic biomass, wet weight, on the Bering Sea shelf annually, or between 2 and 4% of the observed 79 g wet/m^2 or 79 tons/km^2 winter standing stock of food species (Table 14). While seemingly an insignificant percentage, the actual percentage of the benthos consumed over limited areas may be much higher due to walrus concentrations in traditional winter feeding grounds. During the late winter and early spring, for instance, the bulk of the population seems normally to be concentrated in an area just southwest of St. Lawrence Island and in another area just northeast of St. Matthew (F. Fay, personal communication). Over these areas, intensity and high trophic level of walrus feeding may indicate high levels of benthic productivity in a region where the standing stock appears to remain the highest on the eastern Bering Sea shelf (Neyman, 1960). Applying the above means and estimates, each individual walrus would require between 0.3 and 0.4 km^2 feeding area per year, or about 1,000 m^2 per day, provided that they were not size selective and removed all food species from that area, which is hardly likely. For purposes of conjecture, however, if that were the case, the walrus population would require annually between 36,000 and 48,000 km^2 of benthos, or between 3.5 and 4.7% of the total shelf.

A major complication encountered in any distributional study of Bering shelf benthic fauna is the extremely patchy nature of that fauna, as apparent in this study and from past studies (Neyman, 1960). The reasons for this patchiness are uncertain. It seems that environmental factors do not sufficiently explain such variation, which may be due therefore to interspecific and intraspecific biological interactions, or to environmental factors not yet recognized. One of the problems of explaining such variation in terms of environmental factors is the present lack of seasonal data. Several conditions, such as temperature and sedimentation rates, may be decisive limiting factors during seasonal extremes but may appear to have little influence over the rest of the year, i.e. when the studies are undertaken and samples collected.

The bivalve, *Clinocardium ciliatum*, appears at only 2 stations, 7 and 16, over what would seem to be a broad area of suitable habitat, and at each station it is found in great numbers of only one size class. It is suggested, from this limited sampling, that this is the result of biological conditioning of the substrate by newly settled spat so that the habitat is rendered unsuitable for successive recruitments. The established population could then grow to maturity with no admixture of age classes. Upon death or removal of these adults, the recently vacated habitats may lie fallow for some time before the conditioning effects, whatever they are, have ammeliorated to allow recolonization. If one of these *C. ciliatum* stations, Station 7 is deleted from the standing stock computations, the average wet weight biomass estimate for this study over the eastern shelf would drop to 82.7 g wet/m^2, a figure probably not significantly different from that of Neyman for summer studies. Unfortunately, I cannot be certain just how much of this sort of extreme patchiness Neyman encountered in her study, and so can neither support nor deny the validity of including Station 7. For the present study, however, it will be included.

The distribution of *Macoma calcarea* shows the same trend toward extreme patchiness, particularly as regards Station 23. *Macoma calcarea*, however, and *Yoldia hyperborea*, appear to be subject to heavy gastropod predation, judging from the number of drilled shells found, a circumstance which may partially explain their erratic distribution.

C. Ciliatum did not appear to be heavily preyed upon by gastropod borers, though it, as well as the other two bivalve species above, is a major item in the walrus diet (personal observation).

Of the 129 species or taxa encountered, 35 accounted for about 80% of the total density, wet weight biomass or organic carbon biomass, and 8 species accounted for over 50% of all these values. Thus, while the benthic fauna of the Bering shelf shows a fair diversity in terms of number of species present, the overall productivity and ecological stability may be dependent upon very few species and is, in effect, a low diversity fauna. If these percentage contributions by major species hold true, then these species should be emphasized in future investigations of distributions and productivity.

While the 16 stations sampled in this study did show very significant differences in standing stock when subjected to analysis of variance tests, no clear correlation could be determined between physical factors, such as depth, temperature, salinity, oxygen, or sediment size, and distribution of biomass. Such correlation probably does exist, but is presently elusive due to the small sample size available.

In past benthic studies, standing stock has been estimated as wet weight, dry weight, or ash-free dry weight, and though acceptable for standing stock and distribution studies, such measurements are felt to be insufficiently sensitive and descriptive when dealing with productivity and food chain studies. For this reason representative samples of species collected were subjected to elemental analysis, and organic carbon and nitrogen ratios determined as percentage wet and dry weight (Table 2). This elemental analysis will be continued and expanded, and the results applied to future productivity and food chain studies. The average organic carbon content of benthic species sampled ran about 5% wet weight, which converts to a total organic carbon standing stock of about 6.4 million metric tons for the Bering Sea shelf, applying the mean biomass of 127 g wet/m^2 to the entire region. When considering walrus food species, the estimate, based on this study, of 80 million tons wet weight for the entire shelf converts to 4 million tons organic carbon, with an annual consumption by walrus of between 80,000 and 160,000 metric tons.

Qualitative Features of the Fauna

When considering the qualitative distribution of benthic fauna over the Bering Sea shelf and reasons for that distribution, only broad generalizations can be drawn. The species affinity groups (Table 15), based upon distribution and density of the major species, are thought to be valid for this study, but will undoubtedly come under criticism and revision as more data becomes available. Little conjecture can be put forward at this time as to controlling factors which define the distribution of these groups, or the reasons for such species affinities as are observed. These affinities may be due to biological interactions, such as predator-prey relationships, creation of species niches by other species through habitat conditioning, or they may be parallel responses of biologically independent species to environmental dictates. When species data and environmental factors are lumped in regression analysis the species correlations mask almost completely the environmental, but when the species are subjected independently to regression analysis with environmental factors some conclusions can be drawn.

Groups 1 and 2 of the affinity associations (Table 15) appear to be influenced, within the respective group, by the same environmental effects, with species in Group 1 influenced by salinity, depth, and sediment mode size, in that order of importance, and species in Group 2 affected by sediment, salinity, and depth. The depth parameter in Group 2 appears to affect only *Lumbrinereis latrelli japonica*, however, which is a predator and so may be present only in a predator-prey relationship. Group 5 likewise appears to be influenced by oxygen content and salinity, and Group 9 by temperature and oxygen, though both of these groups consist of only two species. The other 5 groups show no dominant environmental influence, and even in cases where influence is apparent, environmental effects account for no more than about 40% of the distributional variability, the remainder being presumed due to biological interactions or environmental factors as yet uninvestigated.

According to Neyman (1960) the population density of certain species, such as *Ophiura sarsi*, seems to be rather definitely dependent upon bottom temperatures, though the present study indicates that sediment size and salinity are the major environmental factors influencing the distribution of *O. sarsi* (Table 15). All Soviet studies were conducted in the summer months, however, when bottom temperatures are considerably warmer and bottom thermoclines more definite. It seems, therefore, that the distribution of at least some species may be governed by seasonal extremes of conditions. Temperature, for instance, may be conclusively limiting at warm, summer, temperatures, but may show little influence upon distribution during winter. The definite correlation of distribution and density with environment awaits then an adequate assessment of the environment over all seasons as well as more complete data as to faunal distribution. Such factors as temperature, salinity, and oxygen content are almost certainly seasonally variable, as are primary productivity rates and probably even sedimentation rates in such a winter ice-bound sea. Depth is probably the only environmental or biological variable which is not seasonally dependent.

An attempt was made to correlate feeder type with affinity groups and environmental effects, with inconclusive results. Affinity Group 1 appears to be mostly composed of selective detritus feeders, as does Group 9. Group 1, however, has salinity, depth, and sediment as the dominant physical determinants, while Group 9 seems to be affected primarily by temperature. Groups 4 and 7 are strictly carnivore associations, which is increasingly curious in that neither shows a dominant environmental determinant. The remainder of the affinity groups, the majority, show no dependable trends as to either feeder type or environmental influence. A review of the major species present at stations (Appendix A), shows a similar confusion, with no feeder type or environmental influence showing dominance at any one station.

An apparent abberation worth mentioning is Station 27, located south of the Seward Peninsula (Fig. 1). Large quantities of eelgrass detritus were found in the grabs at this station, and a fauna somewhat atypical of the other stations (Appendix A). The ophiuroid, *Amphipholis squamatma*, was found in great numbers at this station, and occurred at no other station. This species is known to be associated with eelgrass beds (D'Yakonov, 1954). Whether the ophiuroids were transported with the eelgrass, presumably from the lagoons along the south shore of the Seward Peninsula (McRoy, 1970), or whether they congregated there in response to the eelgrass detritus is open to debate. *A. squamatma* is often confused with *Amphipholis pugetana*, and is likely the same species (D'Yakonov, 1954).

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Appendix A. Quantitative characteristics by station, and feeder type of the major benthic species. Listed species contribute greater than 5% in any category unless marked *, which contribute greater than 10%. Feeder types: SD = selective detritus; NSD = nonselective detritus; SS = sessile seston; MPS = mobile or partly mobile seston; C = carnivore.

Station	Species	Feeder Type	Density Indiv./m^2	% Total Indiv. of All Species	Biomass g wet/m^2	% Total Biomass of All Species	Organic Carbon mg/m^2	% Total Organic Carbon of All Species
3	*Cumacea D	SD	260	39.6	0.4	0.8	18	0.7
	*Amphipod H	MPS	114	17.4	0.4	0.7	17	0.6
	*Amphipod A	MPS	84	12.8	0.5	1.0	38	1.4
	Scoloplos armiger	NSD	62	9.2	0.3	0.6	21	0.8
	Leptosynapta sp.	SD	20	3.1	1.5	2.8	156	0.8
	*_Cucumaria populifera_	SD	18	2.7	37.4	72.6	2,183	80.5
	*_Ophiura sarsi_	SD	2	0.3	5.4	10.6	77	2.8
	Nuculana radiata	SD	2	0.3	3.1	6.0	85	3.2
	>5% sums			85.7		95.1		95.7
	>10% sums			72.9		86.3		86.8
4	*_Echinarachnius parma_	MPS	400	42.0	9.1	31.4	149	9.5
	*Amphipod H	MPS	197	20.7	1.1	3.9	60	3.8
	Spiophanes bombyx	SD	62	6.5	0.4	1.2	19	1.2
	Scoloplos armiger	NSD	55	5.8	1.9	6.5	118	7.5
	Venericardium crebricostata	MPS	18	1.9	1.7	5.9	23	1.5
	Diplodonta aleutica	?	13	1.4	0.5	1.9	84	5.3
	*_Travisia brevis_	NSD	5	0.5	4.9	16.9	564	35.8
	>5% sums			78.8		67.8		64.6
	>10% sums			63.2		52.2		49.1

Appendix A Con't.

Station	Species	Feeder Type	Density Indiv./m^2	% Total Indiv. of All Species	Biomass g wet/m^2	% Total Biomass of All Species	Organic Carbon mg/m^2	% Total Organic Carbon of All Species
5	*Cumacea D	SD	142	22.8	4.5	4.2	211	4.9
	*Amphipod A	MPS	116	18.7	16.5	15.4	518	12.0
	*Amphipod H	MPS	102	16.4	1.3	1.2	61	1.4
	Scoloplos armiger	NSD	46	7.4	3.8	3.6	239	5.5
	*_Sternapus fossor_	NSD	40	6.4	28.9	27.0	670	15.5
	*Nemertinea (unident.)	C	4	0.6	16.0	14.9	871	20.2
	>5% sums			72.4		66.2		59.6
	>10% sums			65.0		62.6		54.0
6	*_Scoloplos armiger_	NSD	266	36.1	7.9	5.7	496	8.6
	*Amphipod A	MPS	190	25.8	3.8	2.8	282	4.9
	*_Echinarachnius parma_	MPS	68	9.2	37.0	27.1	609	10.6
	Amphipod J	MPS	38	5.2	3.9	2.9	262	4.6
	*_Turitellopsis reticulata_	C	22	3.0	33.4	24.5	1,462	25.4
	*_Travisia brevis_	NSD	4	0.5	31.1	22.8	1,840	32.0
	Admete couthouyi	C	4	0.5	12.7	9.3	359	6.2
	>5% sums			80.4		95.0		92.3
	>10% sums			74.7		82.8		81.5
7	*Amphipod H	MPS	100	24.3	0.2	0.1	8	.0
	*Amphipod A	MPS	54	13.1	1.1	0.2	83	.5
	*_Nephtys ciliata_	C	42	10.2	6.0	0.8	263	1.4
	*_Clinocardium ciliatum_	MPS	38	9.2	736.9	93.8	17,255	93.3
	Cumacea C	SD	38	9.2	0.1	<0.1	3	<0.1
	>5% sums			66.0		94.7		95.2
	>10% sums			56.8		94.7		95.2

Appendix A Con't.

Station	Species	Feeder Type	Density Indiv./m^2
8	*Amphipod A	MPS	140
	**Scoloplos armiger*	NSD	78
	Amphipod H	MPS	42
	Praxillella praetermissa	NSD	30
	Axiothella catenata	NSD	24
	Cumacea D	SD	24
	**Macoma calcarea*	SD	2
	**Yoldia hyperborea*	SD	2
	>5% sums		
	>10% sums		
10	*Amphipod A	MPS	138
	**Scoloplos armiger*	NSD	110
	*Amphipod H	MPS	96
	**Praxillella praetermissa*	NSD	58
	**Neptunea heros*	C	4
	>5% sums		
	>10% sums		
11	**Scoloplos armiger*	NSD	224
	**Praxillella praetermissa*	NSD	64
	Chaetozone setosa	SD	46
	**Sternapus fossor*	NSD	42
	Lumbrinereis l. japonica	C	38
	**Yoldia hyperborea*	SD	18

% Total Indiv. of All Species	Biomass, g wet/m^2	% Total Biomass of All Species	Organic Carbon mg/m^2	% Total Organic Carbon of All Species
30.4	0.4	1.3	33	2.3
17.0	2.1	6.0	134	9.6
9.1	0.1	0.3	6	0.4
6.5	1.0	3.0	65	4.6
5.2	1.4	4.0	79	5.6
5.2	0.1	0.1	2	0.2
0.4	17.3	49.1	506	36.1
0.4	6.2	17.5	265	18.9
74.3		81.2		77.7
48.3		73.9		66.9
25.7	0.2	0.4	17	0.4
20.5	2.0	3.1	126	2.8
17.8	0.1	0.1	2	0.1
10.8	3.4	5.4	696	15.2
.7	43.8	68.2	3,472	75.7
75.5		77.1		94.0
74.7		68.2		90.8
41.8	2.3	4.3	143	6.2
11.9	3.4	6.5	215	9.3
8.6	0.6	1.1	39	1.7
7.8	6.6	12.5	152	6.6
7.1	0.2	0.4	16	0.7
3.4	31.1	59.1	1,335	57.7

Appendix A Con't.

Station	Species	Feeder Type	Density Indiv./m^2	% Total Indiv. of All Species	Biomass g wet/m^2	% Total Biomass of All Species	Organic Carbon mg/m^2	% Total Organic Carbon of All Species
11	_Nephtys ciliata_	C	8	1.5	3.2	6.0	140	6.1
	>5% sums			82.1		92.7		92.7
	>10% sums			64.9		82.4		79.7
13	*_Scoloplos armiger_	NSD	90	27.3	2.6	4.0	164	6.0
	*_Chaetozone setosa_	SD	60	18.2	0.9	1.4	62	2.3
	*_Nuculana tenuis_	SD	50	15.2	11.0	16.8	458	16.8
	*_Yoldia hyperborea_	SD	20	6.1	13.0	19.8	558	20.5
	Prionospio malgrenia	SD	20	6.1	0.1	0.2	6	0.2
	*_Artcama proboscidea_	NSD	10	3.0	20.9	32.0	989	36.4
	>5% sums			84.8		92.7		92.7
	>10% sums			78.8		92.5		92.5
14	*Amphipod J	MPS	548	78.5	5.5	18.9	365	26.0
	Scoloplos armiger	NSD	54	7.7	1.5	5.3	96	6.8
	*_Yoldia hyperborea_	SD	8	1.2	10.6	36.6	453	32.2
	Sternapsus fossor	NSD	8	1.2	1.7	5.9	39	2.8
	Nucula tenuis	SD	6	0.9	2.4	8.4	101	7.2
	*_Terebellides stroemi_	SD	4	0.6	3.5	12.1	163	11.6
	>5% sums			90.0		87.1		86.6
	>10% sums			80.2		67.6		69.8

Appendix A Con't.

Station	Species	Feeder Type	Density Indiv./m^2
16	**Clinocardium ciliatum*	MPS	350
	**Ophiura flagellata*	SD	304
	Macoma calcarea	SD	64
	**Yoldia hyperborea*	SD	60
	**Yoldia thraciaeformis*	SD	2
	Pista cristata	SD	2
	>5% sums		
	>10% sums		
23	*Amphipod J	MPS	1,562
	**Maldane sarsi*	NSD	1,090
	**Macoma calcarea*	SD	684
	Ophiura sarsi	SD	68
	>5% sums		
	>10% sums		
24	*Amphipod J	MPS	3,512
	**Scoloplos armiger*	NSD	460
	**Macoma calcarea*	SD	68
	Nucula tenuis	SD	30
	**Pectinaria hyperborea*	SD	26
	Praxillella praetermissa	NSD	26
	Nuculana radiata	SD	24
	>5% sums		
	>10% sums		

% Total Indiv. of All Species	Biomass, g wet/m^2	% Total Biomass of All Species	Organic Carbon mg/m^2	% Total Organic Carbon of All Species
34.8	58.3	42.2	1,221	29.1
30.2	2.8	2.1	46	1.1
6.4	9.8	7.1	24	5.8
6.0	19.1	13.8	820	19.5
0.2	28.9	20.9	904	21.5
0.2	7.1	5.1	341	3.1
77.7		91.1		85.2
71.2		78.9		71.3
42.2	11.2	4.0	754	7.2
29.4	54.9	19.6	2,686	25.7
18.5	143.1	51.0	4,447	42.5
1.8	23.3	8.3	329	3.1
92.0		82.9		78.5
90.1		74.5		75.4
79.6	18.1	11.5	1,210	20.0
10.4	7.8	4.9	489	8.1
1.5	37.4	23.8	1,278	21.1
0.7	9.6	6.1	401	6.6
0.6	21.2	13.5	711	11.7
0.6	5.7	3.7	358	5.9
0.5	10.0	6.4	202	3.3
93.9		69.8		76.7
92.1		53.7		60.8

Appendix A Con't.

Station	Species	Feeder Type	Density Indiv./m^2
25	*Amphipod A	MPS	418
	*Amphipod J	MPS	190
	**Pelonia corrugata*	SS	20
	Macoma calcarea	SD	16
	Ammotrypane aulogaster	NSD	8
	**Ophiura sarsi*	SD	2
	**Assiminea* sp.	C	2
	>5% sums		
	>10% sums		
26	*Amphipod A	MPS	1,158
	*Anthozoa (unident.)	C	12
	Hiatella arctica	?	12
	*Ascidacea (unident.)	SS	4
	Solariella obscura	C	2
	>5% sums		
	>10% sums		
27	*Amphipod A	MPS	224
	*Cumacea A	SP	150
	**Sternapus fossor*	NSD	110
	Amphipholis squamatma	SD	66
	Serripes groenlandicus	MPS	44
	**Yoldia hyperborea*	SD	26
	*Anthozoa (unident.)	C	6

% Total Indiv. of All Species	Biomass, g wet/m^2	% Total Biomass of All Species	Organic Carbon mg/m^2	% Total Organic Carbon of All Species
49.1	2.2	5.7	160	9.0
22.3	4.1	10.9	277	15.6
2.4	9.2	24.2	376	21.2
1.9	2.4	6.4	81	4.5
0.9	1.9	4.9	109	6.2
0.2	6.1	16.3	87	4.9
0.2	5.5	14.6	305	17.2
77.0		83.1		78.5
74.2		71.7		67.8
82.0	3.1	13.6	227	17.7
0.9	8.9	39.4	472	36.9
0.9	2.2	9.9	98	7.6
0.3	3.0	13.3	60	4.6
0.1	1.2	5.2	96	7.5
84.1		81.3		74.1
83.1		66.2		59.1
28.1	1.0	3.2	77	6.2
18.8	0.8	2.4	36	2.9
13.8	13.6	41.5	315	25.4
8.3	1.5	4.6	33	2.7
5.5	0.8	2.5	15	1.2
3.3	5.2	15.9	224	18.1
0.8	3.8	11.6	202	16.4

Appendix A Con't.

Station	Species	Feeder Type	Density Indiv./m^2	% Total Indiv. of All Species	Biomass g wet/m^2	% Total Biomass of All Species	Organic Carbon mg/m^2	% Total Organic Carbon of All Species
27	*Lumbrinereis l. japonica*	C	2	0.3	1.7	5.1	122	9.9
	>5% sums			78.9		86.8		82.8
	>10% sums			64.8		74.6		69.1