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Mollusks in the Northeastern Chukchi Sea[1]

HOWARD M. FEDER,[2] NORA R. FOSTER,[3] STEPHEN C. JEWETT,[2]
THOMAS J. WEINGARTNER[2] and RAE BAXTER[4]

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ABSTRACT. Infaunal and epifaunal mollusks of the northeastern Chukchi Sea were sampled and 139 molluscan taxa were identified. The pattern of spatial distribution of molluscan species was determined by cluster analysis, which resulted in six infaunal and five epifaunal station groups. Species characterizing various faunal groups are defined. Stepwise multiple discriminant analysis was applied to correlate benthic biological associations with environmental variables. Delineation of infaunal groups was mainly due to percentage of sand and bottom salinity, while epifaunal groups were separated by percent gravel and bottom temperature. An increase in abundance and biomass of infaunal mollusks occurred adjacent to and north and northwest of an identified bottom front between the Bering Shelf and Resident Chukchi Water and Alaska Coastal Water. Epifaunal molluscan abundance and biomass were highest near the coast. Mollusks, especially smaller species and the juvenile stages of larger species, represent a food resource for bottom-feeding predators in the study area.

Key words: Chukchi Sea, mollusk, benthic, infauna, epifauna, bottom front, bottom-feeding predators, cluster analysis, discriminant analysis

RÉSUMÉ. On a fait un échantillonnage des mollusques de l'endofaune et de l'épifaune du nord-est de la mer des Tchouktches et on a identifié 139 taxons de mollusques. On a déterminé le schéma de répartition géographique des espèces de mollusques au moyen d'une analyse typologique, qui a donné six groupes de stations dans l'endofaune et cinq dans l'épifaune. On définit des espèces caractéristiques des divers groupes fauniques. On a appliqué une analyse discriminante multiple séquentielle pour corréler les associations biologiques du benthos aux variables de l'environnement. La délimitation des groupes de l'endofaune était due en grande partie au taux de sable et de salinité au fond, tandis que les groupes de l'épifaune étaient répartis en fonction du taux de gravier et de température au fond. Une augmentation dans la quantité et la biomasse des mollusques de l'endofaune apparaissait près du nord et du nord-ouest d'un front de fond compris entre le plateau continental, les eaux non brassées de la mer des Tchouktches et les eaux côtières de l'Alaska. C'est près de la côte qu'on retrouvait l'abondance et la biomasse maximales des mollusques de l'épifaune. Les mollusques, surtout ceux des petites espèces et ceux des grandes espèces qui étaient au stade juvénile, représentaient une source alimentaire pour les prédateurs benthiques vivant dans la zone d'étude.

Mots clés : mer des Tchouktches, mollusque, benthique, enfofaune, épifaune, front au fond, prédateurs benthiques, analyse typologique, analyse discriminante

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INTRODUCTION

Limited quantitative information is available for marine mollusks of the Chukchi Sea north of 68°21′ latitude and east of 170°00′ west longitude (Figs. 1 and 2). However, an investigation of the infauna of this region by Feder *et al.* (1990a) indicated that this group is an important one, constituting approximately 20% of the abundance, 36% of the wet weight, and 40% of the carbon biomass of infauna collected. Studies by Stoker (1978, 1981) in the northeastern Chukchi Sea examined distribution, abundance, and biomass data for mollusks in conjunction with other infaunal organisms. Both Stoker (1978) and Feder *et al.* (1990a) include interpretations of total infaunal distributions based on environmental parameters. The abundance and distribution of bivalves in the western Chukchi Sea are discussed in Filatova (1957). The distributional ecology of bivalves in the adjacent western Beaufort Sea is presented in Carey *et al.* (1984). Qualitative reports on molluscan fauna in the general area are included in MacGinitie (1955) for the Point Barrow region, Ingham *et al.* (1972) and Mann (1977) in the eastern Chukchi Sea, and Frost and Lowry (1983) in the western Beaufort Sea. Supplemental information on the composition and general distribution of selected mollusks in these northern latitudes is also available from feeding investigations on walrus and bearded seals (Johnson *et al.*, 1966; Fay, 1982; Lowry *et al.*, 1980a,b). Additionally, a number of studies include information for molluscan fauna in the southeastern Chukchi Sea. Sparks and Pereyra (1966) present data from 1959 on the composition and relative abundance of mollusks south of Point Hope, although they include some data from stations north of Cape Lisburne. A trawl survey conducted in 1976 provides quantitative data on the epifauna, inclusive of mollusks and demersal fishes, in the area between Bering Strait and Point Hope (Wolotira *et al.*, 1977; Feder and Jewett, 1978; Jewett and Feder, 1981). Qualitative and quantitative sampling for epifauna and demersal fishes was conducted in 1982 in shallow waters (<15 m) in the Kivalina region, south of Point Hope (Blaylock and Erikson, 1983; Blaylock and Houghton, 1983). Information on infauna, inclusive of mollusks, is included in multi-year studies in the northern Bering and southern Chukchi seas by Feder *et al.* (1985), Grebmeier (1987, 1992), Grebmeier *et al.* (1988, 1989), and Feder *et al.* (1990a,b).

Taxonomic literature on mollusks of the northeastern Chukchi Sea is scattered among many sources. Because most mollusks within the study area are widely distributed in arctic and boreal seas, taxonomic descriptions are primarily included in publications relating to areas adjacent to the Chukchi Sea. MacGinitie (1959) describes the molluscan fauna near Point Barrow; Macpherson (1971) summarizes the gastropods, chitons, and scaphopods from the Canadian

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[1] Institute of Marine Science Contribution 1008.
[2] Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska 99775, U.S.A.
[3] University of Alaska Museum, Fairbanks, Alaska 99775, U.S.A.
[4] Deceased; formerly NOAA/National Ocean Service, Ocean Assessment Division, Alaska Office, Anchorage, Alaska, U.S.A.

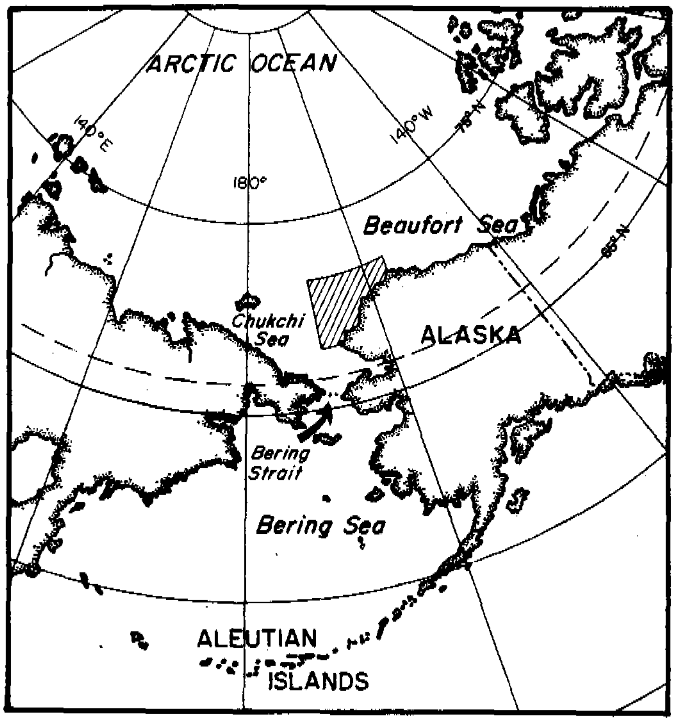

FIG. 1. Location of the study area (cross hatched).

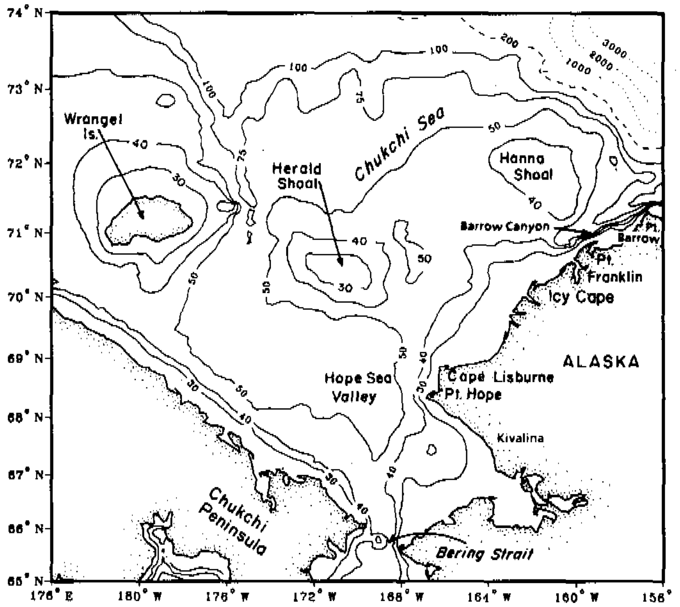

FIG. 2. Bathymetry of the Chukchi Sea.

Archipelago; Bernard (1979) and Lubinsky (1980) provide useful descriptions of the bivalve fauna of the western Beaufort Sea and the eastern Canadian Arctic respectively. Mollusks from adjacent Japanese waters (including the Okhotsk and western Bering seas) are described in Okutani *et al.* (1988, 1989), and reference to these and other mollusks is also found in Pavloskii (1955). Foster (1981) and Baxter (1987) summarize the composition and distribution of molluscan fauna throughout Alaskan waters.

In this paper we consider infaunal and epifaunal mollusks of the northeastern Chukchi Sea, relate their abundance and biomass values to environmental parameters, and consider the importance of mollusks as food for benthic predators in the study area.

THE STUDY AREA

The northeastern Chukchi Sea is relatively shallow, with depths ranging between 30 and 60 m over most of the region (Fig. 2). In general, bottom depth varies smoothly, although there are several important bathymetric features that influence both the flow and distribution of water masses. These features include 1) Barrow Canyon, which strikes northeastward across the continental shelf and slope west of Point Barrow, 2) Hope Sea Valley, a broad, 55 m deep depression trending northwestward from Point Hope, 3) Hanna Shoal, to the west of Barrow Canyon, and 4) Herald Shoal, in the center of the Chukchi Basin. The two shoals have minimum depths of about 25 m.

Circulation features and water-mass properties of the Chukchi Sea are discussed by Coachman *et al.* (1975), Walsh *et al.* (1989), Johnson (1989), and Weingartner (unpubl.). Chukchi Sea waters reflect a combination of both advective and *in situ* processes, with the most important of these being the northward advection of waters through Bering Strait. This flow bifurcates offshore of the Lisburne Peninsula. One branch transports Bering Shelf Water (BSW) northwestward through the Hope Sea Valley, and also northward along the eastern flank of Herald Shoal. This water mass is characterized by low temperatures (−1° to 2°C), high salinity (>32.5), and relatively high nutrient and particulate organic carbon (POC) concentrations (Grebmeier *et al.*, 1988; Walsh *et al.*, 1989). In summer and fall, part of the northeastward flowing branch forms the Alaska Coastal Current (ACC) and consists primarily of Alaska Coastal Water (ACW). This water mass, which is heavily influenced by coastal freshwater discharge from the Yukon River and numerous smaller drainages along the western coast of Alaska, consists of relatively warm (>2°C) and dilute (<31.8‰) water, with a high sediment load but low concentrations of nutrients and POC (Grebmeier *et al.*, 1988). The Alaska Coastal Current flows inshore of and parallel to the 30 and 40 m isobaths and exits the Chukchi Sea through Barrow Canyon. A third water mass, Resident Chukchi Water (RCW), is either advected onshore from the upper layers of the Arctic Ocean and/or is ACW and BSW remnant from the previous winter when its salinity is increased and temperature decreased due to freezing processes. As noted by Johnson (1989) and Weingartner (unpubl.), a bottom-intersecting front paralleling the 30 and 40 m isobaths is typically observed in summer and fall months. The front extends northward from the Lisburne Peninsula to about 71°N and then bends eastward toward Icy Cape and Point Franklin. ACW lies inshore of this front, while BSW, RCW, and mixtures of these water masses lie offshore and to the north of the front (Johnson, 1989). Because ACW is less dense than BSW or RCW, ACW may also be observed at the surface and offshore of the bottom front. Year-long current meter records from 1991/92 and a fall 1992 hydrographic survey identified a persistent northward flow of BSW along the east flank of Herald Shoal

(Weingartner, unpubl.). Coachman and Shigaev (1992) and Whitledge *et al.* (1992) speculate that a fraction of the water flowing north along the Lisburne Peninsula is ultimately derived from the vicinity of Wrangel Island in the northwest Chukchi Sea. This high-salinity, nutrient-rich water is advected into the southeastern Chukchi Sea along the Siberian coast by the Siberian Coastal Current. They suggest that nutrients within this current supplement those derived from the Bering Sea to enhance annual primary production in the southcentral Chukchi Sea and contribute POC to the northeastern shelf (Grebmeier *et al.*, 1988; Walsh *et al.*, 1989). Occasionally, wind-induced reversal of the normal northeastern water flow along the coast is accompanied by upwelling (Wiseman and Rouse, 1980; Johnson, 1989). As discussed later, all the above observations have important effects on the distribution, abundance, and biomass of mollusks in the northeastern Chukchi Sea.

In the northeastern Chukchi Sea, the inner shelf between Point Hope and Point Barrow is carpeted by relatively coarse sediments. Farther seaward are muds containing various proportions of gravel and sand (Naidu, 1987). Sediments of the more northerly offshore region have a higher percentage of water and lower percentage of gravel than the southern offshore area (Feder *et al.*, 1990a). All sediments are very poorly to extremely poorly sorted. The central portion of the northeastern Chukchi Sea receives the major proportion of clayey sediments of Yukon River origin. Sediment is displaced from the Bering Sea via the net northward flow of water masses, presumably as a nepheloid layer (McManus and Smyth, 1970). Sea ice covers the Chukchi Sea from November through June and can affect the benthos by ice gouging (Grantz *et al.*, 1982; Carey, 1991). Polynyas can occur from Cape Lisburne to Point Barrow, generally extending seaward from just beyond the landfast ice (Stringer and Groves, 1991).

MATERIALS AND METHODS

Infaunal mollusks and conductivity, temperature, and depth (CTD) data were collected in August-September 1986 at 37 stations in the study area (Fig. 3a). Five replicate samples using a 0.1 m^2 van Veen grab were taken at each station. Epifaunal mollusks and associated physical oceanographic data were collected in August 1990 at 48 stations at similar depths to the 1986 collection as part of a fish survey in the northeastern Chukchi Sea (Fig. 3b; Smith *et al.*, unpubl.). Epifauna was obtained using a NMFS 83-112 otter trawl. The net had a 90 mm mesh cod end and a 32 mm stretched liner. Effective opening width of the net was 17.0 m. Two 30-minute tows were taken at each station. Sediment data are from Naidu (1987) and Feder *et al.* (1990a).

Specimens were identified to species or lowest possible taxon. Voucher specimens are deposited in the University of Alaska Museum Aquatic Collection, Accessions 1993-3 (specimens collected in 1986) and 1992-16 (specimens collected in 1991). Photographs of nine species that are common in the study area but have not been well illustrated in the literature are included in this paper.

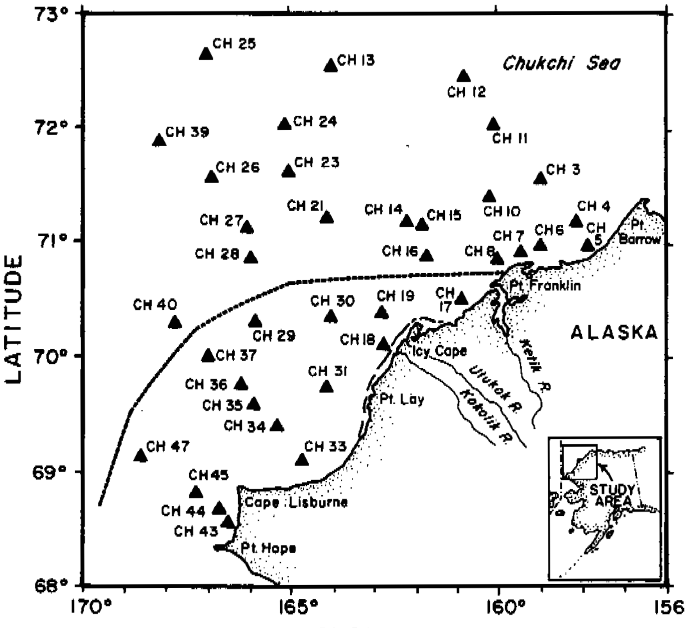

FIG. 3a. Location of the infaunal sampling stations occupied in the northeastern Chukchi Sea by Feder *et al.* (1990a). Dashed line represents a bottom frontal zone that separates Bering Shelf and Resident Chukchi Water, offshore and to the north, from Alaska Coastal Water, inshore of the front.

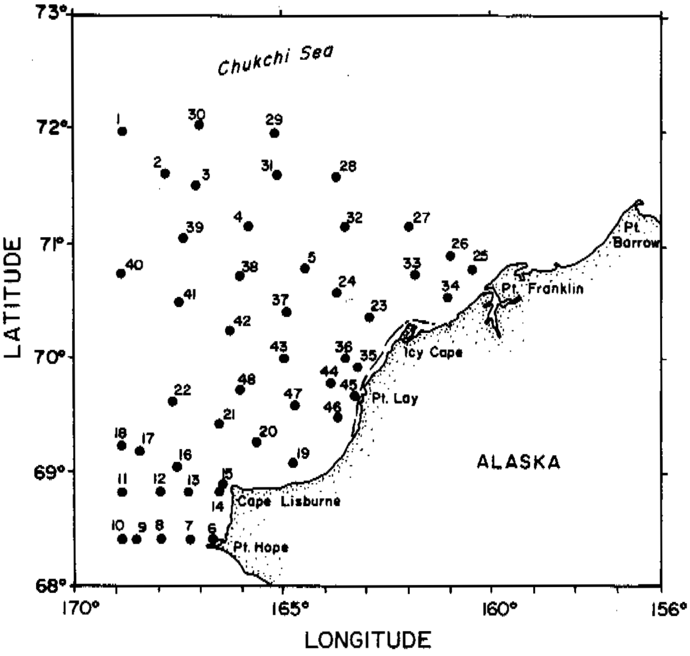

FIG. 3b. Location map showing epifaunal sampling stations occupied in the northeastern Chukchi Sea in 1990 by Smith *et al.* (unpubl.).

The 1986 infaunal collection of Feder *et al.* (1990a) extended farther north than the epifaunal sampling of 1990 (Smith *et al.*, unpubl.). Infaunal and epifaunal samples were collected by different gear types. Each infaunal sample represented a localized area, while epifaunal data were derived from samples taken over a variable distance. Consequently, it was necessary to establish new station numbers for the epifaunal studies in August 1990. Thus, it was not technically possible to pool and analyze all molluscan data.

Infauna and epifauna are treated separately here, with some integrations of data included in the discussion.

Data used in the classification of stations consisted of taxon abundance values (infauna: ind·m^{-2}; epifauna: ind·km^{-2}). One species (*Neptunea heros*) was eliminated in the epifaunal multivariate analysis because its high abundance and ubiquitous occurrence overwhelmed the variations among other species considered dominant. In order to normalize data, a log transformation (*ln* [X+1]) was applied prior to the cluster analysis. The Czekanowski similarity coefficient was used for clustering (Bray and Curtis, 1957; Boesch, 1977). Top-ranked taxa in each station group and percent fidelity of these taxa to stations in each station group are presented. Stepwise multiple discriminant analysis (Davies, 1971) using the BMDP7M and SPSS Discriminant programs was applied to biological data to correlate station group separation by cluster analysis with environmental variables. Such an analysis has been used elsewhere to test a biological model (e.g., station groups) with environmental parameters (Flint, 1981; Shin, 1982; Weston, 1988). Environmental variables used were sediment variables (particle size parameters, organic carbon [C], nitrogen [N], and C/N values) and bottom temperature and salinity. The percentage values for sediment grain-size distribution were arcsine transformed. Wet-weight values of infauna were converted to carbon by applying conversion values of Stoker (1978) determined for taxa in the same region. Only wet-weight values were used for the epifaunal analyses. Standard discriminant function coefficients are presented. These coefficients indicate the relative contribution of the variables in calculating the discriminant scores on each function and are commonly used as measures of the relative importance of the variables in discriminating among groups (Green, 1971; Green and Vascotto, 1978). Infaunal stations were segregated into a northern and a southern group by the frontal zone identified by Johnson (1989), Feder *et al.* (1990a), and Weingartner (unpubl.) and the differences between mean abundance and carbon biomass values for each group were tested statistically. Statistical analysis of these data consisted of *t*-tests utilizing SYSTAT (Wilkinson, 1990). Prior to analysis, a square root transformation was applied to the data (Sokal and Rolf, 1969; Zar, 1974).

RESULTS

General

Approximately 75 and 62 mollusk taxa were identified from the grab and the trawl samples respectively. These taxa included 52 bivalves, 83 gastropods, 3 polyplacophorans, and 1 cephalopod. A total of 139 molluscan taxa were identified. All taxa are listed in the Appendix, along with comments on taxonomy.

Infauna

Abundance values for the 37 stations sampled in 1986 ranged from 16 to 880 ind·m^{-2}, with a mean of 248 ind·m^{-2}. Biomass ranged from 0.007 to 15.02 g C·m^{-2}, with a mean of 3.04 g C·m^{-2}. Highest abundance and biomass values generally occurred north of and adjacent to the bottom front identified by Johnson (1989), Feder *et al.* (1990a), and Weingartner (unpubl.) (Figs. 4a,b). Some high values were also recorded adjacent to Point Hope and north of Cape Lisburne. At stations north and west of the bottom front, mean infaunal molluscan carbon biomass ($\bar{X}$ = 3.97; S.D. = 3.48) was significantly higher (P = 0.01) than at the southern stations ($\bar{X}$ = 1.72; S.D. = 1.53).

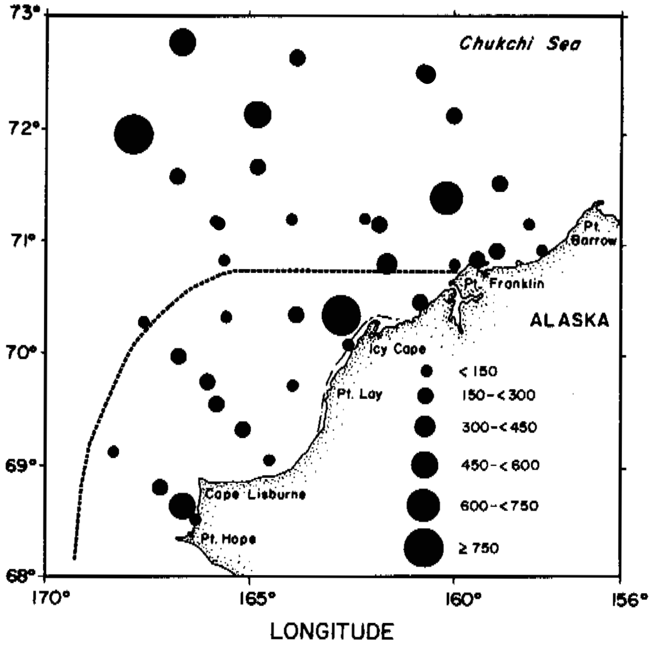

FIG. 4a. Abundance (ind·m^{-2}) of infaunal mollusks in the northeastern Chukchi Sea. Dashed line represents a bottom frontal zone that separates Bering Shelf and Resident Chukchi Water, offshore and to the north, from Alaska Coastal Water, inshore of the front.

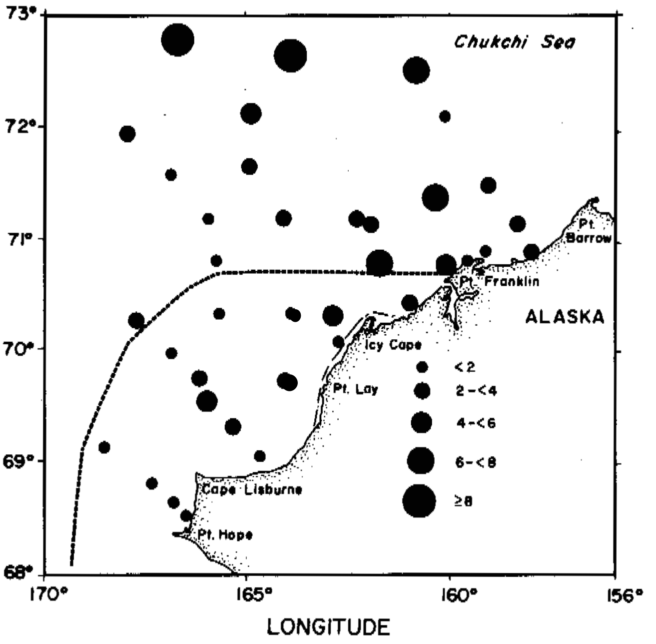

FIG. 4b. Carbon biomass (g C·m^{-2}) of infaunal mollusks in the northeastern Chukchi Sea. Dashed line represents a bottom frontal zone that separates Bering Shelf and Resident Chukchi Water, offshore and to the north, from Alaska Coastal Water, inshore of the front.

Protobranch bivalves dominated infaunal abundance and biomass and were widely distributed. *Nucula tenuis* was present at 29 stations, primarily where muddy substrate prevailed. Other protobranch species — *Nuculana radiata*, *Yoldia hyperborea*, *Y. scissurata*, and *Y. myalis* — were more localized in their distribution. Three species of heterodont bivalves (*Astarte montagui*, *A. borealis*, and *Cyclocardia ovata*) also had high abundance and biomass values but more patchy distributions. The heterodont bivalve *Macoma calcarea* was widely distributed (present at 24 stations) but mainly dominated infaunal abundance and biomass within the muddy, northern offshore region and stations just north of Cape Lisburne. The heterodont bivalves *Astarte montagui*, *A. borealis*, and *C. ovata* were more common in gravelly substrates, while *Thyasira gouldi* (present at 25 stations) was most abundant off Point Hope at Station 44.

Although a few gastropod taxa were relatively common compared to bivalves, they were far less abundant. The relationship between small gastropod species collected in the study area and sediment parameters is not known. The opisthobranch gastropods *Cylichna alba* and *Retusa obtusa* were present at 19 and 11 stations respectively. Common prosobranch gastropods included *Tachyrhynchus erosus* and the trochids *Solariella varicosa* and *S. obscura*. Turridae, mostly unidentified species of *Oenopota*, were occasionally common.

From the recurrence of stations in the cluster analysis of abundance data (Fig. 5), six station groups were determined (Figs. 5 and 6). One station adjacent to Point Hope, Station 43, and one station north of Cape Lisburne, Station 33, were not classified based on the distinct faunal composition of each of these stations (Table 1). The dominant fauna (present in 50% or more of stations in a station group) characterizing each station group and the percent occurrence of dominant taxa at stations constituting the groups are included in Table 1. Abundance varied from 42 ind·m^{-2} within inshore Group VI to 388 ind·m^{-2} in northern offshore Group I; carbon biomass varied from 0.9 g C·m^{-2} within inshore Group IV to 5.4 g C·m^{-2} in Group I (Table 2). The highest abundance and carbon biomass occurred within offshore Station Group I. The largest numbers of *N. tenuis* and *M. calcarea* were found within Group I; abundance of both of these species was considerably less at Groups II and III, the other offshore groups. Group III comprised a mixture of taxa characteristic of inshore and offshore stations and had the second highest carbon biomass value for station groups. Group IV, extending northwest of Cape Lisburne, was distinguished by large numbers of the bivalve *Thyasira gouldi*, with most other taxa in low abundance. Group VI, a sandy-gravelly inshore site just south of Icy Cape, had one of the lowest number of taxa and lowest abundance of mollusks, as well as total infauna (Feder *et al.*, 1990a); also, the lowest carbon biomass of infaunal mollusks occurred within this station group. This station group was the only one at which the protobranch bivalve *Y. scissurata* occurred. Substrate at inshore Group V, north of Group VI, constituted

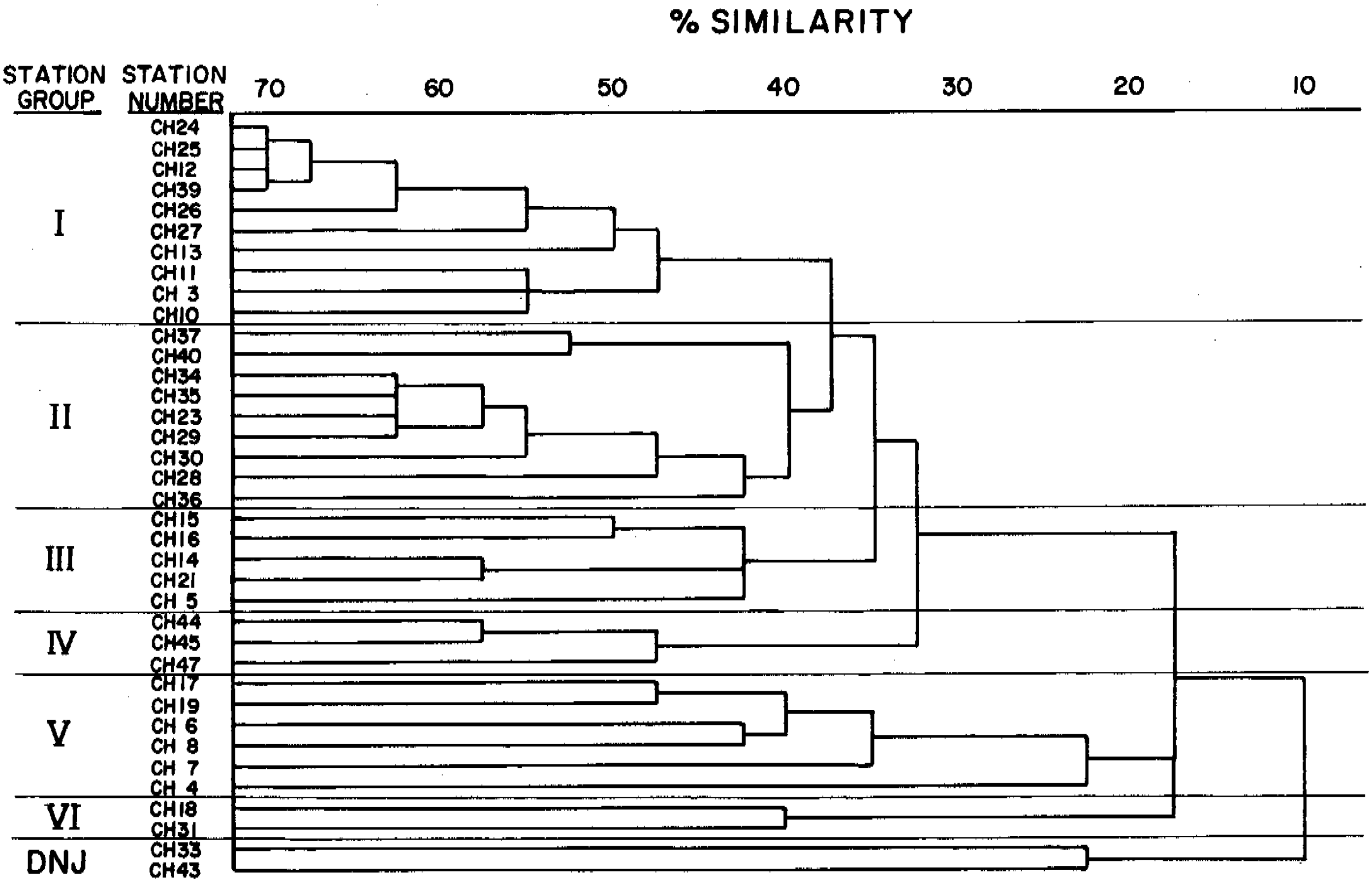

FIG. 5. Dendrogram showing grouping of stations based on a cluster analysis of infaunal molluscan abundance data. DNJ = Did not join any group.

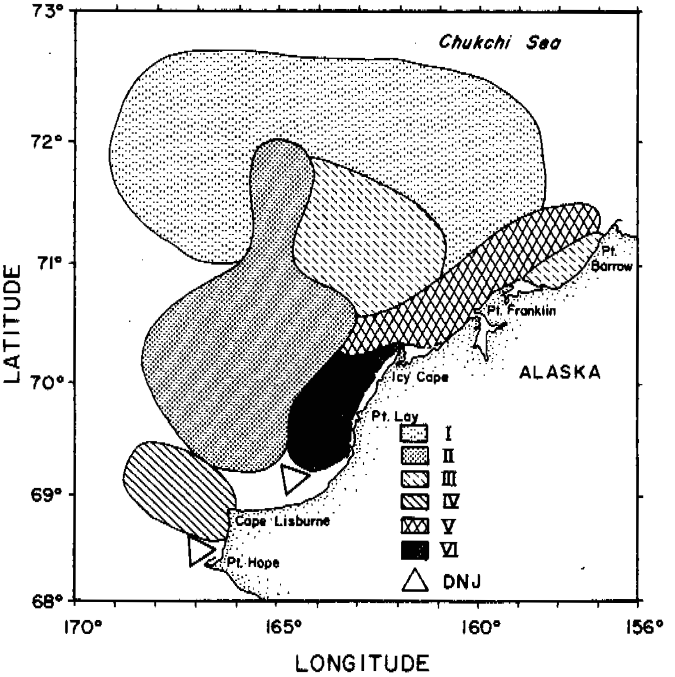

FIG. 6. Infaunal molluscan assemblages in the northeastern Chukchi Sea based on cluster analysis.

a higher percentage of gravel and had the highest number of taxa of all groups.

Table 3 shows the results of multiple discriminant analysis of the environmental conditions relative to infaunal station groups determined by multivariate analysis. The discriminant functions (DF) 1 and 2 contribute nearly 85% of the total separation among the groups ($P \leq 0.001$), and 76% of the stations were classified correctly according to station group. Only these functions are considered further in the interpretation. After the final step in the discriminant analysis, F statistics between pairs of station groups showed significant differences ($P \leq 0.003$) in all comparisons except one (Group I vs Group III). Nevertheless, the comparison between the latter two groups was marginally significant ($P = 0.06$). The low negative value along the DF 1 is due to percentage of sand (Fig. 7). The high positive value along DF 2 is the result of bottom salinity (Fig. 7). The centroid of Group VI is well separated from the other groups along the axis of DF 1. Also, the centroids of Groups II, IV, and V are separated from Groups I and III along DF 1. The centroid of Group IV is well separated from the other groups along the axis of DF 2. Also, the centroids of Groups I, III, and V are separated from Groups II and IV along the axis of DF 2. The separation of inshore Group VI from the other groups is due to the higher percentage of sand at the Group VI stations. Alternatively, offshore Groups I, II and III, and southern inshore Group IV off Cape Lisburne are distinguished by the lower percentage of sand (i.e., presence of more mud) within stations of these groups. The low bottom salinity for Group IV differentiates it from the other station groups. The highest salinity occurs at stations of northern offshore Groups I and III and northern inshore Group V, which separates them from the other groups.

Epifauna

Abundance values from the 48 stations sampled in 1990 varied from 170 to 71 817 ind·km^{-2}, with a mean of 4227 ind·km^{-2}. Wet-weight biomass ranged from 0.29 to 47.28 kg·km^{-2}, with a mean of 6.42 kg·km^{-2}. Abundance and biomass were highest at stations nearest the coast, with particularly high values west and north of Cape Lisburne and near Point Franklin (Figs. 8a,b).

Gastropods made up the greatest portion of the molluscan epifauna in abundance and biomass. The gastropod *Neptunea heros* (Fig. 9a) occurred at all stations and was typically the most abundant mollusk present. Two other species of *Neptunea*, *N. ventricosa* (Fig. 9b) and *N. borealis* (Fig. 9c), were nearly as common, occurring at 35 and 45 of the stations respectively. Other common neptunids included *Volutopsius deformis*, *V. stefanssoni* (Fig. 10a), *V. fragilis* (Fig. 10b,c), *Beringius stimpsoni* (Fig. 11a), and *Plicifusus kroyeri*. Also generally common were buccinids (*Buccinum angulosum*, *B. polare*, *B. scalariforme*, *B. solenum*, and *B. tenellum* [Fig. 11b,c]) and naticids (*Polinices pallidus* and *Natica clausa*). The internal-shelled prosobranch *Onchidiopsis* had a wide distribution, but whether one or more species was present is uncertain.

The most abundant bivalve was the scallop *Chlamys behringiana*, which occurred at 12 stations, with especially high numbers observed (24 000 ind·km^{-2}) at Station 7 off Point Hope (Fig. 12). The scallop was also common at Stations 19 and 22, north of Cape Lisburne, and Stations 25, 26, 27, and 33, adjacent to Point Franklin. The cardiid bivalves *Serripes groenlandicus* and *Clinocardium ciliatum* were abundant at 22 and 13 stations respectively.

The chiton *Amicula vestita* was found at 17 stations, with the greatest abundance just north of Cape Lisburne. An octopus, tentatively identified as *Octopus leioderma*, occurred at 12 stations and, although never abundant, was common offshore (Fig. 13a). Four relatively common gastropods (*Colus spitzbergensis*, *Beringius beringii*, *Buccinum glaciale*, and *Trichotropis bicarinata*) were present in the nearshore areas (see Fig. 13b for example).

Five species (*Beringius stimpsoni*, *C. magna*, *C. behringiana*, *Cyclocardia crassidens*, and *Astarte montagui*) had disjunct distributions, with individuals occurring at stations off Cape Lisburne and at northern stations (see Figs. 13c,d for examples).

From the recurrence of stations in the cluster analysis of abundance data (Fig. 14) five station groups were identified, with three stations not classified (Figs. 14 and 15). Dominant fauna characterizing each of the station groups are found in Table 4.

Number of taxa at station groups varied from 16 in Group IV to 65 at Group V (Table 5). Abundance ranged from 765 in Group III to 18 993 ind·km^{-2} in Group V (Table 5). Biomass ranged from 24 to 292 kg·km^{-2} at Groups IV and V respectively. As observed for offshore infaunal station groups, the northern epifaunal offshore Group I had a larger number of taxa and higher abundance and biomass than southern offshore epifaunal Group III. Also, as noted for the infauna, there is a distinctive epifaunal assemblage (inshore Group IV) in the sandy area between

TABLE 1. Infaunal molluscan abundance dominants within six station groups and two stations not classified (taxa occurred at 50% or more of the stations within a station group; DNJ = Did not join a station group)

Station group	Stations in group	Taxa	Abundance (ind·m^{-2})	% occurrence in group[1]
I	3, 10, 11, 12, 13, 24, 25, 26, 27, 39	*Nucula tenuis*	196	100
		Macoma calcarea	88	100
		Thyasira gouldi	17	90
		Yoldia hyperborea	14	80
		Nuculana radiata	14	50
		Retusa obtusa	11	90
		Mysella sp.	8	60
		Cylichna alba	8	70
II	23, 28, 29, 30, 34, 35, 36, 37, 40	*Nucula tenuis*	98	100
		Thyasira gouldi	14	89
		Macoma calcarea	6	56
		Tachyrhynchus erosus	5	89
		Solariella varicosa	4	78
		Cylichna alba	4	56
III	5, 14, 15, 16, 21	*Nucula tenius*	70	100
		Astarte montagui	16	100
		Cyclocardia ovata	10	100
		Astarte borealis	9	80
		Solariella obscura	6	100
		Cylichna alba	5	80
		Oenopota sp.	5	100
		Propebela sp	5	60
IV	44, 45, 47	*Thyasira gouldi*	105	67
		Nucula tenius	65	100
		Nuculana radiata	57	100
		Retusa obtusa	8	67
		Tachyrhynchus erosus	3	67
		Polinices pallidus	3	100
V	4, 6, 7, 8, 17, 19	*Cyclocardia ovata*	123	83
		Astarte montagui	29	100
		Liocyma viride	25	83
		Yoldia myalis	14	50
		Mysella sp.	13	83
		Axinopsida serricata	8	50
		Musculus spp.	7	100
		Hiatella arctica	5	50
		Polinices pallidus	4	100
VI	18, 31	*Yoldia scissurata*	12	100
		Thyasira gouldi	5	50
		Macoma calcarea	4	100
		Clinocardium ciliatum	4	100
		Liocyma viride	3	50
		Liocyma fluctuosa	2	50
		Natica clausa	2	50
		Tellina lutea	2	50
		Cylichna alba	2	100
DNJ	33	*Musculus* spp.	26	
		Cylichna alba	4	
		Nucula tenuis	2	
		Yoldia myalis	2	
		Oenopota spp.	2	
DNJ	43	*Musculus* spp.	10	
		Hiatella arctica (no other molluscan taxa were present)	6	

[1] The value for each taxon in the column of % occurrence in group is based on the number of stations at which the particular taxon occurs.

TABLE 2. Number of taxa, abundance, and biomass of infaunal taxa by station group

Station group	Number of taxa	Abundance (ind·m^{-2})	Wet weight biomass (g·m^{-2})	Carbon biomass (g C·m^{-2})
I	44	388	147	5.4
II	35	168	51	1.8
III	46	201	134	3.5
IV	13	260	20	0.9
V	50	300	70	2.9
VI	15	42	43	0.28

TABLE 3. Results of the discriminant analysis of the environmental conditions among the six infaunal station groups

Discriminant function	1	2	3
Percent separation	48.73	35.95	15.31
Cumulative percent separation	48.73	84.69	100.00
Test of significance			
Chi-squared value	87.88*	49.99*	18.11
Degrees of freedom	15	8	3
Variables and standardized discriminant function coefficient			
Percent sand	-0.82	0.29	-0.53
Salinity	0.26	1.00	-0.18
OC/N	-0.26	0.49	0.89

*Significance at $P \leq 0.001$.

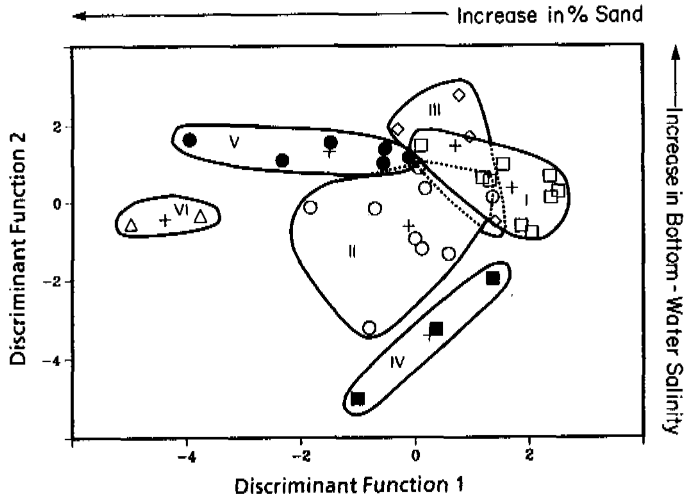

FIG. 7. Station and station group plot from stepwise multiple discriminant analysis of molluscan infauna utilizing environmental variables. + = the centroids of the station groups. Sediment values used in the analysis based on dry weights.

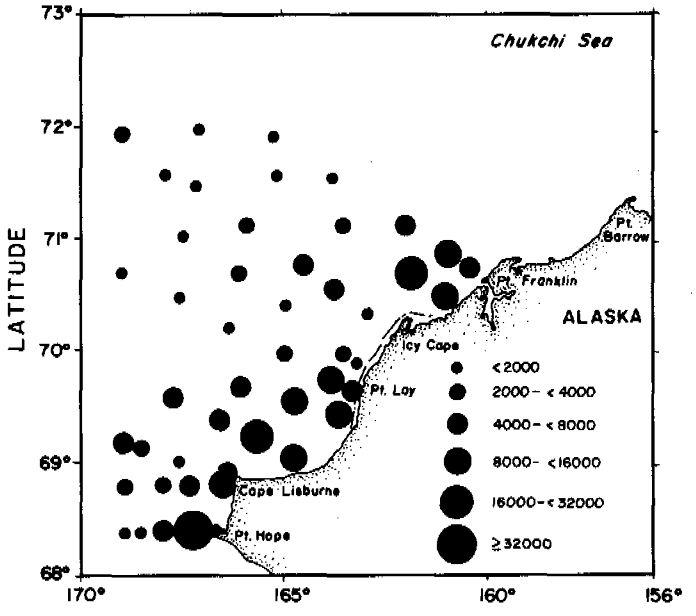

FIG. 8a. Abundance (ind·m^{-2}) of epifaunal mollusks in the northeastern Chukchi Sea.

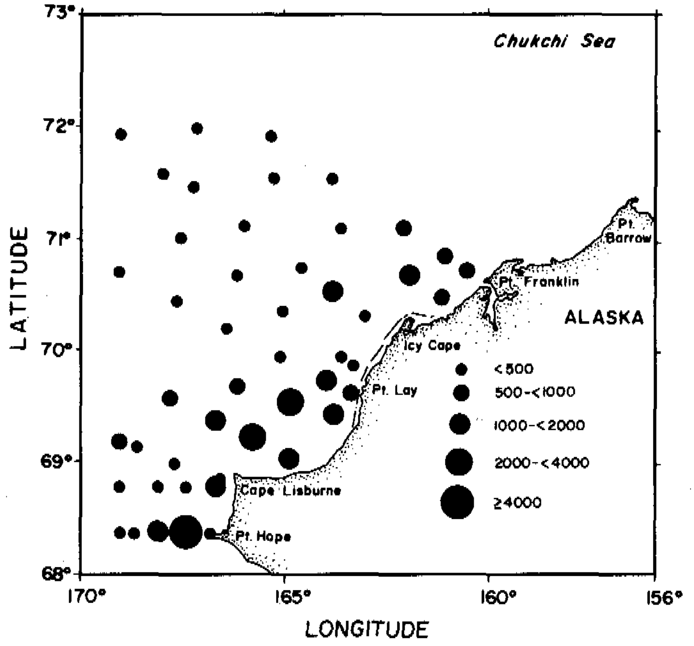

FIG. 8b. Biomass (kg·km^{-2}) of epifaunal mollusks in the northeastern Chukchi Sea.

Icy Cape and Point Lay. The number of taxa, abundance, and biomass here was relatively low. Distinctive species in Group IV were *Buccinum tenellum*, *B. polare*, *B. angulosum*, and *Natica clausa*. The most diverse group, Group V, has a disjunct distribution (Fig. 15). The group was dominated by large numbers of *C. behringiana*. Group II was distinguished by its relatively large number of taxa and high abundance and biomass values.

Table 6 shows the results of the multiple discriminant analysis of the environmental conditions relative to epifaunal station groups identified by multivariate analysis. Discriminant Functions (DF) 1 and 2 contribute 88.8% of the total separation among the groups ($P \leq 0.001$), and only these two functions are considered further in the interpretations. Sixty-one percent of the stations and station groups were correctly classified. After the final step in the discriminant analysis, F statistics between most pairs of station groups showed significant differences ($P \leq 0.001$). Station and station group positions along these two functional axes are plotted in Figure 16 (also see station group locations in Fig. 15). The low negative value along DF 1 is due to higher bottom-water temperature. The low negative value along DF 2 is due to the high percentage of gravel. The centroid of northern offshore Station Group I is well separated from most of the other groups along the axis of DF 1. Also, the centroid of offshore Group III is separated from inshore Groups II, IV, and V on DF 1. The centroids of inshore Group V and inshore Group IV are separated from the other groups along the axis of DF 2. The separation of offshore Groups I and III from the other stations is a result of lower bottom water temperature; both groups share similar sediment characteristics. The separation of Group V from the other groups is due to the high percentage of gravel present at stations of this group, and Group IV differs from the other groups by the low percentage of gravel present (see Figs. 15 and 16).

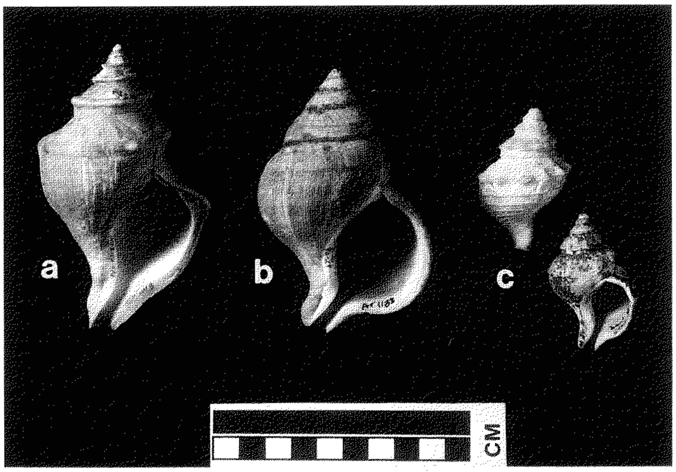

FIG. 9. a) *Neptunea heros*; b) *Neptunea ventricosa*; c) *Neptunea borealis*.

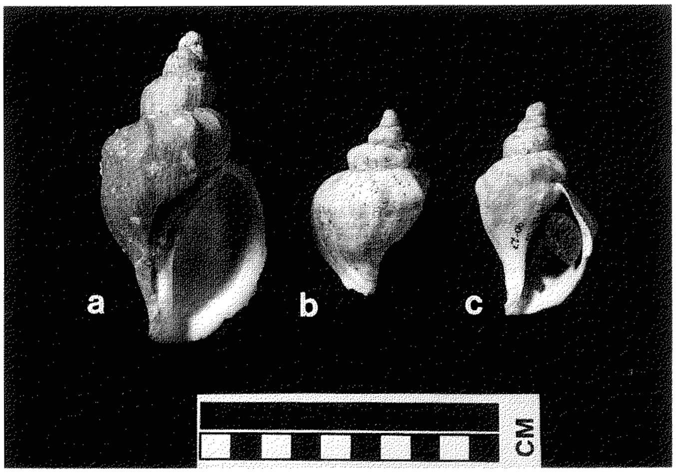

FIG. 10. a) *Volutopsius stefanssoni*; b) *Volutopsius fragilis*; c) *Volutopsius fragilis*.

DISCUSSION

Our results show higher abundance and biomass values for infaunal mollusks adjacent to and north and northwest of the bottom front separating Bering Shelf (BSW) and Resident Chukchi Water (RCW) from Alaska Coastal Water (ACW). A north-south infaunal biomass difference in the northeastern Chukchi Sea was also noted for total infauna by Feder *et al.* (1990a) where higher biomass for the northern region was explained by lower bottom-water temperatures and higher bottom salinities in the northern region. In contrast, epifaunal mollusks have their greatest abundance and biomass within stations adjacent to the coast. Of particular interest is the observed enhancement of infauna at northern stations relative to those farther south. Oceanographic mechanisms that could lead to the observed enhancement of the infaunal benthos to the north include: 1) advection into the area by BSW with its high nutrient and POC load, 2) a flux of ungrazed phytoplankters to the bottom, 3) the recurring presence of polynyas along the coastal region north of Point Franklin (Stringer and Groves, 1991), 4) enhanced primary productivity associated with the summer-fall position of the marginal ice zone (which is typically observed in this region at this time [Grantz *et al.*, 1982]), and 5) enhanced primary production due to upwelling and slope/shelf exchange of nutrient-rich water found at depth along the continental slope to the north of the study area.

The northward flow of BSW along the east flank of Herald Shoal (Weingartner, unpubl.), with its contained nutrients and POC, spreads north and eastward along the bottom, mixes with RCW, and forms a bottom-intersecting front with ACW. The annual water-column primary production north of this front is estimated to be 50-100 g C$\cdot$m^{-2} (Parrish, 1987). Much of the initial pulse of this water-column primary productivity probably remains ungrazed, as observed for the northeastern Bering Sea (Grebmeier *et al.*, 1988). The sinking of ungrazed phytoplankton, as well as POC within the BSW/RCW, would enrich the benthic environment north of the front. Additional nutrient enrichment along the front might also contribute to increases in benthic organisms at stations adjacent to that front. Fronts are characterized by high primary productivity, and it is here that high values for benthic abundance and biomass are often found (Creutzberg, 1986). An increase in benthic organisms along the frontal system in the northeastern Bering and southeastern Chukchi seas was also noted by Grebmeier *et al.* (1988, 1989) and Feder *et al.* (1990b).

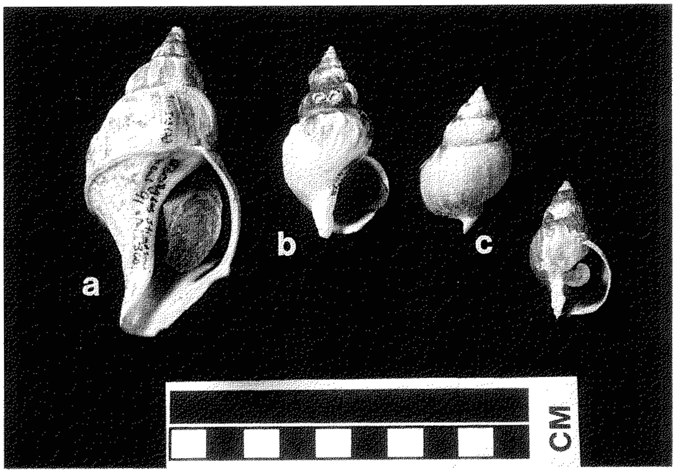

FIG. 11. a) *Beringius stimpsoni*; b) *Buccinum solenum*; c) *Buccinum tenellum*.

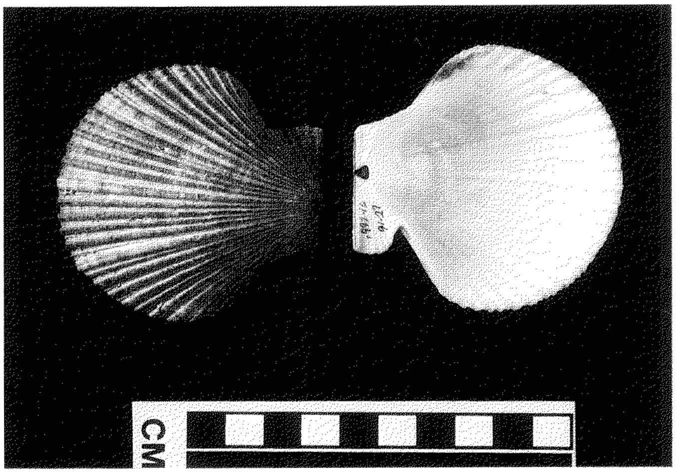

FIG. 12. *Chlamys behringiana*.

TABLE 4. Epifaunal molluscan abundance dominants within five station groups (taxa occurred at 50% or more of stations within a station group; DNJ = Did not join a group)

Station group	Stations in group	Taxa	Abundance (ind·km^{-2})	% occurrence in group[1]
I	1, 2, 3,	*Neptunea heros*	1 021	100
	4, 5, 9,	*Buccinum polare*	390	100
	10, 11,	*Neptunea borealis*	236	100
	18, 27,	*Buccinum scalariforme*	128	100
	28, 30,	*Volutopsius fragilis*	126	50
	31, 32	*Natica aleutica*	97	86
		Polinces pallidus	87	86
		Clinopegma magna	81	93
		Onchidiopsis sp.	76	100
II	8, 12,	*Neptunea heros*	4 256	100
	13, 16,	*Neptunea ventricosa*	668	60
	17, 20,	*Buccinum scalariforme*	506	93
	21, 24,	*Neptunea borealis*	436	100
	34, 43,	*Buccinum angulosum*	147	93
	44, 45,	*Onchidiopsis* sp.	72	67
	46, 47,	*Beringius beringii*	54	73
	48	*Volutopsius fragilis*	33	60
		Serripes groenlandicus	31	67
III	29, 37,	*Neptunea heros*	442	100
	40, 42,	*Neptunea borealis*	72	100
	41	*Buccinum scalariforme*	71	100
		Buccinum polare	51	80
		Neptunea ventricosa	37	60
		Plicifusus kroyeri	17	60
IV	23, 35,	*Neptunea heros*	752	100
	36	*Buccinum tenellum*	98	100
		Buccinum polare	91	67
		Buccinum angulosum	85	67
		Natica clausa	57	67
		Neptunea borealis	56	100
		Polinices pallidus	28	67
		Neptunea ventricosa	28	100
		Bulbus fragilis	3	67
		Buccinum sp.	6	67
V	7, 14,	*Chlamys behringiana*	3 971	100
	15, 19,	*Neptunea heros*	2 363	100
	22, 26,	*Neptunea ventricosa*	1 814	100
	33, 38	*Buccinum angulosum*	1 471	88
		Trichotropis bicarinata	1 457	63
		Amicula vestita	1 168	100
		Margarites costalis	821	50
V (cont'd)				
		Onchidiopsis sp.	794	100
		Plicifusus kroyeri	748	100
		Buccinum scalariforme	477	75
		Cyclocardia crassidens	419	88
		Volutopsius deformis	391	62
		Beringius stimpsoni	431	50
		Volutopsius stefanssoni	341	62
		Buccinum polare	293	50
		Beringius beringii	258	88
		Boreotrophon clathratus	204	63
		Colus spitzbergensis	167	63
		Neptunea borealis	136	50
		Buccinum glaciale	127	75
		Serripes groenlandicus	61	63
		Clinocardium ciliatum	57	75
		Crepidula grandis	35	62
		Musculus discors	32	50
DNJ	25	*Neptunea heros*	3 177	
		Neptunea ventricosa	498	
		Volutopsius deformis	453	
		Buccinum plectrum	199	
		Buccinum glaciale	199	
		Chlamys behringiana	199	
		Beringius beringii	54	
		Beringius stimpsoni	54	
		Buccinum polare	54	
DNJ	39	*Chlamys behringiana*	160	
		Neptunea heros	114	
		Buccinum angulosum	46	
		Plicifusus kroyeri	23	
		Neptunea ventricosa	23	
		Buccinum polare	23	
		Clinopegma magna	23	
DNJ	6	*Neptunea ventricosa*	410	
		Clinocardium californiense	155	
		Neptunea heros	114	
		Musculus discors	68	
		Serripes groenlandicus	46	
		Beringius beringii	33	
		Clinopegma magna	22	

[1] The value for each taxon in the column of % occurrence in group is based on the number of stations at which the particular taxon occurs.

TABLE 5. Number of taxa, abundance (ind·km^{-2}), and biomass (kg·km^{-2}) of epifaunal station groups

Station group	Number of taxa	Abundance (ind·km^{-2})	Wet weight biomass (kg·km^{-2})
I	63	2 770	54
II	52	6 884	188
III	20	765	33
IV	16	1 245	24
V	65	18 993	292

Open-water regions within polynyas are considered important in sustaining primary and secondary productivity in polar regions and are regularly associated with large numbers of sea birds and marine mammals (Dunbar, 1981; Stirling *et al.*, 1981; Massom, 1988; Smith *et al.*, 1990; Grebmeier and Barry, 1991; Deming *et al.*, 1993). The ice-water boundary at marginal ice zones is the site of the earliest spring water-column phytoplankton blooms in polar regions (Alexander and Niebauer, 1981; Johannessen *et al.*, 1982; Niebauer and Alexander, 1985). It is hypothesized that polynyas influence water-column productivity due to ice-edge dynamics at the marginal ice zone, but few studies have investigated pelagic-benthic coupling processes in polynyas (Grebmeier and Barry, 1991). Concentrations of plant-derived pigments and meio-macrofauna were higher in sediments under the Northeast Water (NEW) polynya off the northeast coast of Greenland than under ice-covered regions (Deming *et al.*, 1993). Also, Piepenberg (1988) describes an enhanced epifaunal abundance in the area of the NEW compared to benthos underneath the ice pack. Increased infaunal abundance and biomass north of Icy Cape, observed in our study and by Feder *et al.* (1990a), may reflect in part a flux to the bottom of locally produced POC within polynyas that supplements advected

TABLE 6. Results of the discriminant analysis of environmental factors among the five epifaunal station groups (sediment data used are dry weight values from Naidu [1987] and oceanographic data from Feder *et al.* [1990a].)

Discriminant function	1	2	3
Percent separation	58.31	30.45	11.25
Cumulative percent separation	59.31	88.76	100.00
Test of significance			
Chi-squared value	58.55*	27.71*	8.55
Degrees of freedom	12	6	2
Variables and standardized discriminant function coefficients			
Depth	0.43	-0.60	0.78
Bottom temperature	-0.99	0.27	0.69
Percent gravel	0.54	-0.86	-0.69

*Significance at P≤0.001.

carbon sources. Additionally, the recurring presence of early summer feeding walrus at the ice edge off Point Franklin (Fay, 1982), adjacent to a northern polynya in the northeastern Chukchi Sea, indicates that flux of carbon to the bottom in this area is an annual event that enhances food resources for these animals.

Upwelling of nutrient-rich water along the shelf break might also stimulate primary production on the outer shelf. This upwelling is seasonally modulated and occurs most frequently from October through January, when sea ice covers the region (Aagaard and Roach, 1990). Hence, upwelling could enhance water-column production insofar as it preconditions shelf waters prior to the seasonal sea-ice retreat.

The higher molluscan abundance and biomass values in the northeastern Chukchi Sea compared to the Beaufort Sea can be related in part to the higher primary productivity in the former region (Parrish, 1987). As mentioned above, much of the primary productivity in the northeastern Chukchi Sea probably remains ungrazed and fluxes to the bottom. However, only 1-10% of water-column production in the Beaufort Sea is estimated to reach the bottom (Carey and Ruff, 1977; Carey, 1987). Thus, carbon limitation has an important influence on benthic abundance and biomass in the Beaufort Sea.

Ice scouring of the sea floor disrupts and modifies the sea bed over much of the ice-stressed continental shelf of the Alaskan Arctic and influences faunal abundance and biomass (Barnes and Reimnitz, 1974; Carey and Ruff, 1977; Carey, 1991; Grebmeier and Barry, 1991). Comparison of benthic infaunal biomass in the northeastern Chukchi and adjacent Beaufort Sea shelves indicates regional differences (Carey *et al.*, 1974; Feder *et al.*, 1990a; Grebmeier and Barry, 1991). In the Beaufort Sea, ice gouging contributes to the lowered benthic abundance and biomass in the inner shelf (Feder and Schamel, 1976; Carey and Ruff, 1977; Carey *et al.*, 1984; Braun, 1985) and is also responsible for much of the mid-shelf faunal patchiness (Carey and Ruff, 1977). In contrast, benthic abundance and biomass are higher on the northeastern Chukchi inner and mid-shelf areas. In fact, in the vicinity of Point Franklin there are high molluscan abundance and biomass values inshore (Figs. 4 and 8). Decreased annual ice cover occurs in the northeastern

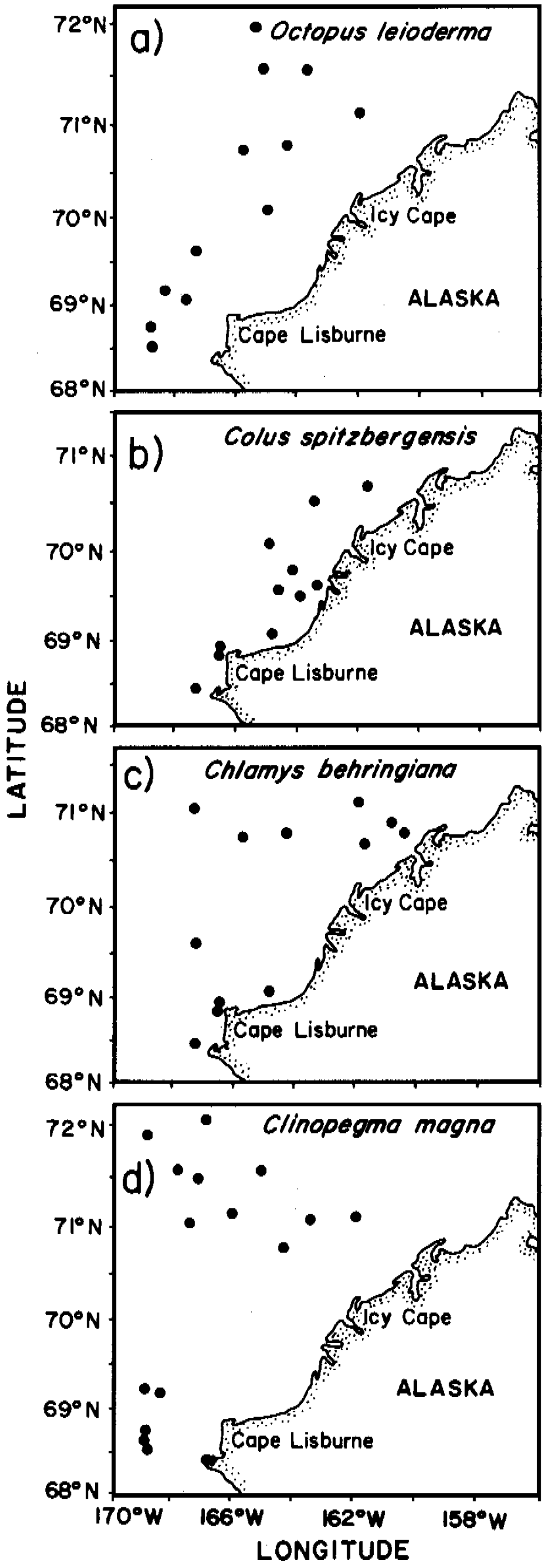

FIG. 13. a) Distribution of *Octopus leioderma*; b) distribution of the gastropod *Colus spitzbergensis*; c) distribution of the scallop *Chlamys behringiana*; d) distribution of the gastropod *Clinopegma magna*.

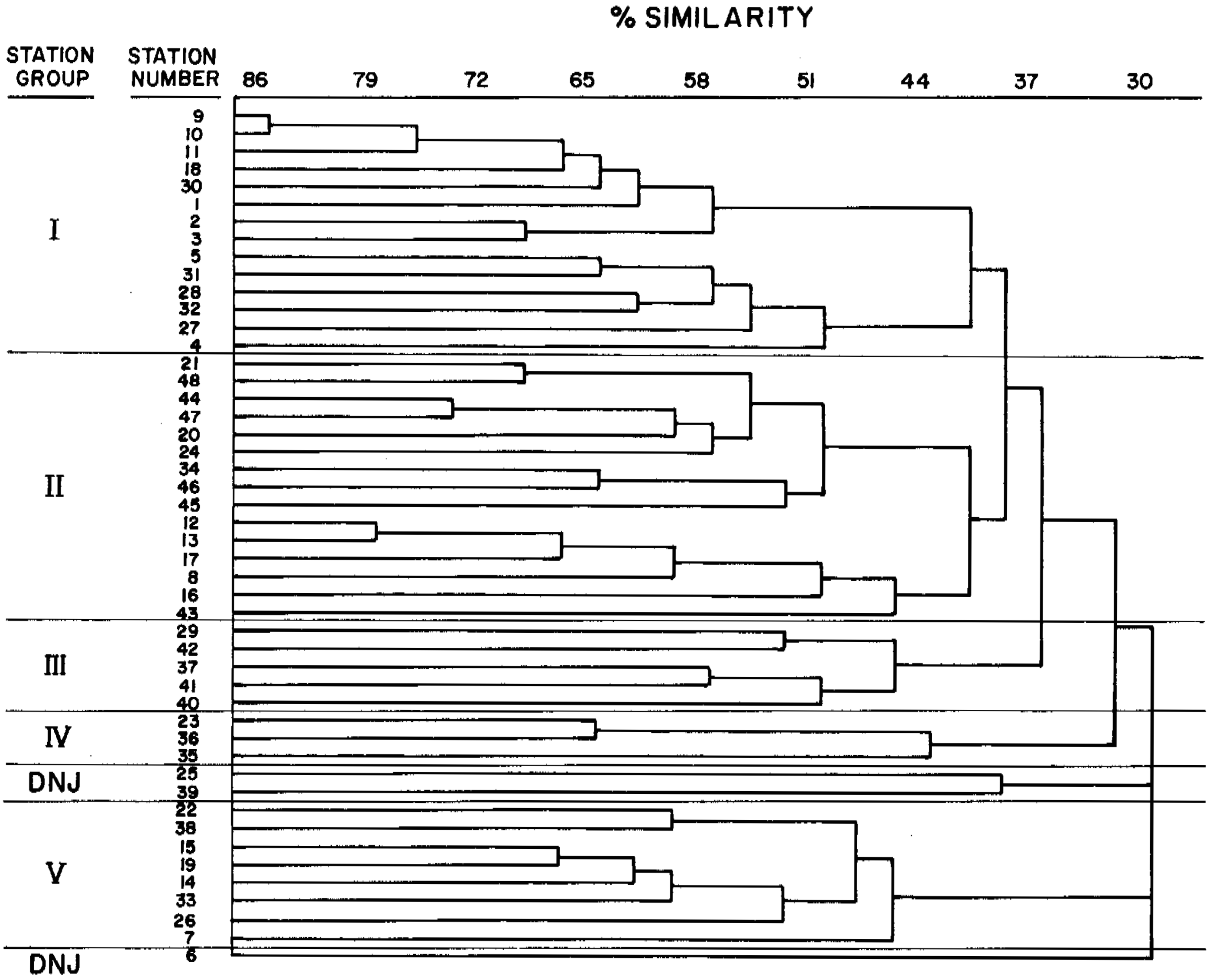

FIG. 14. Dendrogram showing grouping of stations based on a cluster analysis of epifaunal molluscan abundance data. DNJ = did not join any group.

Chukchi Sea as compared to the Beaufort Sea (Grantz *et al.*, 1982). Further, polynyas along the coastal shelf areas of the northeastern Chukchi Sea (Stringer and Groves, 1991) periodically exclude ice in winter. Ice gouging is markedly reduced here during this period. Consequently, the effects of sea ice on benthos of the Chukchi shelf are less intensive and pervasive than on the Beaufort shelf (Grantz *et al.*, 1982).

The large numbers of molluscan epifauna observed in this study adjacent to the coast north of Icy Cape probably represent a response to the abundant infaunal food there. Additionally, increased abundance and biomass of infaunal and epifaunal mollusks at stations adjacent to and northeast of Cape Lisburne appear related to POC originating in Kotzebue Sound (Feder *et al.*, 1990a,b) and the gyre northeast of the Cape (Coachman *et al.*, 1975; Johnson, 1989), which presumably concentrates this POC.

The abundance and biomass of bivalves, the dominant component of the molluscan infauna, appear related to specific physical properties of sediments, bottom salinity, and regional availability of POC. This relationship is reflected by the relatively discrete station groups (composed mainly of bivalves) determined by cluster analysis and the station group affinities shown by discriminant analysis. The dominance of the protobranch bivalve *Nucula tenuis* at infaunal Station Groups I, II, III, and IV is attributed to the presence of muddy sediments where this species typically occurs (Levinton, 1977; Feder and Jewett, 1986; Feder *et al.*, 1990a). However, there are subtle differences in the sediment nature at stations constituting these groups, as illustrated by differences in proportions of coarse grains (gravel + sand) and water (Fig. 17). These sediment differences are reflected by dissimilarities in abundance of dominant species between groups. The relatively higher water content in mud at stations in northern offshore Group I results in a fluidized sediment, which facilitates access to its contained POC for the common deposit-feeding bivalves *N. tenuis* and *Macoma calcarea* present there. Close association of POC with muddy sediments is shown by numerous investigators (e.g., see Weston, 1988, for references). Sediments at stations of northern offshore infaunal Group I generally have a relatively high organic carbon and nitrogen content (Feder *et al.*, 1990a). The importance of muddy, fluidized, and POC-enriched sediments as an environment for deposit-feeding organisms is further demonstrated by the variety of surface and subsurface deposit-feeding infaunal species present offshore (Feder *et al.*, 1990a). Carey *et al.* (1984) observed an increase in the abundance and diversity of protobranch and other deposit-feeding bivalves in muddy sediments of shallow nearshore areas of the southwestern Beaufort Sea. Similarly, Mann (1977) found protobranchs and *Macoma* spp. in greater abundance in soft sediments. The high bottom salinity at northern offshore Groups I and III and northern inshore infaunal Group V, which separates them from inshore Groups IV and VI, indicates the presence of BSW/RCW, with its relatively high POC content in the northern portion of the study area.

The broad distribution of large, epifaunal gastropods, primarily the abundant *Neptunea* spp., in the study area can probably be attributed to their mobility and opportunistic feeding behavior (Golikov, 1963; Feder, 1967; Pearce and Thorson, 1967; Taylor, 1978; MacIntosh and Somerton, 1981). The mobility of molluscan epifauna is reflected by the considerable overlap of station groups in the cluster and discriminant analyses. The relatively low abundance levels of most species of epifaunal gastropods offshore may be related to lack of suitable substrate for egg-laying activities in the muddy sediments there. However, Golikov (1963) and Pearce and Thorson (1967) indicate that the large gastropod *Neptunea* mainly attaches its egg cases to shells of other *Neptunea* spp. and, consequently, do not believe that substrate type explains the distribution of this genus. In our study area, *Neptunea* spp. was common on the muddy offshore substrate.

The surface-deposit feeding clam *Thyasira gouldi* and the suspension-feeding scallop *Chlamys behringiana* occurred in large numbers off Point Hope, and to a lesser extent the deposit-feeding clams *Nucula tenuis* and *Nuculana radiata* were important here (infaunal Group IV and epifaunal Group V). High levels of suspended and deposited organic carbon, which furnish food for these species, were reported for this area (Feder et al., 1990b). South of our study area along the coast from Kivalina to Point Hope, relatively high densities of suspension-feeding organisms (e.g., barnacles and tunicates) occur. Their presence indicates the availability of a stable source of carbon in the water column, derived from Kotzebue Sound, which ultimately contributes POC to the benthos off Point Hope (Feder *et al.*, 1990b; Naidu *et al.*, 1993). This POC is concentrated north of Cape Lisburne by a gyre, where it sustains another large population of scallops. The scallop, as well as ampeliscid amphipods, were common northwest of Point Franklin in an area where high levels of POC occur (Feder *et al.*, 1990a). Ampeliscid amphipods are utilized as food by gray whales *Eschrichtius glaucus* (Cope) in this region (Moore and Ljungblad, 1984; Moore and Clarke, 1986; Phillips and Colgan, 1987; Feder *et al.*, 1990a).

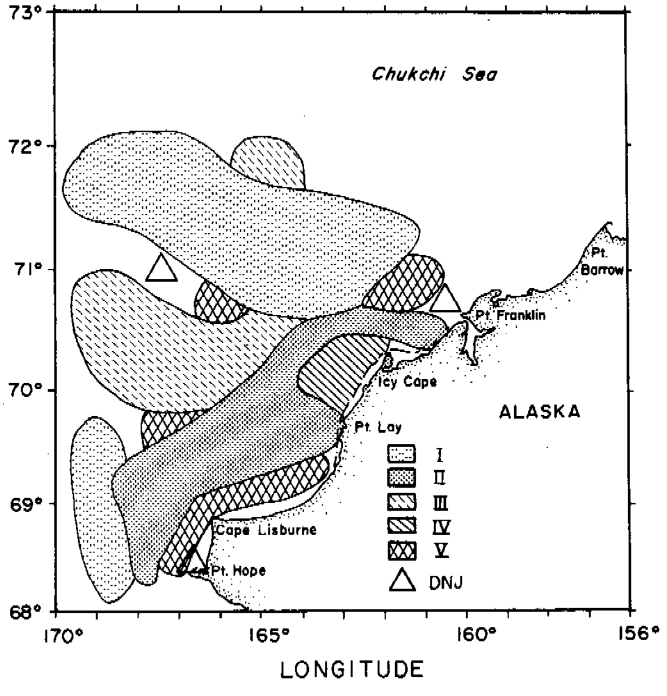

FIG. 15. Epifaunal molluscan assemblages in the northeastern Chukchi Sea based on cluster analysis.

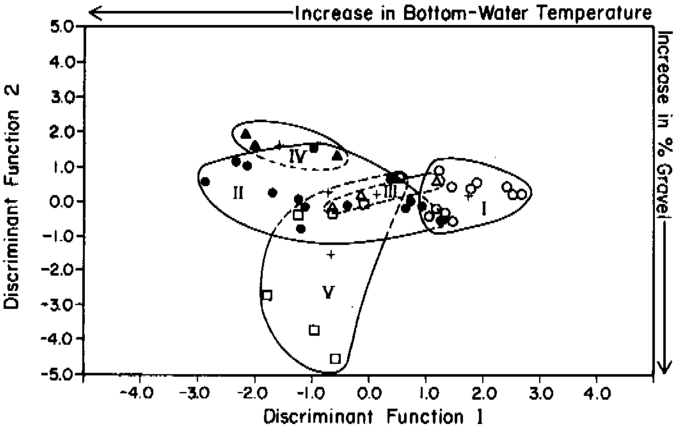

FIG. 16. Station and station group plot from stepwise multiple discriminant analysis of molluscan epifauna utilizing environmental variables. + = centroids of the station groups. Sediment values used in the analysis based on dry weights.

Inshore infaunal Group V is located in a sandy-gravelly environment dominated by suspension-feeding bivalves. The relatively intense longshore currents entrain suspended sediments and associated POC as a food source for the mollusks here (Feder *et al.*, 1990a). A general increase in the proportion of suspension-feeding bivalves with coarser sediments is reported by Mann (1977) in the eastern Chukchi Sea and Carey *et al.* (1984) in the nearshore areas of the southwestern Beaufort Sea. High abundance values of molluscan epifauna, mainly *Neptunea* spp., occurred in the same general inshore area (Fig. 8a), presumably attracted by the abundant infaunal food available here (Feder *et al.*, 1990a).

Stations of inshore infaunal Group VI and epifaunal Group IV are occupied by low numbers of a few molluscan species. This region sustains a large, resident population of suspension-feeding sand dollars, *Echinarachnius parma* Lamarck (Feder *et al.*, 1990a), which presumably excludes other infauna via their sediment-reworking activities (Brenchley, 1981; Smith, 1981; Highsmith, 1982; Highsmith

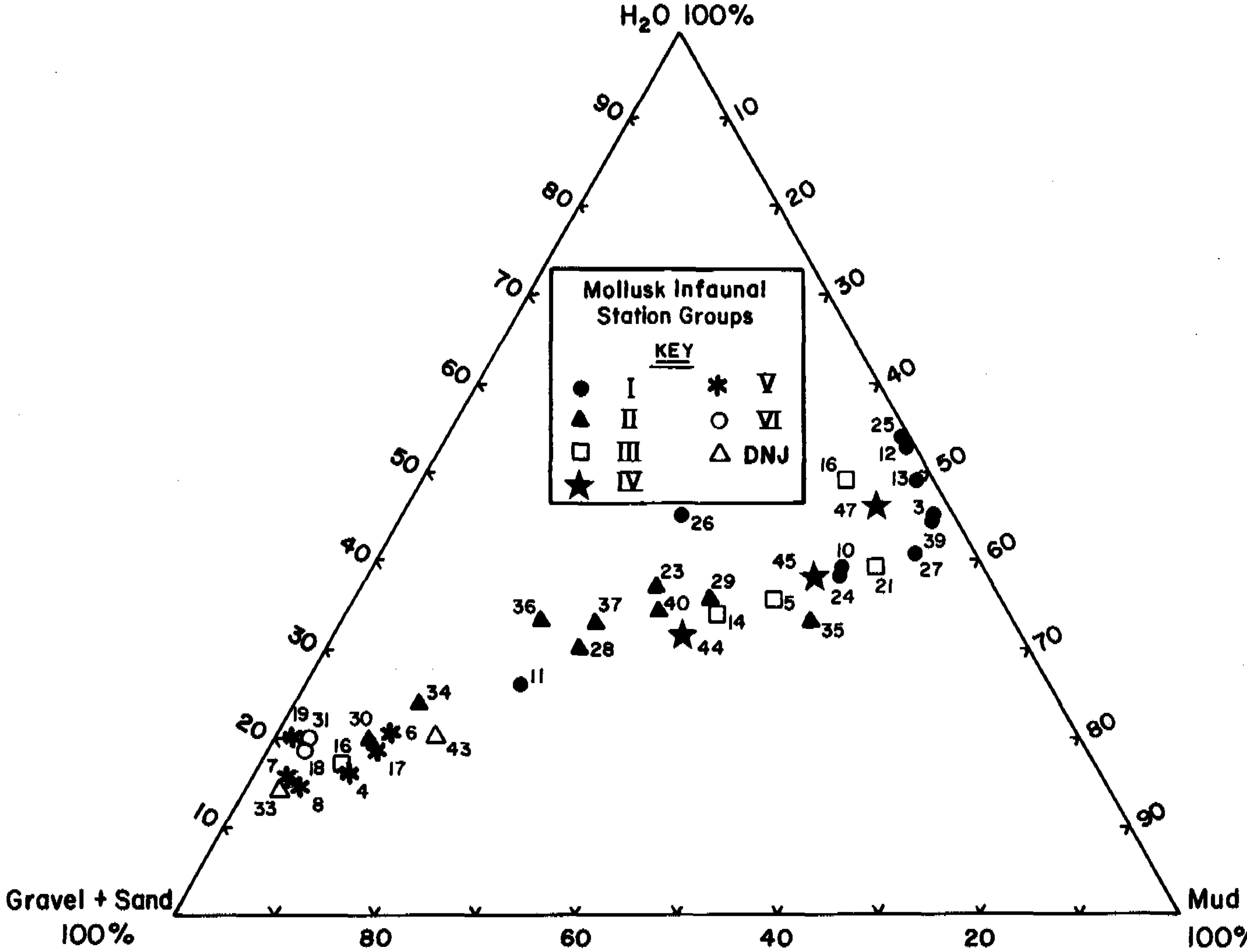

FIG. 17. Ternary diagram relating infaunal molluscan stations and station groups to percent water, gravel + sand, and mud (see Figs. 3a, 5, and 6).

and Coyle, 1991). Reduced numbers of epifaunal gastropods here probably reflect the low abundance of prey species (Feder *et al.*, 1990a).

Mollusks, particularly when small, represent a food resource for bottom-feeding predators in the study area. Documented and potential crustacean predators on mollusks in the northeastern Chukchi Sea include pandalid and crangonid shrimps and pagurid and majid crabs. The pandalid shrimp *Pandalus goniurus* Stimpson and the crangonid shrimps *Sclerocrangon boreas* (Phipps) and *Argis lar* (Owen) were common to abundant at some stations in the study area (Feder *et al.*, 1990a; Foster, unpubl.); these and related species feed on small mollusks in the Gulf of Alaska (Rice, 1980; Rice *et al.*, 1980; Feder and Jewett, 1981; Feder *et al.*, 1981; Feder and Jewett, 1986). Forty-one percent of the majid crab *Chionoecetes opilio* (Fabricius) examined in the southeastern Chukchi Sea were feeding on small bivalve mollusks (Feder and Jewett, 1978), and 61% of those examined in the northeastern Chukchi Sea were utilizing small bivalves (Feder *et al.*, 1990a). This crab also fed on small gastropods to a lesser extent in these areas. Other large, predatory crustaceans in the study area were hermit crabs (Paguridae) and the majid crab *Hyas coarctatus* Brandt (Feder *et al.*, 1990a; Foster, unpubl.). In the Gulf of Alaska some species of hermit crabs and *H. lyratus* Dana feed on small mollusks (Feder *et al.*, 1981).

The distribution of predatory naticid gastropods, *Natica clausa* and *Polinices pallidus*, in the northern portion of the study area overlaps that of the most dense populations of the thin-shelled bivalves *N. tenuis* and *M. calcarea*, on which they probably prey. Evidence that naticids consume infaunal bivalves, and especially *M. calcarea*, comes from observing their characteristic boreholes in shells in the study area (N.R.F.) and from fossil and subfossil assemblages in the Canadian Arctic (Aitken and Risk, 1988). Neptunid snails, abundant in the study area (Table 4), also utilize bivalves as one component of their diet (Pearce and Thorson, 1967; MacIntosh and Somerton, 1981), as do the Muricidae, represented in the study area by *Boreotrophon* spp.

Ophiuroids and asteroids also prey on gastropods and bivalves in the study area. A common ophiuroid in the study area, *Ophiura sarsi* Lütken, fed heavily on small mollusks, with 92% of those examined utilizing bivalves and 50% feeding on gastropods (Feder *et al.*, 1990a). It is suggested by Feder (1981), based on the related *O. ophiura* Linnaeus (= *O. texturata* Lamarck), that where ophiuroids are common they can cause rapid disappearance of bivalve spat after settlement, which subsequently results in low densities of adult clams (also see Thorson, 1966). Large sea stars are abundant in the southeastern (Feder and Jewett, 1978) and northeastern Chukchi Sea (Feder *et al.*, 1990a; Foster, unpubl.). At least nine sea-star taxa (*Asterias amurensis* Lütken, *Crossaster borealis* Fisher, *C. papposus* [Linnaeus], *Evasterias echinosoma* Fisher, *Lethasterias nanimensis* [Verrill], *Leptasterias polaris acervata* [Stimpson], *Leptasterias* spp., *Orthasterias koehleri* [de Loriol], and *Pteraster obscurus* [Perrier]) were identified from epifaunal samples collected in the northeastern Chukchi Sea in 1986 (Feder *et al.*, 1990a) and 1991 (Foster, unpubl.). Feeding observations on *L. polaris acervata* from the southeastern Chukchi Sea revealed that 75% of the prey types were mollusks, with gastropods more frequently taken than bivalves by two to one (Feder and Jewett, 1978). Since *L. polaris acervata* is one of the most abundant sea stars in the northeastern Chukchi Sea (Feder *et al.*, 1990a; Foster, unpubl.), it is probable that mollusks are important prey here as well. Other sea stars documented as predators on mollusks in the southeastern Chukchi Sea and elsewhere in Alaskan waters are *A. amurensis*, *Leptasterias* sp., *E. echinosoma*, and *L. nanimensis* (Feder and Jewett, 1978, 1981; Jewett and Feder, 1981).

Mollusks are a minor component of the diet of fishes in the study area (Coyle *et al.*, unpubl.). Gastropods and bivalves were present, but never important, in the diet of the staghorn sculpin *Gymnocanthus tricuspis* Reinhardt. The arctic flounder *Hippoglossoides robustus* Gill and Townsend utilized bivalve mollusks for food in only a small percentage of fish examined. Mollusks are also a minor portion of the diet of the related flathead sole *H. elassodon* Jordan and Gilbert in the southeastern Bering Sea (Mineva, 1964; Mito, 1974).

Two marine mammals, the walrus *Odobenus rosmarus divergens* Illiger and the bearded seal *Erignathus barbatus* Fabricius, are the most important predators on mollusks in the study area. Bivalves are an important component of the diet of walrus (Fay, 1982). *Macoma calcarea* and other small bivalves were common in our northern offshore infaunal Group I and at stations within the same general region studied by Stoker (1981), an area where walrus feed on these mollusks (Fay, 1982; Fay, pers. comm. in Feder *et al.*, 1990a). Neptunid and buccinid snails are occasionally reported as prey for walrus (Fay, 1982). Limited data from the northwestern and northeastern Chukchi Sea suggest that mainly smaller molluscan species are consumed by walrus (Krylov, 1971; Feder *et al.*, 1990a). The bearded seal feeds on the cockle *Serripes groenlandicus*, the clam *Mactromeris* (= *Spisula*) *polynyma* Stimpson and the gastropods *Buccinum* spp. and *Polinices* spp. in the Bering Sea (Lowry *et al.*, 1979, 1980a). Snails are of minor importance (1% of invertebrate prey volume) as food for the bearded seal in the northeastern Chukchi Sea, but the clams *S. groenlandicus* and *M. polynyma* (this species was not taken in our study) can be important dietary components for this mammal in the area (Lowry *et al.*, 1980a).

In summary, the northeastern Chukchi Sea has an abundant and diverse molluscan fauna. Distribution, abundance, and biomass can be related to several environmental factors. Dissimilarities in abundance of particular infaunal molluscan species are primarily related to specific sediment parameters, but also to bottom salinity. Epifaunal species are more abundant inshore where sandy-gravelly substrate prevails, although the large gastropods *Neptunea* spp. are common throughout the study area. Increase in biomass for infaunal mollusks north of 71° north latitude appears to be influenced by the presence of a bottom front adjacent to Point Franklin. Further, advection of POC-enriched water from the southeast Chukchi Sea to north of the front appears to support in part an enhanced infaunal molluscan fauna there. Although mollusks are not the dominant food utilized by invertebrate, fish, and mammal predators in the study area, they can occur in the diet of most of these organisms. However, it seems that small molluscan species and juvenile stages of large mollusks are mainly consumed by these predators. Clams, but rarely gastropods, serve as prey for the bearded seal. Mollusks in general are long lived in arctic seas (Thorson, 1936, 1957; Ockelmann, 1958; Golikov, 1963; Dunbar, 1968; Chia, 1970). Consequently, larger species as adults, particularly gastropods, represent a carbon sink that mainly contributes carbon to the system via gamete production and death (see discussions in Isaacs, 1976, and Feder and Jewett, 1981.)

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APPENDIX

List of molluscan taxa. Infaunal taxa are those reported in Feder *et al.* (1990a). Taxa designated "sp." were generally too small to be determined to species. Epifaunal mollusks were identified in the field by Rae Baxter. Name changes are based, in part, on specimens collected in the same area in 1991 by N. Foster. Other suggested name changes are by N. Foster.

T = species collected by otter trawl, primarily epifauna, except *Mya* spp.

G = species collected by grab, primarily infauna.

These designations may not always be consistent with the life habits of the animals, as the grab may pick up small epifauna, and, on soft sediments, the otter trawl may dig in and collect larger infaunal species.

Gastropoda

T		*Lepeta caeca* (Müller, 1776)
T		*Margarites argentatus* (Gould, 1841)
T	G	*Margarites costalis* (Gould, 1841)
T		*Margarites giganteus* (Leche, 1878)
T		*Margarites vorticifer* (Dall, 1873)
T	G	*Solariella obscura* (Couthouy, 1838)
T	G	*Solariella varicosa* (Mighels and C.B. Adams, 1842)
	G	Trochidae, not determined
	G	*Moelleria costulata* (Møller, 1842)
	G	*Alvania* sp.
T	G	*Tachyrhynchus erosus* (Couthouy, 1838)
T	G	*Tachyrhynchus reticulatus* (Mighels and C.B. Adams, 1842)
	G	*Boreoscala greenlandica* (G. Perry, 1811)
T		*Asterophila japonica* Randall and Heath, 1912 [endoparasitic in sea stars (Hoberg *et al.*, 1980); biomass was not calculated]
T	G	*Crepidula grandis* Middendorff, 1849
T		*Trichotropis bicarinata* (Sowerby, 1825)
T	G	*Trichotropis borealis* Broderip and Sowerby, 1829
T		*Trichotropis coronata* Gould, 1860
	G	*Trichotropis kroyeri* Philippi, 1848
	G	*Trichotropis* sp.
T		*Bulbus fragilis* (Leach, 1819)
T		*Natica aleutica* Dall, 1919 [may = *N. clausa*][1]
T	G	*Natica clausa* Broderip and Sowerby, 1829
T	G	*Polinices pallidus* (Broderip and Sowerby, 1829)
T		*Marsenina glabra* (Couthouy, 1832) [id. by N. Foster][2]
T		*Onchidiopsis* spp.
T		*Capulacmaea commoda* (Middendorff, 1851)
T		*Velutina plicatilis* (Müller, 1776)
T		*Velutina undata* (T. Brown, 1839)
T		*Velutina velutina* (Müller, 1776)
T	G	*Boreotrophon clathratus* (Linnaeus, 1758)
T		*Boreotrophon muriciformis* (Dall, 1877)
	G	*Boreotrophon beringi* Dall, 1902
T		*Boreotrophon pacificus* (Dall, 1902) [may = *B. beringi*][3]
	G	*Boreotrophon* sp.
T		*Buccinum angulosum* J.E. Gray, 1839
T		*Buccinum ciliatum* Fabricius, 1780
T		*Buccinum glaciale* Linnaeus, 1761
T		*Buccinum plectrum* Simpson, 1865
T		*Buccinum polare* J.E. Gray, 1839
T	G	*Buccinum scalariforme* Møller, 1842
T		*Buccinum solenum* Dall, 1919
T		*Buccinum tenellum* Dall in Kobelt, 1883
T	G	*Buccinum* spp.
T		*Beringius beringii* (Middendorff, 1848)
T		*Beringius stimpsoni* (Gould, 1860)
T		*Clinopegma magna* (Dall, 1895)
T		*Colus* cf. *C. capponius* (Dall, 1919)
T		*Colus dautzenbergi* Dall, 1916
T		*Colus ombronius* (Dall, 1919)
T		*Colus* cf. *C. roseus* (Dall, 1877)
T	G	*Colus* sp.
T		*Liomesus ooides* (Middendorff, 1848)
	G	*Liomesus* sp.
T		*Neptunea borealis* (Philippi, 1850)
T	G	*Neptunea heros* J.E. Gray, 1850
T		*Neptunea middendorffiana* MacGinitie, 1959
T		*Neptunea ventricosa* (Gmelin, 1791)
	G	*Neptunea* sp.
T		*Plicifusus kroyeri* (Møller, 1842)
	G	*Plicifusus* sp.
T		*Volutopsius callorhinus* (Dall, 1877)
T		*Volutopsius deformis* (Reeve, 1847)
T		*Volutopsius attenuatus* (Dall, 1874)
T		*Volutopsius fragilis* (Dall, 1891)
T		*Volutopsius stefanssoni* Dall, 1919
	G	*Admete couthouyi* (Jay, 1839)
T		*Admete regina* Dall, 1911
	G	*Admete* sp.
T		*Oenopota harpa* (Dall, 1885)
T		*Oenopota murdochianus* (Dall, 1885)
T		*Oenopota simplex* (Middendorff, 1849)
T		*Oenopota turricula* (Montagu, 1803)
	G	*Oenopota* spp.
	G	*Propebela* spp. [= *Oenopota* spp.][4]
	G	*Cylichna alba* (Brown, 1827)
T		*Cylichna attonsa* (Carpenter, 1865) [questionable identification][5]
	G	*Cylichna occulta* (Mighels, 1841)
	G	*Philine* sp.
	G	*Retusa obtusa* (Montagu, 1803)
T		*Tochuina tetraquetra* Pallas, 1788
T		unidentified nudibranchs [in part, *Calycidoris geuntheri* Abraham, 1876, id. by N. Foster][2]

Bivalvia

T	G	*Nucula tenuis* (Montagu, 1808) [= *N. bellotti* A. Adams, 1856][6]
T		*Nuculana buccata* (Møller, 1842) [= *N. pernula* Müller, 1779][6]
T		*Nuculana fossa* (Baird, 1863) [questionable identification][5]
	G	*Nuculana minuta* (Fabricius, 1776)
	G	*Nuculana radiata* (Krause 1885) [= *N. pernula*][6]
	G	*Yoldia amygdalea* (Valenciennes, 1846) [= *Y. hyperborea*][6]
T	G	*Yoldia hyperborea* Torell, 1859
T	G	*Yoldia myalis* (Couthouy, 1838)
T	G	*Yoldia scissurata* Dall, 1897 [= *Y. seminuda* Dall, 1871][6]
	G	*Musculus corrugatus* (Stimpson, 1851) [may = *M. glacialis* Leche, 1883 or *M. discors*][6]
T		*Musculus discors* (Linnaeus, 1767)
T		*Musculus niger* (J.E. Gray, 1824)
T		*Chlamys behringiana* (Middendorff, 1849) [id. by N. Foster][2,6]
T		*Pododesmus macroschisma* (Deshayes, 1839)
	G	*Axinopsida serricata* (Carpenter, 1864)
T		*Thyasira equalis* A.E. Verrill and Bush, 1898
	G	*Thyasira gouldii* (Philippi, 1845)
	G	*Diplodonta* sp.
	G	*Montacuta* sp.
	G	*Mysella planata* (Krause, 1885)
	G	*Mysella* sp.
	G	Montacutidae, unidentified
T	G	*Astarte borealis* (Schumaker, 1817)
T	G	*Astarte montagui* Dillwyn, 1817
T		*Cyclocardia crassidens* (Broderip and Sowerby, 1829)
T		*Cyclocardia crebricostata* (Krause, 1885)
	G	*Cyclocardia ovata* (Rjabinina, 1952)
T		*Cyclocardia* cf. *C. ventricosa* (Gould, 1850)
T		*Clinocardium californiense* (Deshayes, 1839)
T	G	*Clinocardium ciliatum* (Fabricius, 1780)
T	G	*Serripes groenlandicus* (Bruguière, 1789) [may include *Yagudinella notabilis* (Sowerby, 1815)][6]
T	G	*Serripes laperousii* (Deshayes, 1839)
T	G	*Macoma calcarea* (Gmelin, 1791)
	G	*Macoma loveni* (A.S. Jensen, 1905)

T *Macoma middendorffi* Dall, 1884
G *Macoma moesta* (Deshayes, 1855)
G *Tellina lutea* W. Wood, 1828
T G *Liocyma fluctuosa* (Gould, 1841)
G *Liocyma viride* Dall, 1871 [may = *L. fluctuosa*][6]
G *Psephidia lordi* (Baird, 1863)
T *Mya pseudoarenaria* Schlesch, 1931
T *Mya truncata* Linnaeus, 1758
G *Mya* sp.
T G *Hiatella arctica* (Linnaeus, 1767)
T G *Lyonsia arenosa* (Møller, 1842)
T *Lyonsia bracteata* (Gould, 1850) [questionable identification][5]
G *Lyonsia* sp.
T *Pandora filosa* (Carpenter, 1864)
G *Pandora glacialis* Leach, 1819
G *Thracia devexa* G.O. Sars, 1878
G *Lampeia adamsi* (MacGinitie, 1959)
G *Periploma aleuticum* (Krause, 1885)

Polyplacophora
T *Amicula vestita* (Broderip and Sowerby, 1829)
T G *Stenosemus albus* (Linnaeus, 1767)
G *Tonicella rubra* (Linnaeus, 1767) [questionable identification][5]

Cephalopoda
T *Octopus leioderma* (S.S. Berry, 1911) [questionable identification][7]

[1] Baxter (1987) separated the northern Pacific *Natica* into three species, based on shell color and morphology and on the shape of egg cases (see Kessler, 1985).

[2] Based on specimens collected in 1991.

[3] The taxonomy of boreal and arctic species of *Boreotrophon* is in need of revision. Baxter (1987) called both *B. pacificus* and *B. beringi* subspecies of *B. truncatus* (Strøm). There is much variation in the shape and proportions of the shells and number of varices, among the species of *Boreotrophon*.

[4] Vaught, 1989.

[5] Specimens were not found among the UA Museum voucher specimens. This species has not been reported in the northeastern Chukchi Sea (Baxter, 1987).

[6] E.V. Coan and P.H. Scott, pers. comm. 1992, based on an unpublished manuscript revision of northeastern Pacific bivalves.

[7] *Octopus leioderma* appeared in Baxter's species list. Cephalopod specimens collected in the northeastern Chukchi Sea in 1991 were sent to J. Voight, cephalopod taxonomist at the Field Museum. She placed them in the genus *Benthoctopus* but could not determine the species with confidence (J. Voight, pers. comm. 1993).

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