FROST / LOWRY

VERTEBRATE CONSUMERS IN THE BEAUFORT

NMFS FINAL REPORT

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FINAL REPORT

Project Title: Feeding and trophic relationships of bowhead whales and other vertebrate consumers in the Beaufort Sea

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TABLE OF CONTENTS

Appendices

LIST OF FIGURES

LIST OF TABLES

List of Tables, cont.

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I. Introduction

Until very recently the marine waters along the north coast of Alaska, commonly called the Beaufort Sea, had received little scientific attention. This region, which lies almost entirely north of 70° north latitude, is characterized in winter by long periods of darkness, extensive sea ice cover, and very few visible animals. During this period of cold and darkness the Beaufort Sea indeed appears to be a biological desert. However, as daylight lengthens, temperatures increase, and the ice cover becomes less continuous, thousands of marine mammals and millions of birds appear in the area. The presence of these animals, most of which have migrated to the Beaufort from more temperate regions, suggests an area of high summer productivity. Indeed, it was Yankee whalers pursuing the bowhead whale (Balaena mysticetus) to its summer feeding grounds who provided the first major influx of non-native people to the region (Bockstoce 1977). Observations made by these whalers during the late 19th and early 20th centuries greatly increased the generally available information on the geography, meteorology, and ice conditions of the area but provided meager data on the biology of the Beaufort Sea region. The excellent observations of explorer/naturalists such as Stefansson (1913) and Leffingwell (1919) dealt primarily with terrestrial fauna and flora and the more obvious marine birds and mammals.

Subsequent to the demise of commercial bowhead whaling in the early 1900's, activity in the Beaufort Sea declined markedly. The establishment of the Naval Arctic Research Laboratory (NARL) at Barrow in 1947 provided the first permanent research facility on the northern coast of Alaska. Several major studies of the local fauna and flora were conducted from NARL (e.g., MacGinitie 1955; Redburn 1974). In addition, NARL provided a support base for work conducted from icebreakers (e.g., Hufford 1974; Watson and Divoky 1974) and drifting ice islands (e.g., Barnard 1959; Mohr and Geiger 1968).

The discovery of oil in Prudhoe Bay in 1968 and the need to transport materials and equipment to Prudhoe by sea initiated the second major surge of interest in the Beaufort Sea. A major study (Alexander et al. 1975) was conducted in the nearby Colville River system which provided some of the first baseline data on the biology and ecology of nearshore waters of the central Beaufort.

The planned extension of oil and gas exploration and development to the nearshore marine waters of the Beaufort Sea provided impetus for a major program of physical, biological, and oceanographic studies. For the first time, a major commitment to logistics provided researchers with the means to carry out their investigations in both nearshore and offshore areas throughout the year. These studies, sponsored by the Bureau of Land Management (BLM) and planned and supervised by the National Oceanic and Atmospheric Administration (NOAA) Outer Continental Shelf Environmental Assessment Program (OCSEAP), greatly increased the available information on the biology and ecology of the Beaufort Sea (see NOAA/OCSEAP 1978). A program of research conducted prior to development of oil and gas reserves in the Mackenzie Delta area of Canada provided complementary information for the Canadian portion of the Beaufort (e.g., Blood 1977).

Concurrent with the development of the OCSEAP program, a concern for the well-being of the bowhead whale population and its habitat arose. Initial studies focused on population assessment and harvest monitoring (Tillman 1980), but later work involved a broad array of topics dealing with distribution, ecology, physiology, etc. (Braham et al. 1980a; NARL 1980).

Studies of foods of bowhead whales in the Alaskan Beaufort Sea began on an opportunistic basis in 1976 with partial support provided by the OCSEAP program and samples collected by National Marine Fisheries Service (NMFS) personnel. Results of analysis of those samples (Lowry et al. 1978) indicated that euphausiids were the primary foods of bowheads taken in September 1976 and also of ringed seals (Phoca hispida) harvested in summer 1975 and 1976. Lowry et al. (1978) briefly discussed the possibility that changes in population levels of bowheads and ringed seals might be interrelated and that competition for food might affect the recovery of the bowhead population. Further studies of bowhead foods supported by NMFS, OCSEAP, and Project Whales (BLM/NARL) indicated that copepods, in addition to euphausiids, are major prey in the Beaufort Sea (Marquette 1979; Lowry and Burns 1980). Copepods were also found to comprise a major portion of the diet of arctic cod in that area (Lowry and Frost 1981a), suggesting the possibility for competition for food between bowheads and arctic cod (Lowry and Burns 1980; Lowry and Frost 1981a). Further studies of foods of ringed seals in the Beaufort indicated that arctic cod were by far the major food during fall and winter (Lowry et al. 1980; Frost and Lowry, in prep.), suggesting an abundance of arctic cod in the area.

The above-mentioned studies, although suggestive, did not provide a thorough and adequate treatment of the foods and trophic relationships of bowheads in the Alaskan Beaufort Sea. Such a treatment appeared timely for several reasons. First, due to the obvious significance of bowheads to Alaskan Eskimos and other people, and suggestions that competition for food might be delaying recovery of other baleen whale stocks (Mitchell 1975), an assessment of possible trophic competitors of bowheads seemed desirable. The apparent simplicity of the pelagic food web of the Beaufort Sea (Frost 1978) made the system appear comparatively tractable. Secondly, it was felt that much of the recently collected data had been inadequately analyzed and synthesized, and synthesis and evaluation of the data were needed in order to adequately plan future research. Third, some major data gaps were evident which were of considerable importance in determining estimates of food consumption by the major consumers of the area. We therefore designed and conducted a study, with funding provided by NMFS, to address the following three primary objectives.

1. Analyze and synthesize all available data on foods and feeding of bowhead whales in the Alaskan Beaufort Sea.

2. Conduct field studies in the eastern portion of the Alaskan Beaufort Sea in September 1980 to examine the foods used by ringed seals and arctic cod in an area where bowheads were known to feed.

3. Synthesize and analyze data from 1 and 2 above with other information on major vertebrate consumers in the Alaskan Beaufort to provide an assessment of the kinds and quantities of prey required on an annual basis to support populations of bowheads and their potential trophic competitors.

II. Methods

A. Literature Search

The primary purpose of the literature survey we conducted was to obtain estimates of productivity and availability of food, and food habits and population biomasses of major vertebrate consumers in the Alaskan Beaufort Sea. For our purposes the study area was defined as the area bounded by a line north from Point Barrow (156°30'W) on the west and the U.S.-Canada demarcation line on the east (141°W) and from the outside of the nearshore barrier islands to the 200-m depth contour (Figure 1). The study area, therefore, includes the entire continental shelf of the Alaskan Beaufort Sea with the exception of the nearshore lagoon systems. The size of the study area was calculated as approximately 50,000 km^2.

Prior to surveying the literature and investigating trophic interactions among consumers we selected four groups of organisms which we considered to be of greatest ecological importance to consumers in the pelagic food web of the Beaufort Sea (Figure 2). The selection of these organisms--copepods, euphausiids, hyperiid amphipods, and arctic cod--was based on results of previous studies of the ecology and trophic relationships among Beaufort Sea vertebrate consumers (Frost 1978; Lowry et al. 1978; Lowry and Burns 1980; Lowry and Frost 1981a).

The literature survey was done by conventional means. Whenever possible we tried to locate information specific to the study area. Where such information was not available, relevant data from other areas were compiled and used. Principal sources of information were reports of the Alaska Outer Continental Shelf Environmental Assessment Program and the Canadian Beaufort Sea Project. Direct contacts with investigators were made when important information was available that had not yet been published. It should be noted, however, that results of some significant studies were not completely analyzed and available to us when this report was prepared.

B. Field Work

The primary field work associated with this project was conducted in the vicinity of Beaufort Lagoon from 4-19 September 1980. Additional

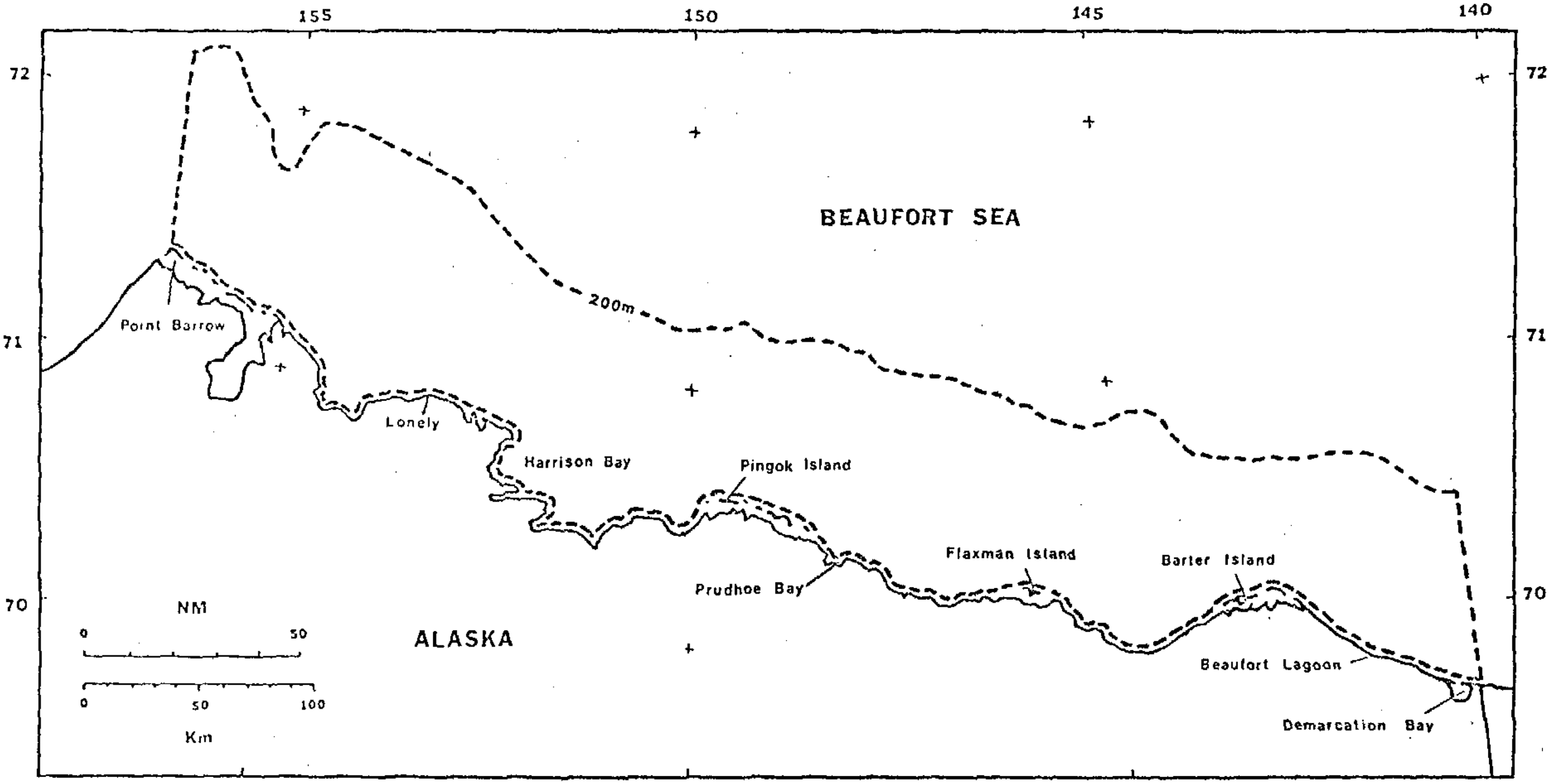
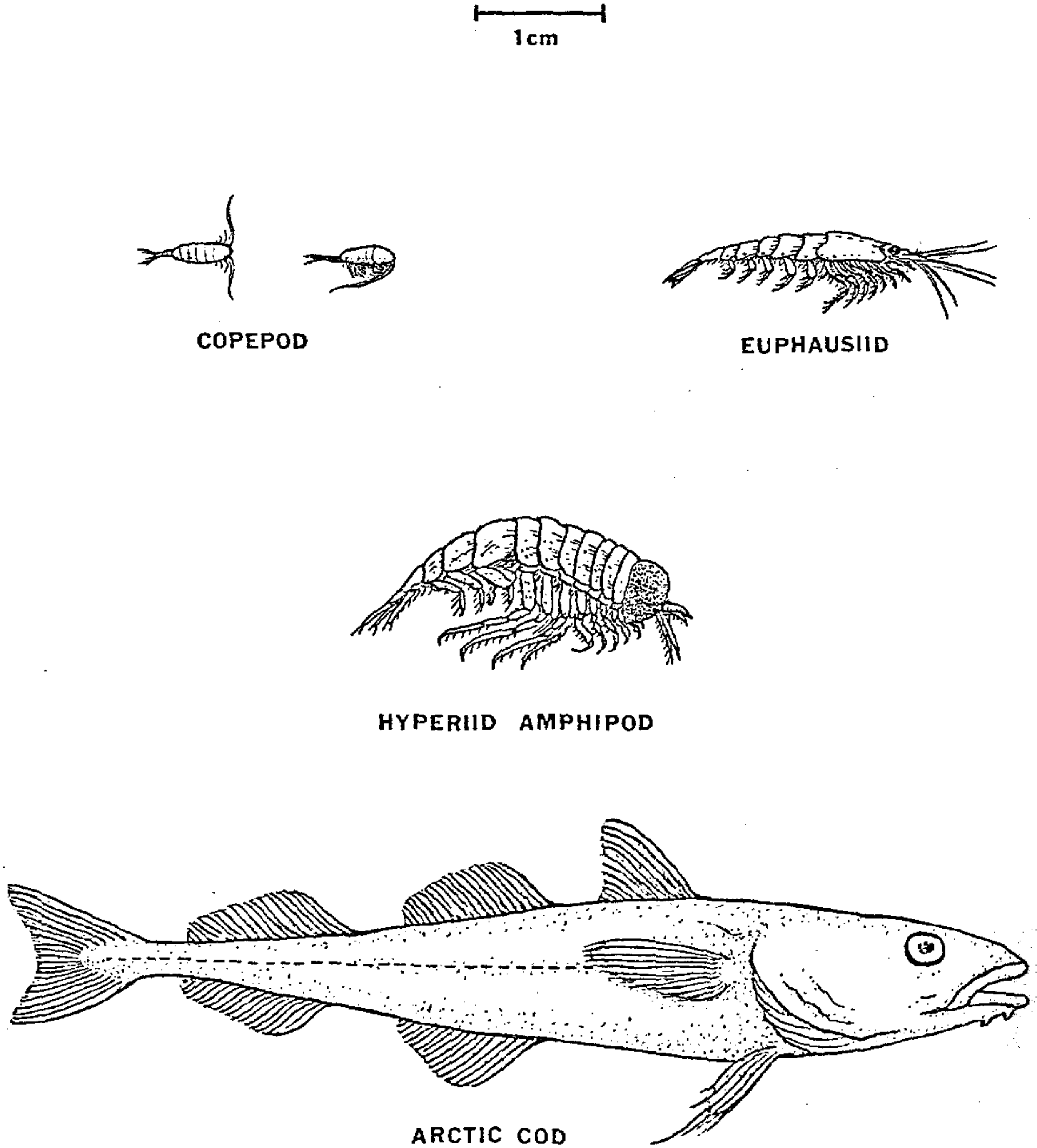


Figure 1. Map of the Alaskan Beaufort Sea indicating the study area (enclosed by dashed line).

Figure 2. Drawings of representative prey species considered in this report.



related work (funded by OCSEAP) was conducted near Pingok Island from 20 August through 1 September 1980. The primary base of operations at Pingok was a small facility constructed and maintained by the NARL, while at Beaufort Lagoon we operated from an abandoned DEW line site which is presently maintained as a research facility by the U.S. Fish and Wildlife Service.

The selection of Beaufort Lagoon as a base of operations was based on the sighting of numerous bowheads apparently feeding near there (Ljungblad et al. 1980) and the occurrence of food in the stomachs of bowheads taken near Kaktovik, the Eskimo village on Barter Island a short distance to the west (Lowry and Burns 1980). Based on the dates of the sightings reported by Ljungblad et al. (24 and 26 September) and the usual timing of the bowhead harvest at Kaktovik, usually the latter half of September (Marquette 1976, 1979), we planned to commence field work early in September and continue if possible until the end of the month. Field work was begun on 3 September and terminated on 19 September due to a rapid and early freeze-up.

A 20-foot (6.1 m) long Boston Whaler was purchased and equipped as a research vessel for this project. The boat was powered by twin 90-horsepower Mercury engines and equipped with standard steering, controls, and safety equipment. A stainless steel A-frame was designed, constructed, and installed. The A-frame allowed nets to be handled either over the stern or alongside the boat. A small gasoline-powered capstan (Gowan Nu-Way Hauler) was installed to facilitate retrieval of nets. A depth sounder (Datamarine Model S200D) provided a digital read-out of depths from 0-200 feet (0-60 m) in 1-foot (0.3 m) intervals.

We attempted to do five types of sampling from the research vessel (Figure 3) whenever weather and ice conditions permitted. These are briefly described as follows:

1. A record was kept of all marine mammals sighted. Number and identity of marine mammals involved was noted along with time of day, water depth, general location, ice conditions, and any other relevant observations.

2. Ringed seals were collected for stomach contents analysis. Seals were shot with a high-powered rifle and retrieved by harpooning. They were then weighed, measured, and necropsied. Samples collected included stomachs, reproductive tracts, and claws and lower jaws which were used for age determination.

3. In areas where ringed seals were collected, as well as at several other locations, otter trawls were conducted. The net used was a semi-balloon design with a 3.8-m headrope, with 3.6-cm stretch mesh body, 3.2-cm stretch mesh cod end, and a 2.5-cm stretch mesh knotless cod end liner. The net was rigged with 30.5-cm by 50.8-cm trawl doors, four floats on the headrope, and galvanized chain on the footrope. Bridles from the trawl doors were attached by swivels

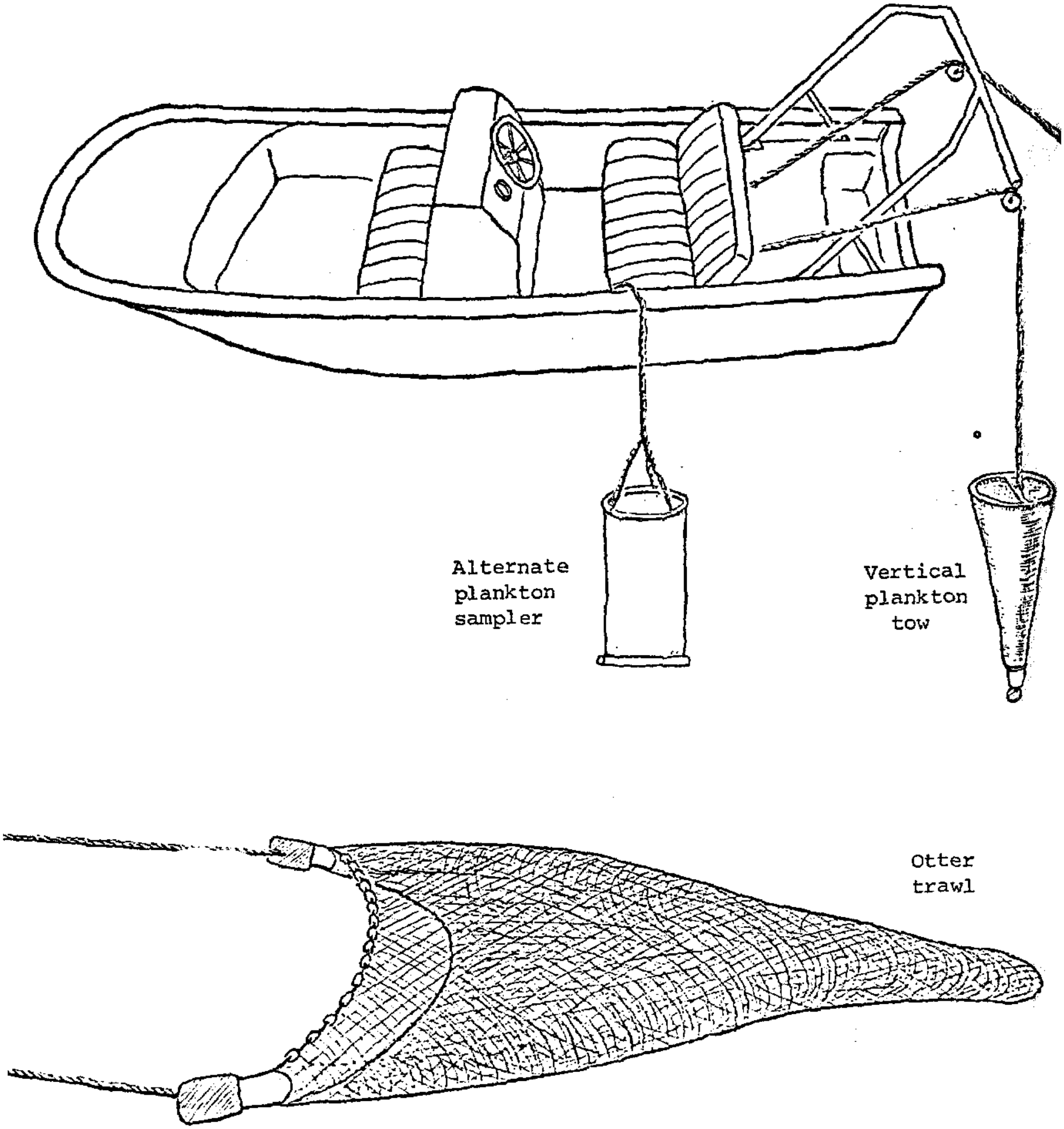


Figure 3. Drawing of research vessel and sampling gear.

to 183 m long, 1.0-cm diameter double-braided nylon rope which was used to tow the net. The towline was marked at 5-m intervals for the first 50 m and at 50-m intervals thereafter. The towline was run through a block on the A-frame and enough towline was let out (approximately 4-5 times the water depth) for the net to reach the bottom. It was towed on the bottom at a speed of 2-4 km/hr for 20 minutes. The net was retrieved using the capstan. Contents of the catch were washed and sorted, and the body cavities of all arctic cod caught were injected with 10% formalin using a syringe. Organisms were then placed in fine-mesh nylon bags, labeled, and immersed in a 10% formalin-seawater solution.

4. Vertical plankton tows were done wherever otter trawls were conducted or bowhead whales were sighted, as well as at 5-m water depth intervals along two selected transects (Figure 4). The net used was 0.5 m in diameter with a 4:1 open area ratio, 505-micron mesh net, quick-release sampling cup, and a crossbar with single-tow bridle. A 5-kg weight was attached to the sampling cup. The towline was run through a block on the A-frame and attached to the tow bridle. The net was allowed to sink to the desired depth, then was retrieved by hand at a speed of 30-40 m/minute. The net was washed at the surface, then collected samples were poured into labeled whirl-pac containers and preserved with 10% formalin-seawater. At locations where otter trawls were conducted, one to three replicate tows were made from the bottom to the surface. Near whale sightings and along transects, vertically stratified tows were sometimes done in addition to tows from the bottom to the surface. In those instances the net was lowered to the first full 5-m depth increment above the bottom (e.g., to 25 m in an area 28 m deep) and hauled to the surface, washed, and the contents labeled and preserved. These were commonly repeated at progressively shallower 5-m increments.

5. We attempted to design and construct an Alternate Plankton Sampler of the type described by Brodie (1978). The purpose of such a sampling device was to adequately collect comparatively large, mobile nektonic organisms such as euphausiids and hyperiid amphipods. The device used by Brodie consisted of a 40-cm sheet-metal cylinder on which was loaded a length of thin polyethylene tubing. The tubing was tied shut at one end so that as the sheet-metal cylinder moved through the water the polyethylene bag became filled. In principle such a sampler eliminates the "bow wave effect" caused by nets and simulates the gulping action of baleen whales which should allow the capture of motile organisms. Using the design suggestions of Brodie (1978), we designed and constructed a sampler that could store up to 50 m of tubing wrapped around a filter apparatus constructed of 5.0-cm diameter plastic pipe. Unfortunately, time did not allow testing of the sampler before field work commenced. The sampler proved deficient in several respects, particularly in the rate of water filtration allowed by the plastic-pipe filtering apparatus. We modified the filtering arrangement of the sampler, but the modifications were not successful. Further development and

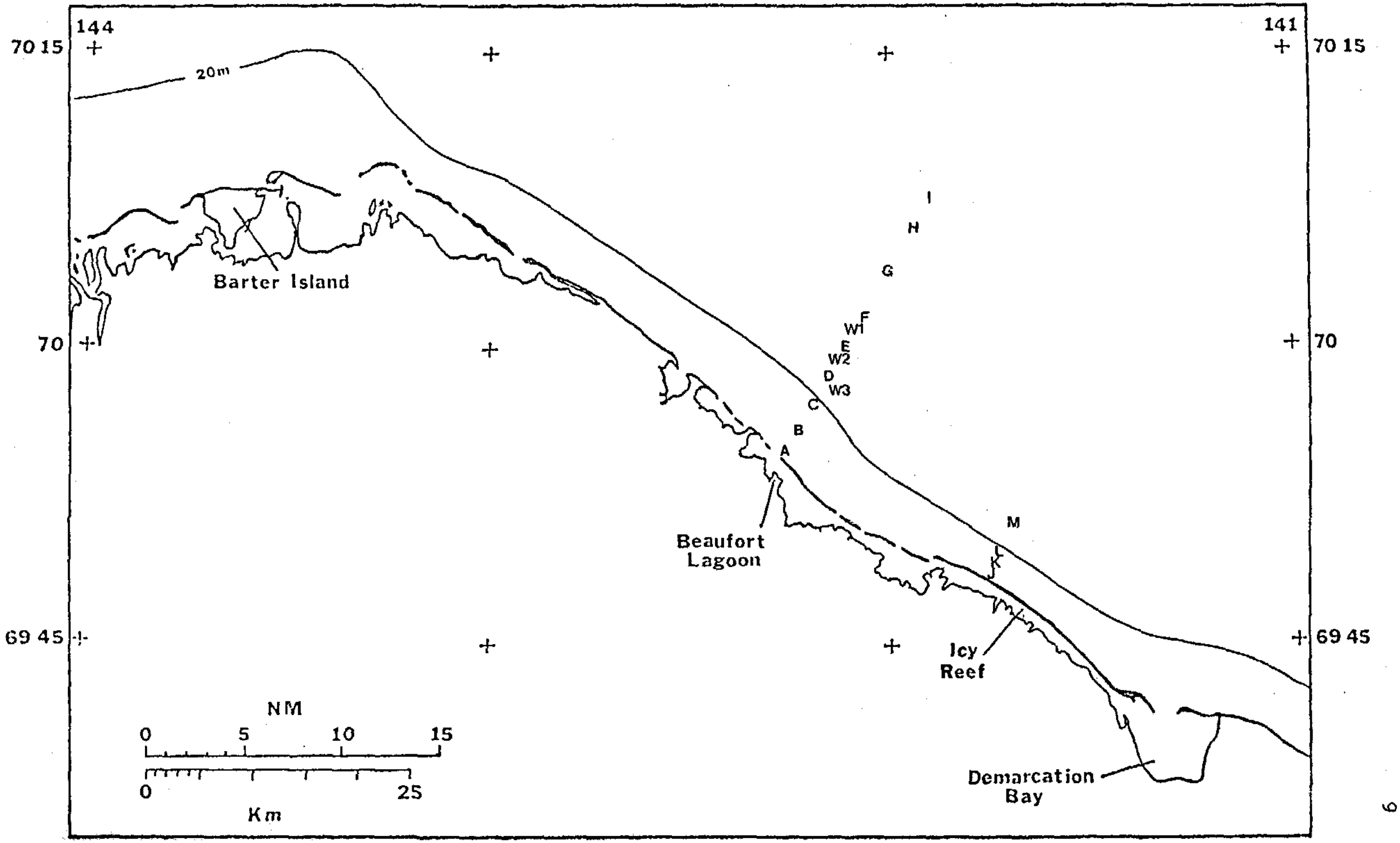


Figure 4. Locations where vertical plankton tow transects were made off Beaufort

testing are required before equipment of this type will be useful on a routine basis. Some such testing has been planned (Brodie, pers. comm.).

C. Laboratory and Analytical Procedures

1. Vertical plankton tows

Organisms caught in the vertical plankton tows were sorted, identified, and enumerated by Kenneth Coyle, University of Alaska, Institute of Marine Sciences. Samples were washed from the whirl-pacs and the excess fluid removed. In most tows the entire catch was processed. For a few tows in which very large numbers of copepods were caught, large organisms were removed from the sample and counted, the remainder was then diluted and several (usually 3-4) subsamples were taken and examined until a total of 100-200 of the most common species was counted. Organisms were identified to the lowest possible taxonomic level which, with the exception of some larval forms, was usually to species. Copepods were identified by age category and sex where possible and were enumerated separately by age and sex class.

Computer programs were developed for entry and analysis of zooplankton data. In analysis programs a subsampling factor was applied to subsample counts (based on the ratio of the volume counted to total sample volume) to derive for all species the estimated total number in the sample. This was then expressed as the number of individuals of each species per cubic meter of water by dividing by the amount of water filtered by the tow (area of net opening x tow depth). For stations with replicate tows, results were expressed as the mean and range in number of individuals caught.

At stations where vertically stratified tows were made, abundance of plankton was computed for each possible depth increment. We assumed that each of the tows in a stratified series sampled a portion of an identical water column. Therefore, in an area 15 m deep, the tow made from 10 m depth to the surface contained all the organisms in the upper 10 m, while the tow from bottom to surface contained those organisms plus those living in the bottom 5 m. The number of organisms of each species caught in the 10-0 m tow would be subtracted from the 15-0 m tow and the result divided by the difference in volume of water filtered. This process was repeated using each progressively shallower pair of tows. If more organisms of a species were caught in a particular tow than were caught in the next deeper tow, the abundance of that species in the depth zone between the tows was considered zero.

2. Otter trawls

Contents of otter trawl catches were washed and sorted into major taxonomic groups which were then enumerated where appropriate and weighed (wet weight to 0.1 g). Fishes were usually identified to species. Arctic cod were individually measured (fork length to 1.0 mm) and weighed (wet weight to 0.1 g), and the sex was noted and the stomach removed. Contents of the stomach were examined under a binocular microscope, components of the stomach contents were sorted to species, enumerated to the extent possible, and weighed (wet weight to 0.01 g).

Computer programs were written for entry and analysis of arctic cod data. One program calculated the mean length and length distribution of cod caught in tows. Measured lengths of specimens were increased by 2.1% to compensate for shrinkage due to preservation (Lowry and Frost 1981a). A second program analyzed the contents of stomachs in terms of mean weight and number of individuals and frequency of occurrence (number of stomachs in which an item occurred/total number of stomachs in sample) of each item in the stomachs examined. Only stomachs containing recognizable food were included in this analysis.

3. Ringed seal stomach contents

Preserved stomach contents from ringed seals were gently washed on a 1.00-mm fine-mesh sieve, then sorted into major categories. Prey items were identified to the lowest possible taxonomic category, counted, and the water displacement volume measured (to the nearest 0.1 ml) in graduated cylinders. Estimates of the number of individuals of each prey consumed were based on counts of intact organisms and characteristic parts such as otoliths of fishes. Otoliths from arctic cod eaten were measured (to the nearest 0.1 mm) with vernier calipers. All otoliths were measured in those stomachs containing fewer than 20. In those containing more than 20 otoliths, a randomly selected subsample of 20 was measured.

Existing computer programs were used to analyze components of ringed seal stomach contents. For each of the two major collection areas the percent of the total stomach contents volume comprised of each category and the frequency of occurrence was calculated. The percent of the total number of fishes eaten which belonged to each taxon was also calculated. The estimated lengths of arctic cod eaten were calculated based on otolith measurements using the formula: Fish fork length (cm) = 2.198 otolith length (mm) + 1.588 (Frost and Lowry, in press a).

4. Bowhead whale stomach contents

Techniques used for examination of bowhead whale stomach contents were generally similar to those just described for ringed seals. Stomach contents were washed on a fine-mesh (usually 0.355 mm) sieve. Large obvious organisms were removed and counted, and the remainder was examined and sorted using a binocular microscope. Prey were identified to the lowest possible taxonomic level and enumerated, using subsamples to estimate numbers of small, abundant organisms such as copepods. Volume of each prey category was determined by water displacement in graduated cylinders. Percent of the total sample volume and percent of the total number of prey which were comprised of each prey category were calculated.

III. Availability and Production of Food

A. Oceanography and Sea Ice

The Beaufort Sea forms a southern embayment of the Arctic Ocean and is bounded by a line drawn from Point Barrow, Alaska, to the tip of Prince Patrick Sound, Northwest Territories. The continental shelf in the Beaufort Sea is narrow, generally less than 150 km wide, and shallow, averaging about 65 m in depth, with a well-defined shelf break at about the 200-m isobath (Hufford 1974).

The Beaufort Sea, like the remainder of the Arctic Ocean, can be divided vertically into three water masses: arctic surface water, Atlantic water, and arctic bottom water (O'Rourke 1974; Herlinveaux and Boom 1975). Arctic surface water extends from the surface to about 200 m and generally covers the continental shelf. The upper 25-50 m originates in the Arctic, mainly as terrestrial runoff, and is generally characterized by relatively low salinities (28.5-33.5 ppt). The remainder of this layer is a mixture of runoff, Atlantic water, and somewhat warmer Bering Sea water (O'Rourke 1974). Circulation off the shelf is predominantly clockwise in the form of the Beaufort Sea Gyre which moves westward off the Alaskan coast at about 10 cm/sec (0.4 km/hr) (Herlinveaux and Boom 1975). On the shelf surface currents are driven by the wind which in summer is usually from the east with intermittent northwesterly winds during storms which reverse the the flow. Subsurface currents are generally to the east, although reversals are common (Mountain 1974, Aagaard 1978). Bering Sea water is often present on the outer shelf at depths of 50 to 100 m. Penetration eastward is very variable but in some years Bering Sea water is present at least as far east as Barter Island (Johnson 1956). Wind-induced mixing of the water column occurs to about 25 m during summer (O'Rourke 1974). Upwelling probably occurs mostly on the outer shelf, east of 146°, when easterly winds move surface water off shore and deeper, poorly oxygenated but nutrient-rich water comes up onto the shelf to replace it (Hufford 1974). Upwelling apparently does not occur every year (Mountain 1974).

Atlantic water, entering the Arctic through the passage between Greenland and Spitsbergen, is found from about 200 to 900 m. Circulation of Atlantic water is counter-clockwise in the main Arctic Basin. This water mass is relatively warm, usually above 0°C, and saline (O'Rourke 1974). Below 900 m, subzero temperatures and salinities of almost 35 ppt characterize arctic bottom waters.

Input into the Beaufort Sea from river runoff varies throughout the year, with maximum flow in June (approximately 80% of the total discharge) and minimum flow in December. The Mackenzie River in the eastern Beaufort Sea contributes about half of the total runoff, with most of the remainder from the Colville, Kuparuk, Sagavanirktok, and Canning (Hufford 1974). The vertical effects of river runoff and spring ice melt are generally limited to the upper 30 m and usually to the upper 15 m (Hufford 1974).

Nearshore waters of the Beaufort Sea are ice-covered for almost 10 months of the year. Freeze-up usually begins in late September or October and the ice continues to grow throughout the winter until it reaches maximum thickness in late April or May (Shapiro and Barry 1978). During winter two major categories of ice are present: landfast ice which is attached to the shore and extends for variable distances seaward, and pack ice which occupies the remainder of the Beaufort Sea and Arctic Ocean, drifting with the winds and the clockwise Beaufort Sea Gyre. Landfast ice and pack ice interact in a zone of shear forces and pressure ridges. The shear zone is usually found at water depths of 15 to 20 m where the moving pack ice impacts the stationary fast-ice edge (Shapiro and Barry 1978). Large pieces of ice commonly ground in this zone, protecting and providing added stability to the ice in shore.

In late May or early June melting begins, initiated by increasing sunlight and warming temperatures (Shapiro and Barry 1978; Burns et al. 1980). Rivers flood out onto the fast ice, ice melts along the shoreline, and melt ponds form on top of the ice. Most years in late June-July the partially melted, weakened fast ice either disintegrates in place or breaks up and moves off shore under the influence of winds and currents. The pack ice also melts and decays, and the southern edge becomes a zone of broken, moving floes (Shapiro and Barry 1978).

The timing and progression of breakup and fall freeze-up, and thus the duration of the open water period, are highly variable. In some years, as in 1975, the ice moved off shore very little and areas of open water were extremely limited. In 1977 the ice moved far off shore, creating vast areas of open water (Frost and Burns, unpubl. obser.). In 1980 freeze-up occured much earlier than "normal," reducing the open water season by several weeks. Such annual variation in the open water period greatly affects the amount of light reaching the water column in a summer and therefore the total annual primary production.

To bowhead whales and other summer visitors, the geographic as well as temporal progression of breakup is important. Their spring migration from the Bering Sea through the Chukchi and into the eastern Beaufort depends on the opening of leads in northwest Alaska in March. In an "average" year those leads gradually spread north and east in an arch across the Beaufort Sea from Point Barrow to the northwest corner of Banks Island (Marko 1975; Burns et al. 1980). It is through these leads that bowheads move. The first major areas of open water in spring lie to the west of Banks Island, spreading south to outer Amundsen Gulf (Marko 1975) and west to Tuktoyaktuk Peninsula by June. A persistent lead, often referred to as the "terminal lead," is present at about the 30-m contour along the Tuktoyaktuk Peninsula (Marko 1975). That lead opens first in Amundsen Gulf and spreads west to Mackenzie Bay, widening as spring progresses. Open water occurs off Herschel Island and the Alaskan coast by July or August (Markham 1975). Although the extent of open water varies annually, the terminal lead is almost always present in some form in the southern Amundsen Gulf-Tuktoyaktuk region. Consequently, it may be particularly important to bowheads as a reliably open water area in severe ice years.

B. Primary Production

In the oceans, the photosynthetic organisms responsible for converting inorganic carbon (carbon dioxide) to organic carbons (simple sugars) which are readily usable by the rest of the food web are small one-celled plants known as phytoplankton. Although they survive and flourish in a wide variety of circumstances these phytoplankton, like all plants, have basic requirements for light and nutrients. In the Arctic, both light which provides the energy source for the photosynthetic reactions and nutrients which provide needed building blocks may be limiting.

The availability of light is highly variable on a seasonal basis. From November until January the Beaufort Sea receives no direct sunlight. In mid-March days and nights are of equal length, while from May through July direct light is present for 24 hours a day. By late August light levels have significantly decreased and in early October days and nights are once again of equal length. For the phytoplankton, light levels are generally adequate for photosynthesis and growth from March until October (Bursa 1961). Major factors affecting the availability of light include the angle of the sun, cloud and fog cover, wave action, turbidity in the water column caused by sediment or organic matter, and the presence of ice, including its thickness and snow cover (Bursa 1961; Grainger 1975). Most of those factors vary annually and in combination greatly affect the magnitude of phytoplankton production in any particular year.

Although incident solar radiation is adequate for plant growth by late March or early April, little of that light reaches plankton in the water column. Surface albedo (reflectivity) is high and light attenuation through one to several meters of snow-covered ice is great. As little as 1-2% of the incident radiation reaches the ice-water interface (English and Horner 1977), and "drastic light attenuation can be expected to persist almost as long as the ice cover lasts" (Schell 1980). Solar radiation is greatest in June, but maximum penetration into the water column does not occur until July when snow on the surface of the ice has melted and much of the seasonal sea ice has melted, broken up, or moved off shore. In the Arctic the depth of the euphotic zone (the zone where light is adequate for photosynthesis) varies but is usually less than 50 m (Bursa 1961; Grainger 1975; Davis et al. 1980).

Phytoplankton productivity in arctic waters is considered to be quite low in comparison to similarly cold antarctic waters, a fact which is generally attributed to differences in the availability of nutrients. Those nutrients--primarily nitrates, phosphates, and, in the case of diatoms, silicates--are required in various amounts for successful growth and reproduction of the phytoplankton community. In the Beaufort Sea the availability of nutrients fluctuates seasonally (Horner 1981). During the summer nutrient levels (particularly nitrogen) are low or undetectable and the system is nitrogen limited (Grainger 1975; Horner 1981). This is due to a combination of rapid nutrient utilization by phytoplankton populations and the extreme stability of the water column. Stability is caused by decreased salinities due to melting ice and warming by the sun which in combination result in a strong density gradient or pycnocline (Horner 1981). Although a strong pycnocline tends to keep phytoplankton from sinking through it and out of the euphotic zone, it also prevents the exchange of nutrients between deep nutrient-rich waters and near-surface nutrient-depleted waters. Upwelling is responsible for nutrient replenishment and thus high productivity in many parts of the world such as the antarctic convergence and off the coasts of Peru and California. However, throughout much of the arctic upwelling probably does not occur, which results in a generally nitrogen-depleted system with relatively low productivity (Thordardottir 1977). Upwelling apparently does occur in at least some years on the outer shelf of the Beaufort Sea east of 146°W (Hufford 1974, Mountain 1974). Productivity values are higher in that area. It is possible that persistent nearshore ice in the western portion of the Beaufort Sea reduces the amount of open water, thus limiting upwelling. In general, nitrates decrease from the shore to the shelf break, whereas phosphates increase, largely because terrestrial runoff is high in nitrogen and low in phosphates (Horner 1981).

Stratification of the water column breaks down in fall and winter as a result of wind mixing caused by storms, declining water temperatures, and formation of ice. Deep mixing occurs, bringing up nutrients from deep waters to the surface layers. In situ regeneration of nutrients by microbial populations also takes place at this time (Hsiao 1976; Horner 1981). According to Schell (1980), "Nutrient concentrations rise steadily in the under-ice waters of the nearshore Beaufort Sea following cessation of plant uptake in the fall." In spring, additional nutrients, especially nitrates, are supplied by river runoff and desaltation of the ice, but are rapidly depleted by the developing phytoplankton blooms (Meguro et al. 1967, Alexander 1974).

Temperature and salinity are important factors for the survival of individual species and thus greatly affect the species composition of the phytoplankton. They do not, however, regulate productivity since high productivity can occur in cold as well as warm waters and at either high or low salinities. Thus, unlike the availability of light and nutrients, temperature and salinity are not strictly limiting factors to primary production.

The species composition of the primary producers in arctic waters changes seasonally with changing light, nutrient, temperature, and salinity regimes. Early in the year, from about April until June, most production is attributable to "ice algae" which grow in brine pockets in the ice at light levels considerably below the 1% level generally considered necessary for phytoplankton in the water column. Primary productivity in the water column at that time is quite low (Hsiao 1980). The ice algal community appears with ice formation in the fall, persists at low numbers through the winter, then undergoes a rapid increase in spring as light and nutrient levels increase. Ice algae are dispersed throughout the ice in winter, but by April or May are concentrated in a thin layer (2-3 cm) at the bottom of the ice (Horner and Alexander 1972; Hsiao 1980). That layer is comprised almost entirely of pennate diatoms, particularly of the genus Nitzschia, although dinoflagellates, flagellates, and ciliates are also present (Meguro et al. 1967; Horner and Alexander 1972; Hsiao 1980). The peak ice algae bloom usually occurs in late June, just before breakup, as light penetration is greatest due to melting snow and decreased surface albedo (Hsiao 1980). Production declines thereafter, in part due to light inhibition and in part because the dark algal layer differentially absorbs light and melts, releasing algae into the water column (Hsiao 1980). Nutrients are probably not limiting to the ice algae since the top layer of ice acts as a reservoir, providing nutrients to the plants below through desaltation and drainage through brine channels (Meguro et al. 1967; Hsiao 1980). Exchange with seawater makes available additional nutrients which are in abundant supply following a winter of replenishment and low utilization.

The contribution of the ice algae to total annual primary production is difficult to evaluate and undoubtedly varies from year to year in relation to ice and snow conditions. The only available information for the area outside the barrier islands in the central Beaufort Sea is from Schell (1980) who estimated annual production of ice algae in that area to be about 2 g/m^2. Comparable estimates for the eastern Chukchi Sea (Alexander 1974) and the Bering Sea (McRoy 1976) are 5 g $C/m^2/yr$ and 24 g $C/m^2/yr$.

Although total ice algal production is not great, the ice algae standing stock in early spring may be 40-500 times greater than that of the water column, and thus may provide a relatively concentrated food source for zooplankton well before the regular phytoplankton bloom occurs. There is probably less annual variation in ice algal production than in phytoplankton production since factors affecting ice algal growth are annually less variable than those affecting the phytoplankton. Consequently, in years of poor phytoplankton production the ice algae may account for 25% or more of the total annual production (Alexander 1974), whereas in good years for phytoplankton it may comprise as little as 5-10%.

During April-June while ice algal productivity is high, the water column phytoplankton are just beginning their seasonal increase. Throughout the winter months, chlorophyll a is barely detectable in the water column. Diatom numbers are low and small flagellates predominate. During March-early May flagellates are still most abundant, but diatom numbers (and chlorophyll a) are steadily increasing. In much of the Arctic there are two major phytoplankton production peaks (Bursa 1961; English and Horner 1977; Horner 1981). The first usually occurs in late June-early July just before or during breakup and is comprised primarily of pennate diatoms, particularly the genus Nitzschia. Bain et al. (1977) reported a 300-fold increase in Nitzschia numbers from the 1st to the 19th of June in Wellington Channel, N.W.T. Pennate diatoms decrease in number after the June-July peak, and during most years there is a rapid increase of centric diatoms, particularly Chaetoceros, during July with a peak in mid-August (Bursa 1961; Bain et al. 1977). In 1976, 1977, and 1978 the major genera of diatoms in the central and western Beaufort Sea were Chaetoceros, Thalassiosira, and Nitzschia (Horner 1980). At Igloolik (69°N in the Canadian Arctic) Bursa (1961) found that the centric diatoms peaked approximately 1 month after the pennates. There is a major decrease in diatom numbers and production in late August-September as light decreases, nutrients are depleted, and grazers reach maximum numbers. This decline continues through October until the winter minimum is reached in about November. During late summer-fall, as diatom numbers decrease, other groups are numerous. Flagellates reach their annual maximum in late July-August, ciliates from late July-September, and dinoflagellates in August-September. Flagellates are the most numerous group through the winter (Bursa 1961; English and Horner 1977). In general, diatoms make up over 90% of the phytoplankton during summer, particularly in areas of high productivity. Flagellates predominate off shore where nutrient levels are low and in surface waters where light intensity is greatest (Hsiao 1976, English and Horner 1977).

The timing and intensity of phytoplankton blooms vary annually depending on a variety of factors such as ice conditions, weather patterns, and nutrient availability. Bursa (1963) reported that development of the phytoplankton bloom in leads was up to 2 months ahead of that in completely ice-covered areas and suggested that the persistence of ice may delay the spring bloom 1-2 weeks. English and Horner (1977) found that phytoplankton assimilation rates were consistently lower in water under snow-covered ice than under melt ponds on the ice or in leads. In 1975, the most severe ice year on record since 1953 (Brower et al. 1977), Horner (1978) reported a September phytoplankton bloom with the characteristics of the spring bloom. Pennates were the most numerous diatoms and nutrients were still high a full 2 months after the "usual" time for the pennate bloom. This suggested that the centric bloom had not yet occurred and, furthermore, that it probably did not occur before winter conditions set in. The data of Hsiao et al. (1977) from the Mackenzie Delta area in August indicated that production at ice-covered stations was about 65% of that in open water. Horner (1978) estimated that total annual production in 1976, which she termed a "heavy ice year," was about 64% of production in 1977, a relatively light ice year.

Nutrient availability may vary substantially on an annual basis, although this has not been quantified in the Beaufort Sea. Hufford (1974) suggested that upwelling occurs in the central Beaufort, but Mountain (1974) was quite sure that it did not occur every year. Since upwelling is often caused by wind acting across open water, it may occur infrequently or not at all in heavy ice years or in geographic areas where ice is especially persistent. Years of unusually low river runoff may also substantially reduce nutrient input.

Estimates of total annual primary production in our study area are difficult to make and are imprecise at best. Many of the estimates that have been made are based on data from the western Beaufort Sea, between

Prudhoe Bay and Point Barrow. Virtually all samples have been collected in August-September, very probably after the peak of productivity.

Estimates of annual primary production for the Alaskan sector of the Beaufort Sea range from 2 to 10-15 g C/m^2/yr (Table 1). In the Canadian sector of the Beaufort, estimates are considerably greater, ranging from about 18 g C/m^2/yr at offshore stations to as much as 96 g C/m^2/yr near shore. Comparable values for other locations in the Canadian Arctic range from 9 g C/m^2/yr at Alert, N.W.T., to 42 g C/m^2/yr in Frobisher Bay, N.W.T. (Davis et al. 1980). Horner's (1981) data indicate that, in the years she sampled, productivity and standing stock were usually higher, often substantially so, east of Prudhoe Bay, particularly east of 147°W, than between Prudhoe Bay and Barrow. In 1977 highest integrated productivity was at a station in 28 m of water off Demarcation Bay.

Based on the estimates of Alexander (1974) and Horner (1981) for phytoplankton productivity and Alexander (1974) and Schell (1980) for ice algae, the estimated total annual primary production in the study area (50,000 km^2) would be 2-10 X 10^5 metric tons (t) C/yr. If estimates from the Canadian Beaufort are used, total production would range from 10-26 X 10^5 t C/yr. It is probably reasonable to assume that annual production is at least 2 X 10^5 t C/yr and possibly as great as 26 X 10^5 t C/yr, or 4-52 t C/km^2/yr. This compares favorably to a similar estimate by Davis et al. (1980) for the Canadian Arctic of 41 t C/km^2/yr. Using a Carbon:wet weight conversion factor of 0.058 (Sheldon et al. 1977), our estimates translate to 3-44 million metric tons of phytoplankton per year. Since the proportion of diatoms in relation to other non-silicified groups in a sample greatly affects the Carbon:wet weight ratio, the use of 0.058 as a conversion factor provides only an approximation of the actual biomass.

Estimates such as those in the previous paragraph are useful for making gross generalizations about the total amount of food available to secondary consumers in the Beaufort Sea. It is important to remember, however, that these numbers are averages for a broad geographic area over a wide time frame. The entire process of integrating and averaging values removes the local, small-scale patchiness which is so important to consumers. As Brodie et al. (1978) pointed out, although average estimates of prey density may fit satisfactorily into generalized food webs, they may not be at all satisfactory in explaining specific predator-prey relationships. Thus, in our study area local differences in phytoplankton productivity are probably far more important to copepods, and thus to bowhead whales, than estimates of total tons of carbon per square kilometer. Although the Alaskan sector of the Beaufort Sea is apparently a relatively low productivity area in comparison with the Canadian Arctic, it may be very productive in localized areas such as the region around and east of Barter Island. In 1977 integrated carbon values were 10-20 times greater off Demarcation Bay than they were at most other Beaufort Sea stations (Horner 1981). Herbivorous zooplankton may be correspondingly more abundant there.

Table 1. Estimates of total annual phytoplankton productivity in the southern Beaufort Sea.

Source	Location	mg C/m^2/hr	g C/m^2/yr
Alexander 1974	Central Beaufort - outside barrier islands	7	10-15
Horner 1981	Western Beaufort - 1976	4-150	9
	Central and western Beaufort - 1977	9-170	14
	Central and western Beaufort - 1978	1-32	2
Hsiao 1976	Mackenzie R. Delta - inshore - 1975	45-49 ($\bar{x}$ 47)	96[1]
	Mackenzie R. Delta - offshore - 1975	4-18 ($\bar{x}$ 9)	18[1]
Hsiao et al. 1977	Off Mackenzie R. Delta - ice covered	15	31[1]
	Off Mackenzie R. Delta - open water	23	47[1]

[1] Calculated from mg C/m^2/hr estimates, assuming 30 days/month and 24 hrs daylight in June and July, 20 hrs in August.

C. Secondary Production

Herbivorous zooplankters such as copepods and euphausiids convert plant tissue into animal tissue which can then be utilized by other consumers. The efficiency of that conversion is difficult to quantify but has been estimated at about 15-20% for temperate oceans (Mullen 1969, cited in Davis et al. 1980). Raymont (1963) suggested that 25% is probably the upper limit for gross ecological efficiency in natural communities. Gulland (1974), in discussing the abundance of whales in relation to productivity, assumed a 10% transfer efficiency from phytoplankton to zooplankton. In the Arctic, net energy transfer from phytoplankton to consumers may be somewhat less than in temperate waters since animal life cycles are longer and more energy is required for maintenance activities over the extended life span. However, in northern waters maintenance requirements and growth efficiency are not constant year-round; growth rates increase during summer when phytoplankton productivity is high and decrease during winter when little food is available.

Measured assimilation efficiencies (proportion of ingested food which is digested) range from 40 to 90% in copepods and euphausiids (Raymont 1963; Lasker 1966; Pechen-Finenko 1977; Vyshkvartzeva 1977). Of the assimilated proportion, most is used for respiration and the remainder for growth and reproduction. Clutter and Theilacker (1971) estimated that 19-29% of the calories ingested by *Metamysidopsis* over its life span are available for transfer to the rest of the trophic web, with the remainder lost to maintenance activities. For *Euphausia pacifica*, Lasker (1966) suggested that a somewhat higher proportion (32%, including eggs, molts, and growth, with a range of 11-74%) was available for transfer. In field studies he found that approximately 9% of assimilated calories went to growth, 15% to molts, 9% to eggs, and 66% to respiration. During periods of rapid growth, growth efficiency was as high as 30%, while during slow growth periods it was as low as 6%. Raymont (1963) suggested that growth efficiency in copepods also varies greatly on a seasonal basis.

There are many groups of animals which are not of direct importance to fishes, birds, and marine mammals but which may greatly affect the composition and abundance of both phytoplankton and zooplankton. Among those groups in the arctic are the herbivorous larvaceans (*Oikopleura* and *Fritillaria*) and pteropods (*Limacina*), and the predominantly carnivorous medusae (*Aglantha*, *Aeginopsis*, *Rathhea*, *Obelia*, and *Cyanea*), chaetognaths (*Sagitta*), and ctenophores (*Beroe*) (Grainger 1959, 1962, 1975). In areas where medusae, ctenophores, or hydrozoans are abundant they may greatly reduce the standing stock of copepods (Raymont 1963; Huntley and Hobson 1978).

The availability of zooplankton to consumers is frequently discussed in terms of productivity of prey populations. From a practical standpoint, however, it is high standing stock, rather than productivity, that enables animals such as whales to successfully feed (Gulland 1974). In the Arctic, individuals grow relatively slowly and generation times are two to several times longer than they are in warmer southern waters (Dunbar 1957; Grainger 1965; Berkes 1976). Consequently, productivity may be relatively low but standing stock quite high since it represents several years of production. Furthermore, since many consumers, for example seabirds and bowheads, are migratory and spend only summer in the Beaufort Sea, exploitation of prey populations by those species is limited to a few months of the year.

The actual caloric value of prey is obviously of great importance to consumer species. Caloric values of major prey species are discussed in Section VII and summarized in Table 2. In comparing the differing prey, it is apparent that caloric values of all groups are quite similar. The exception is Calanus copepods, for which values are about 25-35% higher. Several sources confirm that Calanus copepods are higher in calories than other copepods and other groups (Laurence 1966; Cummins and Wuycheck 1971). This is probably due to the substantial lipid reserves (15-40% of total body weight) which are accumulated in summer and fall (Brodskii 1950; Vyshkvartzeva 1977). Caloric value of those lipids is about 9,500 cal/g (Laurence 1976). The importance of lipids in accumulation of whale blubber has been discussed by Ackman et al. (1975) and Brodie (1975).

Although distributional records for zooplankton species in the Beaufort Sea are quite good, data on the standing stocks of important prey species are largely unavailable. Most extant zooplankton data pertinent to our study area were collected on a series of icebreaker cruises during August-September 1975-79 (English and Horner 1977; Horner 1980; Horner 1981). Those data do not include biomass estimates but are presented instead as number of individuals/1,000 m^3. Numbers are averaged over the entire water column and therefore do not show differential depth distribution of species.

Horner (1981) found Calanus glacialis, C. hyperboreus, and Metridia longa to be the most abundant copepods in the study area. In general, copepods comprised a greater proportion of the zooplankton east of Prudhoe Bay than to the west, and C. hyperboreus and M. longa were more abundant than C. glacialis in that region. Metridia was most abundant in deep water.

Hyperiid amphipods and euphausiids are not adequately sampled by plankton nets. Nonetheless, hyperiids were caught at 75% of all stations in all years except 1976 (Horner 1981). The greatest density reported was off Harrison Bay in 1977 when $8/m^3$ were caught. Horner (1981) caught Thysanoessa euphausiids in 54% of all samples. Thysanoessa raschii was most abundant, with a maximum reported density of $0.5/m^3$, off Demarcation Point in 1977. Euphausiids were generally most abundant along the 20-m contour between Demarcation Point and Beaufort Lagoon, along the 40-m contour off Camden Bay, and at the 200-m contour off Barrow. It may be significant that the area where euphausiid numbers were greatest--Demarcation Point to Beaufort Lagoon--is an area where

Table 2. Caloric values of major prey of ringed seals, bowhead whales, and arctic cod in the Beaufort Sea.

Prey	Cal/g Wet Weight	Cal/g Dry Weight	Cal/g Ash-free Dry Weight	Source
Copepod	--	5,252	5,626	Laurence 1976
Calanus sp.	--	6,425	6,835	Laurence 1976
C. hyperboreus	--	--	7,432	Cummins and Wuycheck 1971
Pseudocalanus sp.	--	5,071	5,542	Laurence 1976
Euphausiid				
Thysanoessa sp.	1,173-1,204	--	5,414-5,554	Nishiyama 1977
T. raschii	--	4,950	5,861	Nishiyama 1977
Hyperiid Amphipod				
Parathemisto libellula	652	3,415	4,458	Nishiyama 1977
			6,300	Griffiths and Dillinger 1981
Mysid				
Mysis litoralis	--	--	5,470	Griffiths and Dillinger 1981

bowheads are thought to feed on their fall migration. Euphausiids occurred in stomachs of bowheads taken at Kaktovik in 1979 (Lowry and Burns 1980) and ringed seals collected off Beaufort Lagoon in 1980 (see Section V).

We collected zooplankton samples during our September 1980 field program in order to gather more information on distribution and abundance of zooplankton species, particularly copepods, which are foods of arctic cod. Since bowheads also eat copepods, our samples yielded some information about the distribution and relative abundance of potential bowhead foods. It was our original intention to also sample nektonic species (hyperiid amphipods and euphausiids), but since our alternate plankton sampling device did not work adequately we were unable to do so. Thus, we are unable to comment on the distribution of the nektonic groups, except as indicated by the stomach contents of ringed seals (see Section V).

Plankton tows were made at all locations where otter trawls were done for direct comparison to arctic cod stomach contents (see Section V). Tows were also made where bowhead whales were sighted (W1-W3) and at 5-m depth intervals along four onshore-offshore transects (Figure 4 and Appendix I). Three of those transects (Stations A-I) were conducted off the mouth of Beaufort Lagoon on 10, 14, and 17 September. The fourth (Stations J-M) was made off Icy Reef on 12 September. During the week preceding the 10 September transect the weather was good, with light and variable winds. Stormy weather and 20-30 knot winds preceded transects conducted on 14 and 17 September.

Only four species (or species groups) of copepods were recurrently present in our samples: Pseudocalanus sp., Calanus hyperboreus, C. glacialis, and Derjuginia tolli (Table 3). Metridia longa, which Horner (1981) listed as one of the three most common copepod species, was not common in our samples. Along all transects Pseudocalanus was the most abundant species. Average densities of particular species on the four transects varied by factors of up to 400. Abundance of the two Calanus species was less variable than Derjuginia or Pseudocalanus.

Calanus hyperboreus (stage III and larger) were absent from surface waters on all days and at all depths except at the shallowest (5-m) stations where densities were 1-2/m^3. They were most abundant near the bottom at stations where water depth was 20 m or more. Densities were never high, averaging 1-2/m^3 for all stations combined and reaching a maximum of 30/m^3 at 10-15 m depth at Station F (30 m water depth) on 14 September. There were no substantial differences in densities between transects off Icy Reef and Beaufort Lagoon.

Calanus glacialis were somewhat more abundant than C. hyperboreus, averaging about 10/m^3 for all stations combined and reaching a maximum density of 70/m at 10-15 m depth at Station F on 14 September. They were usually more abundant near the bottom than near the surface, and at stations where water depth was 20 m or more. They were markedly more abundant on 14 September, when the average density for all stations was 24/m^3, than on 10 September (4/m^3) and 17 September (6/m^3).

Table 3. Average abundance (number individuals/m^3 in entire water column) of copepods along Transects 1-3 off Beaufort Lagoon (Stations A-I) and Transect 4 off Icy Reef (Stations J-M).

	Water Depth (m)								
Copepod Species	5	10	15	20	25	30	35	40	45
Calanus hyperboreus									
Transect 1	2	0	2	<1	<1	<1	<1	<1	<1
Transect 2	1	2	1	<1	3	5			
Transect 3	1	<1	<1	<1	<1	<1			
Transect 4	0	1	<1	10					
Calanus glacialis									
Transect 1	3	0	0	<1	1	4	7	5	16
Transect 2	27	38	15	19	26	21			
Transect 3	1	<1	<1	7	18	9			
Transect 4	0	2	<1	3					
Pseudocalanus sp.									
Transect 1	42	4	4	73	117	3	<1	4	8
Transect 2	5,909	537	13	12	8	4			
Transect 3	889	1,722	517	20	7	4			
Transect 4	78	304	10	12					
Derjuginia tolli									
Transect 1	0	1	2	<1	255	25	2	2	0
Transect 2	7	<1	<1	<1	<1	<1			
Transect 3	1	<1	4	<1	<1	<1			
Transect 4	0	<1	2	10					

Derjuginia tolli were very abundant only on the 10 September transect off Beaufort Lagoon. They were extremely numerous at Station E (25 m water depth) near the bottom (Figure 5). Average density for the entire water column was $225/m^3$ and in the bottom 5 m of water reached $1,277/m^3$. Distribution was apparently quite patchy, since on the same day samples at Stations D and F contained relatively few individuals ($<1/m^3$ and $25/m^3$). On the other three transects, densities were low, usually less than $1/m^3$, with a maximum of $43/m^3$ at Station C on 17 September.

Pseudocalanus was the most abundant copepod species on all transects. They were least numerous off Icy Reef ($10-303/m^3$), with maximum densities there occurring at the 5- and 10-m stations (J and K). On two of the three Beaufort Lagoon transects (14 and 17 September), maximum numbers of Pseudocalanus were also found at the 5-m ($5,909/m^3$) and 10-m ($1,722/m^3$) stations (A and B). On the 14th most individuals were near the bottom, whereas on the 17th they were near the surface. On 10 September, before the period of stormy weather, distribution was quite different (Figure 5). Very few Pseudocalanus were caught at the 5-m and 10-m stations. Maximum densities were found at Stations D (20 m) and E (25 m), and vertical layering was pronounced. Almost all individuals were within 5 m of the bottom where the number/m^3 was four to five times higher than the average density for the water column.

Estimates of copepod biomass in the western and central Beaufort Sea are not available in the published literature. In a recent study in Amundsen Gulf, Griffiths (1981) reported an average copepod biomass (for the entire water column) in areas where whales were seen of $0.0999\ g/m^3$. We measured and weighed representative specimens of the major copepod species caught in our samples (Table 4). Based on those data we calculated a similar average water column biomass for copepods of $0.1005\ g/m^3$ in the area where the first whale was sighted. In the dense layer of copepods near the bottom, the calculated copepod biomass was $0.8390\ g/m^3$, or eight times that of the water column as a whole. Considering the variation in densities among replicate samples, where the maximum number of copepods was twice the average number, copepod biomass could be at least as high as $1.3\ g/m^3$ in the dense bottom layer.

As a result of our zooplankton sampling, two important facets of copepod distribution were evident:

1. Copepods are not distributed uniformly throughout the water column. Traditional data presented as number/m^3 averaged for the entire water column may underestimate densities in layers by a factor of as much as 10. We observed dense layers of copepods near the bottom, particularly in water depths of 20-30 m.

2. Copepod distribution and abundance, as well as being patchy on a given day, are highly variable from one day to the next. Daily fluctuations we observed involved changes in abundance of three orders of magnitude.

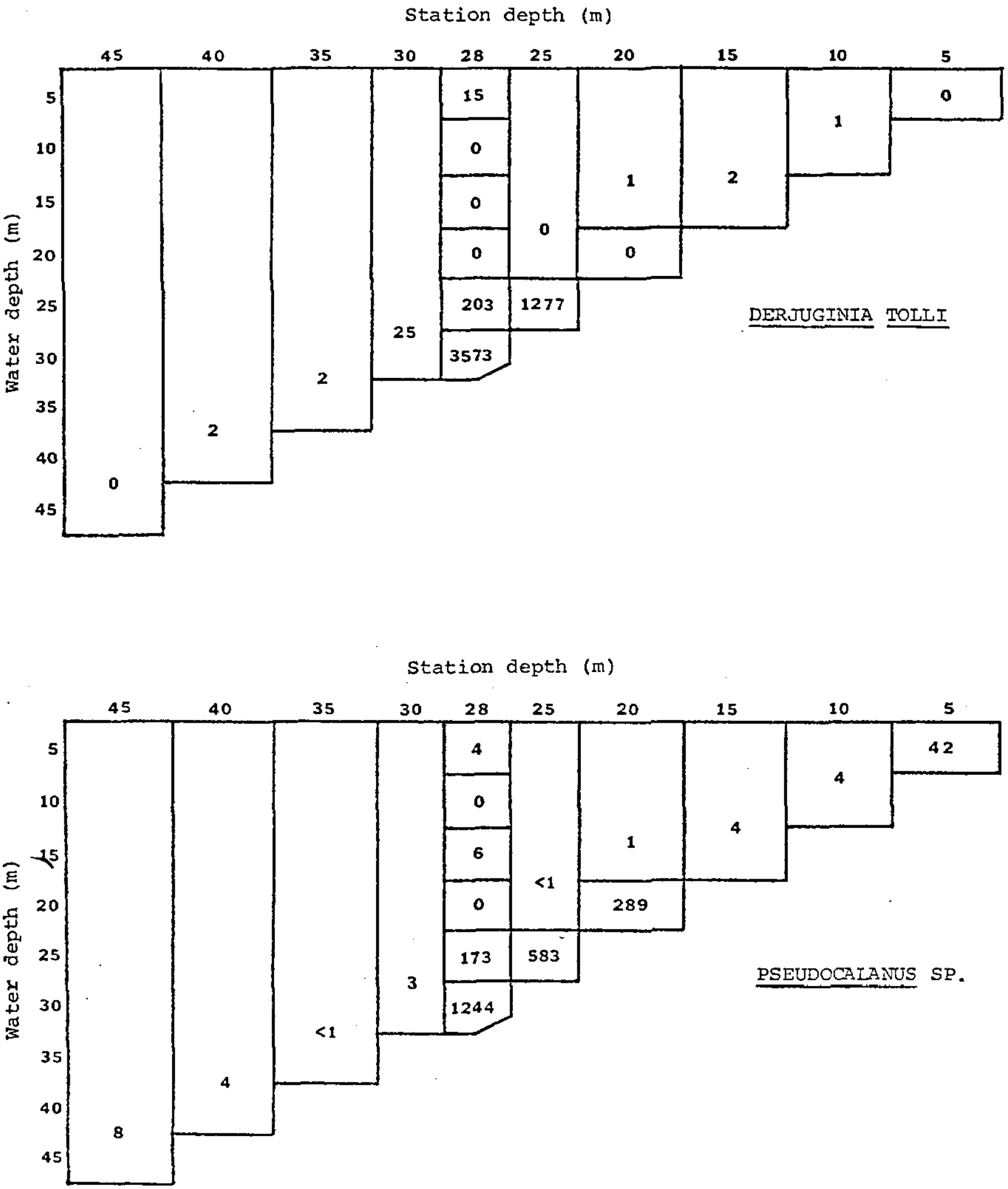


Figure 5. Vertical distribution of copepods (# individuals/cubic meter) along transect 1 off Beaufort Lagoon, 10 September 1980. Tows at the 28m station were done the previous day in the immediate vicinity of the first bowhead whale sighting.

Table 4. Average length, width, and weight of major copepod species. Length measurements are of the prosome or cephalothorax as described in Pearre (1980).

Species	Length (mm) n=10	Width (mm) n=10	Weight (mg) n=20
Calanus glacialis			
stage III	$\bar{x}$ = 1.96 (1.72-2.28)	$\bar{x}$ = 0.55 (0.48-0.72)	0.5
stage IV-adult	$\bar{x}$ = 2.74 (2.40-3.32)	$\bar{x}$ = 0.83 (0.64-1.04)	1.8
Pseudocalanus sp.	$\bar{x}$ = 1.32 (1.12-1.56)	$\bar{x}$ = 0.55 (0.48-0.64)	0.1
Derjuginia tolli	$\bar{x}$ = 1.64 (1.40-1.80)	$\bar{x}$ = 0.60 (0.52-0.72)	0.2
Calanus hyperboreus[1]			
stage IV			1.0
stage V			4.0
adult			9.0

[1] Taken from Bain et al. (1977)

Bowheads were sighted off Beaufort Lagoon on 3 days: 9, 17, and 18 September. On only the first of those days were copepods extremely abundant (Table 5). Both Derjuginia and Pseudocalanus were strongly layered. There were 1,244 Pseudocalanus/m^3 and 3,573 Derjuginia/m^3 within 3 m of the bottom, whereas average densities for the water column were 165/m^3 and 420/m^3, or 12-13% the density of the bottom layer. The first whale sighting and Transect 1 occurred on consecutive days. Both were preceded by a period of calm, stable weather which presumably did not cause unusual mixing of the water column or disruption of water column stability. Plankton samples from similar depths on the 2 days were similar; Derjuginia and Pseudocalanus were very abundant near the bottom at water depths of 20-30 m. Both species were two to three times more abundant in the immediate vicinity of the whale sighting than they were the following day, suggesting that the whale, and our plankton net, were sampling a very concentrated "patch." The three replicate bottom-to-surface tows made near the first whale provide further evidence for patchiness. Both species of copepods were four to five times more abundant in the last replicate than in the first. This whale appeared to be feeding. We observed it make four dives of 16-20 minutes each, surfacing after each in the same general location.

The whale sighted on 17 September may also have been feeding. It dove and surfaced several times in the same area, and while it could be observed it swam in a variety of directions. Unlike the previous sighting, this whale did not show its flukes when it dove; two dives were timed at 12 and 13 minutes. Copepods were not particularly abundant in tows taken near this whale (Table 5). We speculate that the whale may have been feeding on euphausiids since euphausiids occurred in ringed seals (BLP-15-80 and BLP-16-80) collected very near where the whale was sighted.

The whale sighted on 18 September was seen only briefly as it dove and was not seen again. Copepods were not abundant in tows made near this whale (Table 5). The sighting was near the location where a whale was sighted and seals were collected on the previous day. This whale may have been eating euphausiids or perhaps was not feeding at the time it was sighted.

IV. Population and Biomass of Major Vertebrate Consumers

A. Marine Mammals

At least nine species of mammals regularly occur in the Beaufort Sea during some part of most years (Eley and Lowry 1978). Seasonal abundance and primary prey of those species are summarized in Table 6. Sea ice distribution and characteristics seasonally limit the distribution of all species except ringed seals and polar bears which are the only marine mammal species common in the area throughout the year. Bowhead and belukha whales are common during parts of the summer and early fall. Three species, walrus, bearded seals, and grey whales, are primarily benthic feeders (Frost and Lowry 1981; Lowry and Frost 1981b), although

Table 5. Average abundance (number individuals/m^3 in entire water column) of copepods near whale sightings.

	Whale 1 9 September 28.0 m	Whale 2 17 September 23.0 m	Whale 3 18 September 20.5 m
Calanus hyperboreus	0	<1	<1
Calanus glacialis	0	13	7
Pseudocalanus spp.	165	20	36
Derjuginia tolli	420	9	<1

Table 6. Seasonal abundance and primary foods of mammals which regularly occur in the Alaskan Beaufort Sea.

Common Name	Scientific Name	Abundance Winter/ Spring	 Summer/ Fall	Primary Foods
Bowhead whale	*Balaena mysticetus*	absent	common	small - medium-sized zooplankton and nekton
Grey whale	*Eschrichtius robustus*	absent	rare	epibenthos
Belukha whale	*Delphinapterus leucas*	absent	common	fishes, crustaceans, and cephalopods
Bearded seal	*Erignathus barbatus*	uncommon	uncommon	epibenthos and infauna
Ringed seal	*Phoca hispida*	common	common	fishes, medium-sized nekton, epibenthos
Spotted seal	*Phoca largha*	absent	uncommon	fishes, crustaceans, and cephalopods
Walrus	*Odobenus rosmarus*	absent	uncommon	infauna and epibenthos
Polar bear	*Ursus maritimus*	common	common	ringed seals and carrion
Arctic fox	*Alopex lagopus*	common	rare	carrion and ringed seal pups

bearded seals at times consume arctic cod, perhaps when in areas too deep for efficient benthic feeding (Frost and Lowry, unpubl.). Although some bearded seals occur in the Beaufort Sea throughout the year, the center of the range of all three bottom feeding species is the Bering-Chukchi platform. Polar bears and arctic foxes while on the sea ice feed primarily on ringed seals and carrion from dead marine mammals (Stirling and Smith 1975). Spotted seals feed on fishes, crustaceans, and cephalopods (Bukhtiyarov et al., in prep.) and are therefore trophically connected to the pelagic food web. However, with the exception of a hauling area east of Barrow on Oarlock Island which is regularly used by 100 to 200 spotted seals, they are not common along the Beaufort Sea coast (Frost, Lowry, and Burns, unpubl. observations). Three species, belukha and bowhead whales, and ringed seals, are at least seasonally abundant and are directly linked to the pelagic food web. Populations of each are discussed separately in the following sections.

Bowhead whales

General characteristics of the annual migration pattern of bowhead whales are quite well known (Sergeant and Hoek 1974; Braham and Krogman 1977; Fraker et al. 1978). Recent studies (Braham et al. 1979; Ljungblad et al. 1980, 1981) have greatly increased our knowledge of seasonal distribution patterns.

Recent sightings of bowheads during winter and early spring are quite limited. We made one sighting of a bowhead on 19 April 1976 in 4-5 octas of ice, near the southern edge of the ice front 150 km west of the Pribilof Islands. The whale was swimming slowly in a large polynya just south of the edge of consolidated 8-octa pack ice.

Braham et al. (1979) reported numerous sightings of bowheads in the ice front in March-April 1979. Whales were seen in the northwestern sector of the Bering Sea, generally between St. Matthew and St. Lawrence Islands and the Gulf of Anadyr, in close association with ice. None were seen in open water, even large polynyi. Other reported sightings during April have been in the same general area (Braham and Krogman 1977). All available information indicates a close association with the ice front from at least January through early April. Characteristics of the front provide an area where whales can reside among the ice while maintaining regular access to air between the generally dispersed and mobile floes. Since the geographical distribution of the ice front zone varies seasonally as well as from year to year (Burns et al. 1980), the location of bowhead wintering areas would be expected to show similar variations.

The northward migration of bowheads begins in early spring and has been well documented since the whales commonly pass near Eskimo settlements where they are hunted (Marquette 1977, Durham 1979). Since the migration precedes the major period of ice degradation, the route taken and the timing of arrival at various locations depend on features of the ice pack, particularly recurrent and persistent leads and polynyi. Whales generally travel through the shore lead which extends north from Bering Strait to Point Hope then northeastward near the Alaskan coast to Point Barrow (Marquette 1977, Shapiro and Burns 1975). Whales pass Barrow from late April to at least early June with a usual peak in numbers in early to mid-May (Durham 1979). At the time bowheads pass Barrow, the nearshore areas of the Beaufort Sea are covered with continuous, generally unbroken sea ice. Satellite photos of spring sea ice conditions show regularly occurring leads running west to east from north of Point Barrow to the northwestern portion of Banks Island. Speculations that bowheads migrated through these offshore leads (Braham and Krogman 1977) have been confirmed by extensive survey efforts (Braham et al. 1980b; Ljungblad et al. 1981). The earliest sightings of bowheads near Banks Island have occurred in May (Braham et al. 1980b), with later sightings in the polynya which forms at the mouth of Amundsen Gulf between Cape Bathhurst and Banks Island (Fraker et al. 1978).

Recent and historical summer sightings of bowheads in the western Canadian Arctic have been summarized by Fraker et al. (1978) and Fraker and Bockstoce (1980). With very few exceptions, sightings in July and August were in the southeastern Beaufort Sea and outer Amundsen Gulf west of 122°W longitude. The majority of recent sightings has been within 50 km of the mainland coast between Cape Parry and the Alaska-Yukon border in water less than 50 m deep. Bowheads were numerous along and northwest of the Tuktoyaktuk Peninsula during August and September 1980 (Hobbs, pers. comm.). They were not regularly reported from other areas in spite of extensive survey efforts.

The number of bowheads summering in the Alaskan portion of the Beaufort Sea is poorly known. A single bowhead was sighted on 8 August 1976 about 1 km offshore from the barrier islands just east of Point Barrow (L. Lowry, unpubl. observation). No bowheads were seen by us during icebreaker and small boat work in the Alaskan Beaufort Sea during 17 August-3 September 1976, 9 August-6 September 1977, 13-22 August 1978, and 20 August-8 September 1980. Ljungblad et al. (1981) saw no live bowheads in the central Alaskan Beaufort during aerial surveys conducted during July and August 1980.

Factors influencing the westward migration of bowheads from the eastern Beaufort Sea are poorly understood, but formation of sea ice is undoubtedly important. Sightings of whales in recent years were most common off the Mackenzie Delta and Tuktoyaktuk Peninsula in August and west of there along the Yukon Territory coast in September (Fraker and Bockstoce 1980). Ljungblad et al. (1980) reported sightings of groups of bowheads along the Alaskan coast east of Barter Island near Demarcation Bay on 24 and 26 September 1979. In that area in 1980 we sighted a bowhead on 9 September and heard blows that were likely made by bowheads on the previous day. Groups of bowheads have been sighted near and to the east of Barrow on 21 September 1972 (Fraker et al. 1978), 12-22 September 1974, and 16-26 September 1976 (Braham and Krogman 1977). During August through October 1979, Ljungblad et al. (1980) made 134 sightings of bowheads between Point Barrow and Demarcation Bay, primarily along the

18-m depth contour. Behavior of whales seen between Demarcation Bay and Harrison Bay suggested possible feeding, while west of there whales were predominantly swimming westward. In 1980, probably due to an early and rapid freeze-up, fewer sightings were made during the fall migration in the Alaskan Beaufort and, with the exception of possible feeding near Demarcation Bay, most whales were swimming westward (Ljungblad et al., 1981). The last sighting of a bowhead in the Alaskan Beaufort Sea in 1980 occurred on 9 October 1980 (Ljungblad et al. 1981), while in 1977, a year of very late freeze-up, a bowhead was seen near Barrow on 14 November (Lowry and Burns 1980). From 14-19 October 1979, Ljungblad et al. (1980) saw numerous bowheads in the area between Flaxman Island and Harrison Bay, mostly near the 18-m depth contour.

Although historical whaling records indicate catches of bowhead whales in the northern Chukchi Sea during July and August (Sergeant and Hoek 1974), no whales were seen in the Chukchi Sea during shipboard work there from 22-28 August 1976 and 31 July-7 August 1977 (Frost and Burns, unpubl. observations), and during June and July 1978 (Dahlheim et al. 1980). However, during a joint Soviet-American research cruise in September and October 1980, many bowheads were seen nearshore along the Siberian coast northwest of Cape Vankarem in 17-23 m water depth (K. Coyle, pers. comm.). An abundance of bowheads in the Chukchi Sea in September and October is confirmed by commercial whaling records (Sergeant and Hoek 1974; Dahlheim et al. 1980).

Observations of bowhead whales during the months of November through February are virtually nonexistent. Presumably the whales move progressively southward with the advancing sea ice, passing through Bering Strait probably during late November.

The following general conclusions can be drawn from the available data and the preceding discussion:

1. Wintering areas (December-March) occur in the Bering Sea, generally in the central and western portions of the ice front. The geographical location of these areas varies with the position of the front.

2. Spring migration (April-June) occurs through nearshore leads of the Chukchi Sea. Lead systems utilized in the Beaufort Sea are farther off shore, generally north of the continental shelf.

3. Bowheads appear in the Canadian Beaufort Sea off Banks Island in mid-May although some whales are still passing Point Barrow at this time. Whales move south along Banks Island and are commonly seen in the polynya in western Amundsen Gulf by late May.

4. Most bowheads spend June through early September feeding in Canadian waters. The distribution of sightings shows a westward trend through the summer, with sightings common in western Amundsen Gulf in July, off the Mackenzie Delta and Tuktoyaktuk Peninsula in

August, and off the Yukon coast in September. Bowheads are uncommon in the Alaskan Beaufort Sea and the Chukchi Sea in July and August. It seems reasonable to conclude that in most years virtually the entire bowhead population feeds in the Canadian Beaufort Sea and Amundsen Gulf from about 1 June-15 September, approximately 105 days.

5. The bowhead population migrates westward along the continental shelf of the Alaskan Beaufort Sea during September and October. The migration is greatly affected by freezeup but in most years extends for about a month beginning in mid-September. Feeding occurs in the Alaskan Beaufort during this period (see Section V). Since bowheads also appear in the Chukchi Sea in early October, the average bowhead may spend only about 25 days foraging in the Alaskan Beaufort Sea during most years.

6. Bowheads are common in the Chukchi Sea during October and presumably feed in that area. The duration of this early fall feeding is poorly known but it may extend for as much as 30 days.

The best estimate of present bowhead whale abundance is based on counts of animals made near Point Barrow during the spring northward migration. The counts have yielded a mean population estimate of 2,264 bowheads (Braham et al. 1979). Based on analysis of satellite photos and results of aerial surveys, it appears that all animals passing Point Barrow head eastward to the Canadian Beaufort Sea. We will therefore consider that 2,264 bowheads feed in the Canadian Beaufort Sea, then migrate through and feed in the Alaskan Beaufort Sea. It should be noted that surveys conducted in the Alaskan and Canadian Beaufort (Hobbs, pers. comm.) have accounted for fewer than the total estimated number of whales, suggesting that some animals may summer on feeding grounds in the Chukchi Sea or elsewhere in the Canadian Arctic.

The size of an average bowhead whale is not known. Based on the average length of whales harvested by Eskimos in 1973-1977 (10.2 m, Marquette 1977) and the length-weight relationship for black right whales, <u>Balaena glacialis</u>, (weight (t) = 0.0132 X length (m)$^{3.06}$, Lockyer 1976), Draper et al. (1979) calculated that the average whale harvested weighed approximately 15.9 metric tons. Since the relationship between the size distribution of harvested whales and the actual size distribution of whales in the population is poorly known, no more refined estimate of average individual weight is possible. We therefore estimate the biomass of the bowhead population as approximately 36,000 metric tons.

<u>Belukha whales</u>

Many of the general features of distribution and movements of belukha whales are similar to those described for bowheads. Belukhas migrate along the Alaskan coast in spring, generally in association with bowheads. The belukha migration may begin slightly earlier than that of bowheads and they may use offshore lead systems with greater frequency (Braham and Krogman 1977). Belukhas are also thought to move eastward from Point

Barrow through offshore lead systems, arriving in the eastern Beaufort Sea in late May and early June (Fraker et al. 1978). They appear in the Mackenzie estuary in late June or early July. Many whales remain in the estuary until early to mid-August, while others occur in the eastern Beaufort and western Amundsen Gulf (Fraker et al. 1978). Few belukhas occur in the Alaskan Beaufort Sea during July and August. We saw belukhas only once during icebreaker and small boat work in that area from 17 August-3 September 1976, 9 August-6 September 1977, 13-22 August 1978, and 20 August-23 September 1980. That sighting occurred on 21 August 1978 and included 15-25 belukhas in 7-octa heavy ice about 27 km north of Prudhoe Bay (Frost, unpubl. observation). Belukha whales occurred near Barter Island in mid-August 1980 (Frost and Lowry, unpubl.). Harrison and Hall (1978) made four sightings of belukhas (35 individuals) while surveying 6,000 km of trackline in the western Beaufort Sea during July and August. Those sightings occurred about 100 km offshore in water depths of approximately 1,800 m.

Belukhas move westward through the Alaskan Beaufort Sea in the latter half of August and September. With the exception of occasional reports from Barter Island residents, the only confirmed fall sightings known to us of belukhas in nearshore waters of the Alaskan Beaufort are those of Johnson (1979), who sighted whales on 15 September 1977 and 23 September 1978 swimming westward close to the shore of Pingok and nearby Thetis Islands.

During September large groups of belukhas have several times been seen north of Point Barrow in pack ice (C. Ray, cited in Braham and Krogman 1977, ADF&G, unpubl.). These sightings have generally been in deep water beyond the continental shelf. During extensive surveys of the western Beaufort Sea during August-October 1979, Ljungblad et al. (1980) sighted belukha whales only once. That sighting of 15-20 animals occurred on 19 October, approximately 95 km north of Harrison Bay, in deep water off the continental shelf. The relative lack of sightings in nearshore waters of the Alaskan Beaufort strongly suggests that offshore westward migration is the usual pattern. Belukhas pass south through the Chukchi Sea into the Bering Sea in November and December. During winter months they occur in the Bering Sea ice wherever ice characteristics provide adequate access to open water (Seaman and Burns, in press).

Considering the above information, we will assume that belukhas summering in the Mackenzie estuary and eastern Beaufort Sea pass through the Alaskan Beaufort Sea during a period of about 30 days in September. They appear to usually remain in deep water near the continental slope.

Fraker et al. (1978) have summarized estimates of white whale abundance in the Mackenzie estuary. The maximum estimated number in 1976 was 5,500-6,000, while estimates for 1977 and 1978 were 5,500 and 6,600, respectively (Fraker 1978). We consider 6,000 as a reasonable estimate of the number of belukhas which summer in the Mackenzie estuary and migrate through the Beaufort Sea.

There are no direct observations of weights of belukha whales in the Beaufort Sea. Reported mean lengths of whales taken in the Mackenzie region are 4.1 and 4.3 m for males and 3.6 and 3.9 m for females (Sergeant and Brodie 1969, Fraker et al. 1978). Since most of the animals taken are adults (Fraker et al. 1978), these measurements are undoubtedly greater than the length of an average individual in the population. We will use 4.0 m and 3.5 m as the average length of male and female belukhas, respectively. Based on the length-weight relationship determined for belukhas in the St. Lawrence estuary (log weight (kg) = 2.605 X log length (cm) - 3.807; Sergeant and Brodie 1969), the average weight for males and females would be 940 and 660 kg. Assuming a 50:50 sex ratio, an average belukha would weigh about 800 kg; therefore, the total belukha biomass would comprise about 4,800 metric tons.

Ringed seals

Unlike bowhead and belukha whales, ringed seals are present in the Beaufort Sea throughout the year. Although they can and do occur in all sea ice types, the seasonal cycle of sea ice has a great effect on ringed seal distribution and regional abundance (Burns 1970; Burns et al. 1980; Frost and Lowry, in press b).

With the onset of winter freeze-up, movements of ringed seals which have ranged freely during the summer become increasingly restricted. It is generally considered that many seals which have summered in the Beaufort Sea move west and south with the advancing ice and disperse throughout the Chukchi and Bering Seas. Others remain in the Beaufort, probably concentrating in areas of abundant prey (Lowry et al. 1980; Frost and Lowry, in prep.). During periods of ice formation, seals make and maintain breathing holes in the ice, usually in areas which were previously open water or covered by thin ice (Smith et al. 1978). Ice movement which creates new leads and pressure ridges provides additional access to air. By February most pregnant females are in areas covered with shorefast ice, while males and subadults range more widely, making much use of transient leads and polynyi (Lowry, Frost, and Burns, unpubl. observations). Female seals enlarge their breathing holes and excavate lairs in the snow above (Smith et al. 1978). Pups are born and nursed in these lairs from late March through early June. Adult males, some of whom also excavate lairs, breed with the females mostly in May (Burns 1970; Frost and Lowry, in press b).

As the snow cover melts in late spring and early summer, birth and haul-out lairs collapse and warmer temperatures cause leads and holes to generally remain unfrozen. Increasing numbers of seals appear near holes and leads (Burns and Harbo 1972). During this period of molt, seals haul out for long periods of time and are easily observed (Finley 1979). The peak of haul-out activity varies somewhat with locality but generally occurs in mid-June (McLaren 1958; Burns and Harbo 1972; Finley 1979). Frequency of hauling out diminishes in July, and ringed seals are only rarely seen on the ice for the remainder of the year (Frost, Lowry, and Burns, unpubl.).

Distribution of ringed seals during summer months is more dynamic and less well understood. Seals spend virtually all of their time in the water feeding, and their distribution is therefore probably greatly influenced by that of their prey (Frost and Lowry, *in prep.*). During shipboard observations in the Beaufort Sea in August and September 1976-77, seals were very non-uniformly distributed, with high abundance areas off Prudhoe Bay and very low abundance elsewhere (Frost and Lowry, unpubl.). Ljungblad et al. (1980) also noted an abundance of pinnipeds in this same general area in mid-October 1979. During our work in the nearshore ice in August and September 1980, seals appeared much more uniformly distributed, at least off Harrison Bay and Beaufort Lagoon. Although most ringed seals are thought to remain in association with pack ice and ice remnants during summer, some at least occur in open water many miles from the ice (M. Goebel, pers. comm.; Lowry, unpubl.).

The estimation of numbers and residence times of ringed seals in the Alaskan Beaufort Sea is complicated by seasonal movements discussed above. Standard visual survey methods for numerical assessment are useful only during the molt period in June. Many factors complicate the design and execution of reliable surveys. The effects of seasonal and diurnal haulout patterns are well known (McLaren 1958; Burns and Harbo 1972; Finley 1979), as are relationships to sea ice conditions (Johnson et al. 1966; Smith 1975; Burns et al. 1980) and the influence of weather (Burns and Harbo 1972; Finley 1979). In regions where shorefast ice is adjoined by moving pack ice, spring densities of basking seals are much greater on the shorefast ice (e.g., McLaren 1958; Johnson et al. 1966; Smith 1975). Such conditions occur in the Chukchi Sea off Alaska (Burns and Harbo 1972; Burns et al. 1980). However, in the Beaufort Sea, ice conditions are much more stable, particularly during spring months. Shorefast ice is often very extensive and the motion of the large floes of the pack is comparatively slight (Shapiro and Barry 1978). We believe that the shorefast ice and much of the offshore pack of the Alaskan Beaufort are similar with respect to their physical suitability for ringed seal habitat. Data collected by Stirling et al. (1977), who flew extensive rigorous surveys in the southeastern Beaufort Sea and Amundsen Gulf, show no clear relationship between ringed seal abundance and water depth from 0 to over 1,000 m depth. Burns and Harbo (1972) surveyed ringed seals on the shorefast ice of the Alaskan Beaufort Sea. They tested the relationshi between ringed seal abundance and distance from shore and the edge of shorefast ice and found an indication that density increased with distance from shore, and no relationship between density and distance from the seaward edge of the fast ice.

Results of aerial surveys conducted by Burns and Harbo (1972) and Burns and Eley (1978) in the Alaskan Beaufort Sea and those of Stirling et al. (1977) along the adjacent Yukon coast (Table 7) show considerable variation both among sectors and years. Overall, the data suggest a decline in the number of seals the southeastern Beaufort in 1970-77. Surveys conducted by Burns and Harbo (1972) in 1970 and Burns and Eley (1978) in 1975 were comparable in intensity and coverage. However, those flown in 1976 and 1977 were more limited and the densities derived

Table 7. Ringed seal density estimates (number seals sighted/km^2) along various sectors of the Beaufort Sea coast.

Year	Barrow-Lonely[1]	Lonely-Oliktok[1]	Oliktok-Flaxman I.[1]	Flaxman I.-Barter I.[1]	Yukon Coast[2]	Average of Means
1970	0.68	0.32	0.41	0.73	--	0.54
1974	--	--	--	--	0.52	--
1975	0.84	0.42	0.30	0.54	0.21	0.46
1976	0.42	0.33	0.42	0.12	--	0.32
1977	0.30	0.15	0.21	0.36	--	0.26
Average of Means	0.56	0.30	0.34	0.44	0.36	

[1] Burns and Harbo 1972; Burns and Eley 1978

[2] Stirling et al. 1977

from them may therefore be more subject to variations caused by local conditions such as sea ice topography.

Combining the results of surveys conducted in all years in each sector suggests highest densities of seals west of Lonely and lowest densities between Lonely and Flaxman Island. The significance, if any, of this particular pattern cannot be assessed at present. The overall average observed density of ringed seals in the Beaufort Sea, derived from all survey years in all sectors including the Yukon coast, is 0.40 seals/km^2. Given the above discussion we feel this figure is generally applicable as an average observed density of ringed seals in the study area.

In order to estimate the total number of ringed seals in an area during the haul out, it is necessary to know what proportion of the population is counted during surveys. Smith (1973, 1975) considered that 50% of ringed seals were usually in the water at the times of his aerial counts. Detailed observations by Finley (1979) indicated that under ideal circumstances 70% or more of the seals in an area may be hauled out. Considering that not all surveys cover all areas during ideal conditions, we will assume that observed densities in the Beaufort Sea are 50% of actual densities. Actual overall density will therefore be taken as 0.80 seal/km^2, resulting in an estimate of 40,000 seals in the study area in winter.

Freeze-up in the Beaufort Sea is usually well underway by November. By that time ringed seals appear in large numbers at coastal locations in the Bering Sea (ADF&G, unpubl.). At breakup in many areas, a mass influx of seals has been seen in the latter part of June (Finley 1979). We will assume that the overall spring density derived above is applicable for the period 1 November-1 July. Although it has not been documented, an influx of seals into the Beaufort probably occurs in late June or early July. The overall magnitude of the summer increase in ringed seal abundance in the Beaufort Sea is unknown. Results of shipboard observations of swimming ringed seals are not readily expressed as densities. However, those observations show that in certain regions and years seals may be very abundant in limited areas and scarce elsewhere, while in other circumstances they are much more evenly distributed. Causes of these variations are thought to be related to food availability. For the basis of calculations we will assume that the number of ringed seals in the Alaskan Beaufort Sea doubles during summer to about 80,000 individuals, and those animals reside there from 1 July-30 October.

Ringed seals show annual fluctuations in weight and blubber thickness due to changes in levels of feeding (McLaren 1958; Johnson et al. 1966). In addition, weight at age varies greatly among individuals and areas (Frost and Lowry, in press b and unpubl.). Based on weights of 929 ringed seals taken in the Bering, Chukchi, and Beaufort Seas, the average weight of a seal in the population is about 34.3 kg (Frost, Lowry, and Burns, unpubl.). The estimated winter and summer ringed seal biomasses in the Alaskan Beaufort are therefore 1,372 t and 2,744 t, respectively.

B. Seabirds

Birds are virtually absent from the Alaskan Beaufort Sea during winter but are a common and conspicuous component of the summer fauna. Although the summer avifauna comprises many species, few are common in marine habitats of the Beaufort Sea (Watson and Divoky 1974; Schamel 1978). In addition, several of the most abundant species (e.g., oldsquaw (Clangula hymenalis) and eiders (Somateria sp.)) feed almost entirely in nearshore marine waters and lagoons on benthic and near-bottom organisms (Divoky 1978; Schamel 1978; Johnson and Richardson 1981).

Approximately 11 species (or species groups) of seabirds forage in marine waters of the Beaufort Sea on organisms connected to the pelagic food web (Table 8). Estimation of numbers of each species in marine waters is complicated by several factors. Most species are migrants, entering the area in June when open water areas form and leaving prior to freeze-up. Some individuals breed in coastal and barrier island areas and their feeding activities are somewhat restricted to the vicinity of the nest site. Nonbreeders and adults after fledging of young are free to move throughout the area. During migration large numbers of birds are seen at certain localities, but in many instances they are not feeding. Divoky (pers. comm.) provided us data on individual size of birds of each species as well as preliminary estimates of the number of individuals in the study area based on several years of observation and data collection. These population estimates and the average individual biomass values were used to estimate total biomass values for each species in the study area (Table 8).

For most species, estimated total biomasses were quite small due to either small population size (e.g., murres and guillemots) or small individual size (e.g., terns and phalaropes). Loons comprised approximately 63% of the estimated seabird biomass due to their abundance and large size. It should be noted that estimation of numbers of loons is difficult (Divoky, pers. comm.) and there are few data available on their foods in the study area.

Most seabirds arrive in the Beaufort Sea by early June. For breeding adults, nest building and courtship are primary initial activities. Those species which forage in marine waters become more abundant in such areas after fledging of young. Timing of migration west and south from the Beaufort Sea is affected by freezeup but generally occurs in September (Watson and Divoky 1974). For purposes of calculations we will assume that, with the exception of Ross' and ivory gulls, birds in the abundance indicated in Table 8 feed in the study area for an average of 90 days per year (about mid-June to mid-September). Ross' and ivory gulls are not known to breed in the Alaskan Beaufort Sea but migrate through the area in fall (Watson and Divoky 1974). We will consider the average residence times of these species to be about 30 days per year.

Table 8. Summary of abundance and biomass of marine birds in the Alaskan Beaufort Sea (from Divoky, pers. comm.).

Species	Estimated Number of Individuals	Average Individual Size (kg)	Estimated Total Biomass (t)
Black-legged kittiwake (*Rissa tridactyla*)	5,000	0.40	2.0
Glaucous gull (*Larus hyperboreus*)	7,000	1.20	8.4
Ivory gull (*Pagophila eburnea*)	1,000	0.40	0.4
Ross' gull (*Rhodostethia rosea*)	10,000	0.20	2.0
Sabine's gull (*Xema sabini*)	30,000	0.20	6.0
Arctic tern (*Sterna paradisaea*)	100,000	0.12	12.0
Jaegers (*Stercorarius* spp.)	30,000	0.50	15.0
Black guillemot (*Cepphus grylla*)	1,000	0.40	0.4
Thick-billed murre (*Uria lomvia*)	1,000	1.0	1.0
Loons (*Gavia* spp.)	50,000	2.0	100.0
Phalaropes (*Phalaropus fulicarius* and *Lobipes lobatus*)	200,000	0.06	12.0

C. Fishes

Studies of the fish fauna of the Alaskan Beaufort Sea have mostly dealt with nearshore and anadromous species, some of which are of local commercial or subsistence importance. Published studies of marine fishes (Frost et al. 1978) indicate approximately 19 species in marine waters less than 400 m deep (Table 9). Of those, only two, arctic cod and leatherfin lumpsucker, were found to feed predominantly on planktonic organisms, while all others fed mostly on benthos. Food habits data are not available for polar cod but it is likely that they feed on similar foods to arctic cod which are morphologically almost identical. Arctic cod was by far the most abundant species caught.

During field work conducted during August and September 1980, arctic cod were again the most abundant fish we caught, both in terms of number of individuals and biomass (Table 10). The only other commonly encountered fishes, sea snails (Family Liparidae) and sculpins (Family Cottidae), feed on benthic organisms (Frost et al. 1978; Frost and Lowry, unpubl.). Based on the above information, we feel that arctic cod is the only fish species which is regularly common in the study area and feeds to a large extent on planktonic animals. Plankton-eating fishes such as capelin (Mallotus villosus) and herring (Clupea harengus) do appear occasionally in the Beaufort (e.g., McAllister 1962), but their numbers and distribution are unknown and their occurrence seems irregular and infrequent.

General features of the biology of arctic cod are well known (e.g., Andriyashev 1954; Moskalenko 1964; Hognestad 1968; Ponomarenko 1968). They are found near the sea floor, in the water column, and in association with sea ice. Their overall distribution is circumarctic, and they are generally associated with cold water and ice cover, although they sometimes occur in open water far from the ice. Spawning occurs during winter in nearshore waters under the ice at which time they are thought to be concentrated in dense shoals. During other months they appear to be more dispersed in deeper water, although local large schools have been observed (Craig and Haldorson 1981).

Few data are available on arctic cod distribution and abundance in Alaskan waters. Available data for northern areas (Lowry and Frost 1981a, Table 10) are not readily expressed in terms of density of fishes. Wolotira et al. (1977) estimated, based on bottom trawls, that the biomass of arctic cod in the northern Bering and southeastern Chukchi Seas was about 1,234 t in September-October 1976. It should be noted that the survey was conducted during the open water season when arctic cod abundance would be expected to be low. Gjosaeter (1973) estimated a biomass of 3-5 million metric tons in the Barents Sea.

Available data do not allow a direct estimate of arctic cod biomass in the study area, and it is unlikely that an adequate stock assessment will be done in the future. Based on data presented in Sections V and VI, the total amount of arctic cod consumed annually by predators other than arctic cod in the study area is approximately 28,630 metric tons. Arctic

Table 9. Species of fishes caught by otter trawls in offshore waters of the northeastern Chukchi and Alaskan Beaufort Seas during 1976 (n=2) and 1977 (n=33). Species are ranked in order of decreasing catch (from Frost et al. 1978; Frost and Lowry, unpubl.).

Scientific Name	Common Name	No. Individuals	No. Stations	Depth Range (m)
Boreogadus saida	Arctic cod	227	30	40-400
Lycodes polaris	Canadian eelpout	121	16	40-150
Icelus bicornis	Twohorn sculpin	74	13	50-130
Artediellus scaber	Hamecon	36	11	40-70
Aspidophoroides olriki	Arctic alligatorfish	36	6	40-400
Liparis spp.	Snailfish	34	20	40-400
Eumicrotremus derjugini	Leatherfin lumpsucker	29	11	50-110
Gymnelis viridis	Fish doctor	27	12	40-130
Icelus spatula	Spatulate sculpin	20	4	56-123
Lumpenus fabricii	Slender eelblenny	11	2	40-123
Lycodes raridens	Eelpout	10	3	64-123
Gymnocanthus tricuspis	Arctic staghorn sculpin	5	3	40-58
Eumesogrammus praecisus	Fourline snakeblenny	4	4	40-64
Triglops pingeli	Ribbed sculpin	3	3	40-110
Lycodes mucosus	Eelpout	2	2	50-105
Lycodes rossi	Eelpout	2	1	123
Arctogadus glacialis	Polar cod	1	1	150
Lumpenus medius	Stout eelblenny	1	1	40
Lumpenus maculatus	Daubed shanny	1	1	44

Table 10. Summary of abundance of arctic cod and other fishes caught by otter trawls in the Beaufort Sea during August and September 1980.

	Pingok Island 20 Aug.-1 Sept. 1980				Beaufort Lagoon 3-19 Sept. 1980			
Fish Species or Group	Number	% of Total	Weight (g)	% of Total	Number	% of Total	Weight (g)	% of Total
Arctic cod	169	78.2	1785.5	87.4	91	54.2	365.7	79.8
Sea snails	28	13.0	120.1	5.9	28	16.7	21.4	4.7
Sculpins	17	7.9	134.6	6.6	41	24.4	30.1	6.6
Other	2	0.9	2.8	0.1	8	4.8	41.2	9.0
Number of tows	9				14			
Depth range (m)	5-19				3-40			

cod are in some instances cannibalistic (Baranenkova et al. 1966; Section V, this report), usually involving large adults consuming larvae and fry. We will not consider consumption of cod by cod in our calculations since there are few data on this relationship, and such consumption, even if a very low rate is assumed, will greatly influence estimates of total cod stock size (see Section VI). Our estimates of total arctic cod biomass in the area will be conservative and will largely not include biomass of larvae and young fry. A minimum estimate of stock size can be derived by assuming that the total annual consumption by predators is equal to the maximum sustainable yield of the arctic cod stock in the area. Data on the relationship between total stock size and sustainable yield are sparse, particularly for arctic species. Sustained yield for fish stocks in temperate regions should be 1/4 to 1/2 of standing stock (Sheldon et al. 1977); therefore, stock size should be two to four times the sustained yield. For purposes of calculations we will assume the arctic cod stock size to be three times the estimated total amount consumed by predators or 85,890 metric tons.

V. Feeding of Major Vertebrate Consumers

A. Marine Mammals

Bowhead whales

Foods utilized by bowhead whales are poorly known in comparison to other baleen whales. Commercial whalers who took bowheads removed only the baleen and blubber and thus had little opportunity to observe their stomach contents (J. Bockstoce, pers. comm.). Their observations were therefore limited and general, as in the following from Scammon (1874):

> When the Bowhead feeds, it moves through its native element, either below or near the surface, with considerable velocity, its jaws being open, whereby a body of water enters its capacious mouth, and along with it the animalculae (termed by the whalemen "Right Whale feed," or "brit"). The water escapes through the layers of baleen, but the insect food is retained by the fine fringes on its inner edges, and is afterward swallowed.

One might surmise from the reference to "Right Whale feed" that Scammon considered copepods to be the main food of bowheads. More recently Johnson et al. (1966) examined stomachs of three whales taken at Point Hope in spring 1960 and 1961. Two stomachs were empty, while the third contained fragmentary remains of benthic organisms. Durham (1972) reported on examinations of stomachs of 17 whales of which six were empty or contained only sand and the sample from a seventh was lost. Food items found included copepods, euphausiids, mysids, and amphipods, as well as tundra vegetation, silt, and benthic organisms such as isopods, tunicates, and sculpins. Apparently, the only stomachs with appreciable quantities of food contained mysids, euphausiids, and copepods. Other references to bowhead foods (e.g., MacGinitie 1955; Mitchell 1975) state generally that bowheads eat copepods, euphausiids, and mysids as well as benthic amphipods and perhaps pteropods. Based on the morphology of the baleen, bowheads would be expected to feed primarily on copepods and to a lesser extent on euphausiids and other zooplankters (Nemoto 1970). Tomilin (1957), based on indirect evidence such as the types of organisms found near bowheads and the color of the whales' feces, stated that the main food "consists of minute (3-4 mm long) crustaceans Calanus finmarchicus and 4-5 mm long pteropods Limacina helicina."

Since 1976 we have received and examined samples of prey items from the gastrointestinal tracts of 17 whales (Appendix II). With three probable exceptions, all were collected from stomach contents. Eight of the samples were from whales taken near Point Barrow, six from whales taken near Kaktovik, two from Point Hope, and one from Shaktoolik.

Depending on the state of digestion of the samples, it was more or less difficult to determine the specific identity of the prey. Some prey could be identified only to phylum, family, or genus when only fragments were collected. Small, fragile organisms such as copepods were difficult to identify to species except in comparatively fresh stomach content samples. Larger, more durable organisms such as amphipods and molluscs could generally be identified in mostly digested stomach or intestinal samples. The presence of euphausiids was easy to detect due to the persistent and characteristic nature of the eyes which detach from the body during digestion. Entirely soft-bodied animals such as coelenterates, salps, chaetognaths, and pteropods may not have been detected in some samples examined, although they would have been readily observed in those which were in fresh condition.

Eliminating those organisms which could not be identified to species but which probably represented species found in other samples (e.g., Calanus sp., Gammarus sp., Family Lysianassidae, and Family Crangonidae), a probable total of 46 prey species was found in the 17 whales containing identifiable food remains (Table 11). With the exception of three species each of molluscs and fishes, all identified prey were crustaceans. The distribution of prey species among the major groups of crustaceans was: gammarid amphipods - 16; copepods - 10; hyperiid amphipods - 5; euphausiids, mysids, and shrimps - 2 each; and isopods, cumaceans, and ostracods - 1 each. The number of times each of the major prey groups occurred in the samples was: euphausiids - 11; gammarid and hyperiid amphipods - 10 each; copepods - 9; mysids - 6; shrimps - 5; fishes - 4; molluscs -3; and isopods, cumaceans, and ostracods - 1 each. Of the individual prey species, the most frequently encountered were Thysanoessa raschii (11 occurrences), Calanus hyperboreus (7 occurrences), and Parathemisto libellula (7 occurrences). All the remaining prey species occurred in fewer than five stomachs, while 37 species occurred in only one or two samples. Pebbles, generally about 1 cm in size, occurred in five samples.

Copepods or euphausiids were the dominant component of all except four of the samples we examined (Table 11). Two of those four samples were from colons; the remaining two contained a single amphipod and a

Table 11. Prey identified from samples collected from gastrointestinal tracts of bowhead whales. Samples were collected from stomachs unless otherwise indicated. Dominant prey species in each sample are indicated by XX.

	BARROW								KAKTOVIK						OTHER AREAS		
PREY SPECIES	4388[1] May 1969	76-B-6F 10 Sept 1976	76-B-7F 20 Sept 1976	77-B-5 5 May 1977	79-B-32 27 May 1979	80-B-3 25 May 1980	80-B-5 25 May 1980	80-B-9 27 May 1980	79-KK-1 20 Sept 1979	79-KK-2 6 Oct 1979	79-KK-3 8 Oct 1979	79-KK-4 10 Oct 1979	79-KK-5 11 Oct 1979	80-KK-13 14 Sept 1980	78-H-2 Point Hope 4 May 1978	79-H-3 Point Hope 6 May 1979	80-SH-12 Shaktoolik 9 May 1980
COPEPODS														XX			
Calanus cristatus						X											
Calanus finmarchicus												X					
Calanus glacialis				X				X									
Calanus hyperboreus						XX		X	XX	XX	X	XX	X				
Calanus sp.						X				X		X					
Chiridius obtusifrons						X		X				X					
Euchaeta glacialis				X		XX											
Heterorhabdus sp.										X		X					
Metridia longa				XX													
Metridia lucens										X		X					
Pseudocalanus sp.				X													
EUPHAUSIIDS																	
Thysanoessa inermis	XX					X		X					X				
Thysanoessa raschii	XX	XX	XX	X		X	XX	XX		X	XX	X	XX				
MYSIDS																	
Mysis litoralis								X		X	X		X				
Neomysis rayi						X	X	X									
HYPERIID AMPHIPODS																	
Hyperia galba						X		X									
Hyperia medusarum								X		X							
Hyperia sp.									X								
Hyperoche medusarum								X									
Parathemisto abyssorum				X							X						
Parathemisto libellula		X	X						X	X	X	X	X				
GAMMARID AMPHIPODS																	
Acanthostepheia behringiensis			X								X		X				
Acanthostepheia incarinata										X							
Ampelisca macrocephala															X		
Anonyx nugax								X									
Apherusa glacialis												X					
Atylus carinatus											X		X				
Gammaracanthus loricatus											X		X				
Gammarus zadduchi			X														

Table 11. cont.

PREY SPECIES	BARROW 4338[1] May 1969	 76-B-6F 10 Sept 1976	 76-B-7F 20 Sept 1976	 77-B-5 5 May 1977	 79-B-3[2] 27 May 1979	 80-B-3 25 May 1980	 80-B-5 25 May 1980	 80-B-9 27 May 1980	KAKTOVIK 79-KK-1 20 Sept 1979	 79-KK-2 6 Oct 1979	 79-KK-3 8 Oct 1979	 79-KK-4 10 Oct 1979	 79-KK-5 11 Oct 1979	 80-KK-1[3] 14 Sept 1980	OTHER AREAS 78-H-2 Point Hope 4 May 1978	 79-H-3 Point Hope 6 May 1979	 80-SH-1[2] Shaktoolik 9 May 1980
Monoculoides zernovi			X														
Monoculoides c.f. *M. schneideri*											X	X					
Munnopsis c.f. *M. typica*											X						
Onisimus glacialis										X							
Onisimus litoralis									X								
Rozinante fragilis		X	X									X					
Weyprechtia heuglini												X	X				
Weyprechtia pinguis														X			
Family Lysianassidae									X								
ISOPODS																	
Saduria entomon													X				
SHRIMP			X							X							X
Eualus gaimardii												X					
Sabinea septemcarinata												X					
Family Crangonidae									X								
CUMACEANS																	
Diastylis sp.												X					
OSTRACODS				X													
MOLLUSCS																	
Limacina helicina				X													
Natica clausa																X	
Nuculana sp.					X												
FISHES				X													
Boreogadus saida										X			X				
Myoxocephalus quadricornis											X		X				
Pungitius pungitius													X				
PEBBLES		X				X	X		X			X					

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[1] Sample from Floyd Durham via F. H. Fay. Exact collection date and portion of gastrointestinal tract from which sample was collected are not known.

[2] Sample from colon.

[3] Sample probably from small intestine

single snail. In the other 13 samples, euphausiids were the major food in seven and copepods were dominant in six. Other prey groups, although they comprised many species and occurred quite frequently (e.g., gammarid amphipods), were never a major component of those samples which contained more than a few prey items in an identifiable state. In most of the samples, either *Thysanoessa raschii* or *Calanus hyperboreus* was the dominant prey species. At Barrow, *T. raschii* was the dominant prey in both whales taken in September, while in samples from spring *T. raschii* was dominant in three while copepods (*Calanus hyperboreus*, *Euchaeta glacialis*, and *Metridia longa*) predominated in two. In samples from whales at Kaktovik, all of which were taken in late September and early October, copepods (principally *C. hyperboreus*) were dominant in four and *T. raschii* in two.

Available records do not allow a conclusive examination of geographical or temporal patterns of feeding activity. Whale stomachs examined at Barrow and Kaktovik in the fall commonly contained substantial quantities of food, while those taken at Point Hope and Barrow in spring were usually empty or contained small amounts of food (Appendix II). We feel that significant feeding does not occur until the spring migration is complete and the whales have arrived in the eastern Beaufort Sea.

Quantitative data on the composition of bowhead whale stomach contents samples (Lowry et al. 1978; Lowry and Burns 1980) indicate that, as bowheads pass through and feed in the Alaskan Beaufort Sea in fall, copepods and euphausiids comprise the bulk of the food eaten. In stomachs of five whales taken at Kaktovik in fall 1979, copepods and euphausiids comprised approximately 60 and 37% of the overall contents, respectively, while in the only two samples from whales taken at Barrow in the fall copepods did not occur and euphausiids comprised about 92% of the samples (Table 12). Assuming that the food composition observed at Barrow and Kaktovik is each representative of half of the total foraging activity in the Alaskan Beaufort Sea, the overall proportions of prey in the diet would be approximately: copepods - 30%; euphausiids - 65%; hyperiid amphipods - 1%; and other organisms including primarily gammarid amphipods - 4%. We will use those proportions for calculating quantities of the various prey types consumed by bowheads in the study area.

Food consumption rates of large whales are poorly known. Published estimates of daily consumption range from 1 to 4% of total body weight (Sergeant 1969; Brodie 1975, 1980). Brodie (1975) estimated that an average Antarctic fin whale (*Balaenoptera physalus*) which fed for 120 days and fasted for the remainder of the year would consume about 2.1% of its total body weight per day during the feeding season. Since the average fin whale considered by Brodie was much larger (48.0 t) than what we are assuming for bowheads (15.9 t), we will assume the daily food consumption rate of bowheads in the Alaskan Beaufort to be 3% of the total body weight per day. Therefore, the total bowhead population foraging in the area for 25 days would consume about 27,000 t of food.

Table 12. Quantitative composition of stomach contents from bowhead whales. For each whale, numbers indicate percent of the sample volume comprised of each prey type.

	KAKTOVIK, FALL 1979						BARROW, FALL 1976		
	Whale Specimen Number					Overall mean % of contents[1]	Whale Specimen Number		Overall mean % of contents[2]
Prey Type	79-KK-1	79-KK-2	79-KK-3	79-KK-4	79-KK-5		76-B-6F	76-B-7F	
Copepod	99.7	99.0	23.4	88.3	<0.1	59.8	--	--	--
Euphausiid	--	0.3	67.8	4.9	97.9	37.2	97.1	86.7	91.9
Mysid	--	0.3	7.0	--	0.8	0.2	--	--	--
Hyperiid amphipod	<0.1	0.1	0.5	0.4	--	0.1	2.3	3.0	2.6
Gammarid amphipod	0.1	0.1	0.3	2.4	0.1	0.4	0.6	10.3	5.4
Other invertebrate	<0.1	<0.1	--	2.3	1.1	0.6	--	<0.1	<0.1
Fish	<0.1	0.1	1.0	1.7	--	0.4	--	--	--
Sample volume (ml)	2406.2	545.2	399.7	131.3	357.9		17.5	33.0	
Estimated total volume of contents (gallons)	12	5	6	5	10		unknown	30	

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[1] Calculated based on the volume and percent composition of each sample and the estimated total contents of stomachs from which samples were taken.

[2] Calculated as the average of the percent of total volume in each of the two samples.

Belukha whales

There are few direct observations of foods of belukha whales in the Beaufort Sea. Seaman and Lowry (in prep.) report arctic cod as a major food at Barrow and Point Hope during the spring migration, while other fishes such as saffron cod, herring, smelt, and sculpins were eaten during summer at more southern locations. In the Mackenzie Delta in summer Fraker et al. (1978) reported that little feeding occurs within the delta. They speculated that arctic cod is a major food off shore. Based on the importance of arctic cod in the summer diet of belukhas in other areas of the arctic (e.g., Kleinenburg et al. 1964), we agree with Fraker et al. and will assume that 80% of the diet of belukhas in the Alaskan Beaufort is comprised of arctic cod. The remaining 20% may be comprised of organisms such as shrimps, cephalopods, and other fishes.

Sergeant (1969) calculated an estimate of the daily food consumption of belukhas as 5.1% of the total body weight per day. Therefore, 6,000 belukhas feeding in the Alaskan Beaufort Sea for 30 days would consume about 7,344 t of food.

Ringed seals

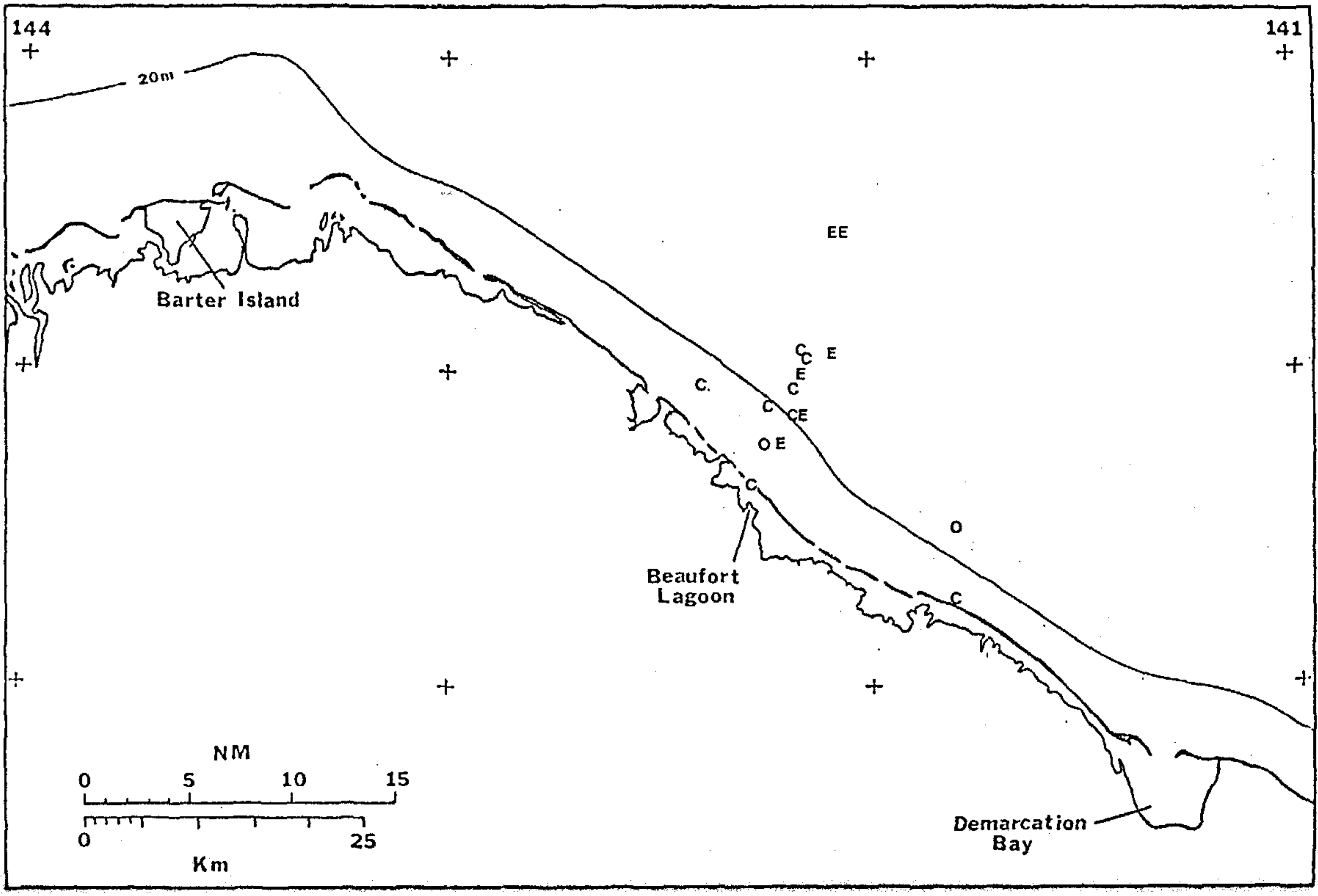
Foods of ringed seals in the Alaskan Beaufort Sea are comparatively well known from previous studies (Lowry et al. 1978, 1979, 1980). Results of those studies, which involved the examination of stomach contents of 246 ringed seals collected from 1972 to 1979, indicate that arctic cod, nektonic crustaceans (hyperiid amphipods and euphausiids), and benthic crustaceans (gammarid amphipods, mysids, shrimps, and isopods) are the major foods eaten. The primary prey type consumed varied seasonally as follows: benthic crustaceans in April-June; nektonic crustaceans in August-September; and arctic cod in November-March. Largest amounts of food were found in seals which were feeding on nektonic crustaceans or arctic cod.

As part of field studies conducted in summer 1980, we collected and examined the stomach contents of an additional 24 ringed seals (Appendix III). Eight seals were collected in the vicinity of Pingok Island between 21 August and 1 September in water 14-21 m deep. Arctic cod comprised 98% of the stomach contents of those seals, and the remainder was primarily benthic crustaceans. Of the 16 seals collected near Beaufort Lagoon, six had eaten primarily euphausiids and eight had eaten mostly arctic cod, while the remaining two had eaten mostly benthic organisms (Table 13, Figure 6). Arctic cod occurred in seals collected throughout the entire depth range investigated (3-40 m), while euphausiids were found only in seals collected in water 15-40 m deep.

Based on a comparison of the length of arctic cod caught in otter trawls and the length of cod eaten by ringed seals at Beaufort Lagoon estimated from otoliths (Frost and Lowry in press a), large arctic cod were either missed by the trawls or selected for by ringed seals (Figure 7).

Table 13. Ringed seal stomach contents, Beaufort Lagoon, September 1980.

Seal No.	Water Depth (m)	Percent of Contents Arctic Cod	Euphausiid	Polychaete	Gammarid	Other	Total Volume (ml)
BLP-1-80	15	100.0	--	--	--	--	9.2
BLP-2-80	14	19.4	--	75.3	5.2	0.2	87.7
BLP-3-80	19	100.0	--	--	--	--	20.0
BLP-4-80	13	89.7	--	0.9	--	9.4	22.3
BLP-5-80	25	0.0	100.0	--	--	--	23.0
BLP-6-80	23	100.0	--	--	--	--	165.0
BLP-7-80	27	95.0	--	--	--	5.0	66.3
BLP-8-80	29	100.0	--	--	--	--	55.0
BLP-9-80	40	12.3	87.7	--	--	--	57.0
BLP-10-80	40	0.0	100.0	--	--	--	160.0
BLP-11-80	20	82.2	--	9.4	1.9	6.6	42.6
BLP-12-80	31	3.0	94.2	--	2.6	0.2	46.7
BLP-14-80	22	0.0	0.0	--	98.2	1.8	33.8
BLP-15-80	15	0.0	99.7	--	--	0.3	70.2
BLP-16-80	20	--	100.0	--	--	--	120.0
BLP-18-80	3	99.2	--	--	0.6	0.2	95.8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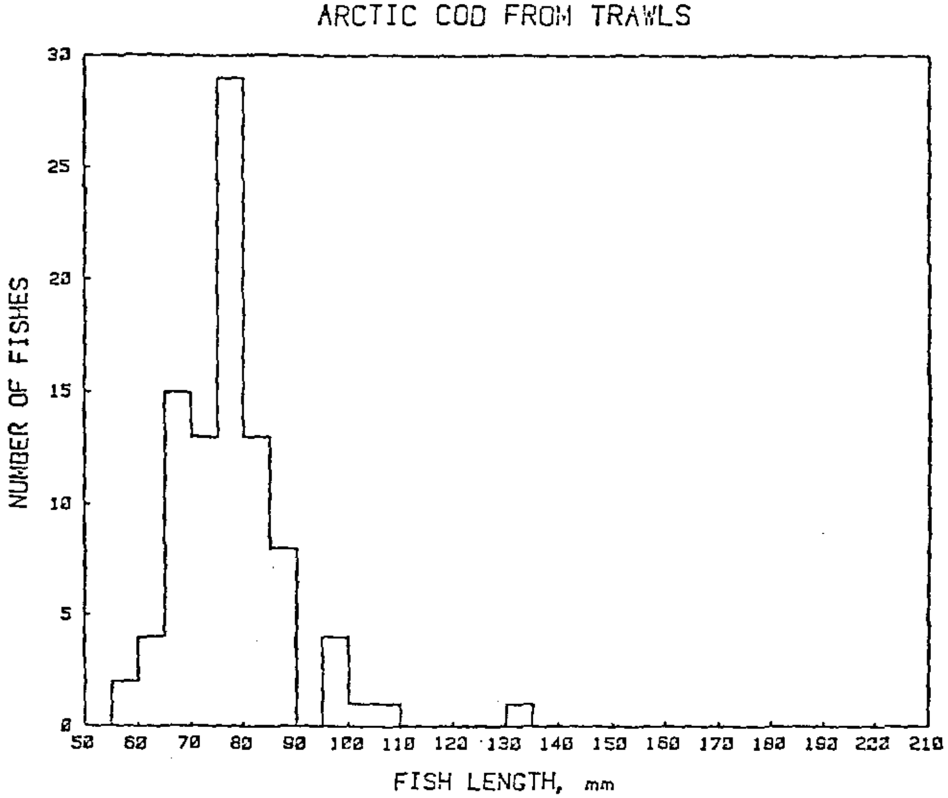
ARCTIC COD FROM TRAWLS

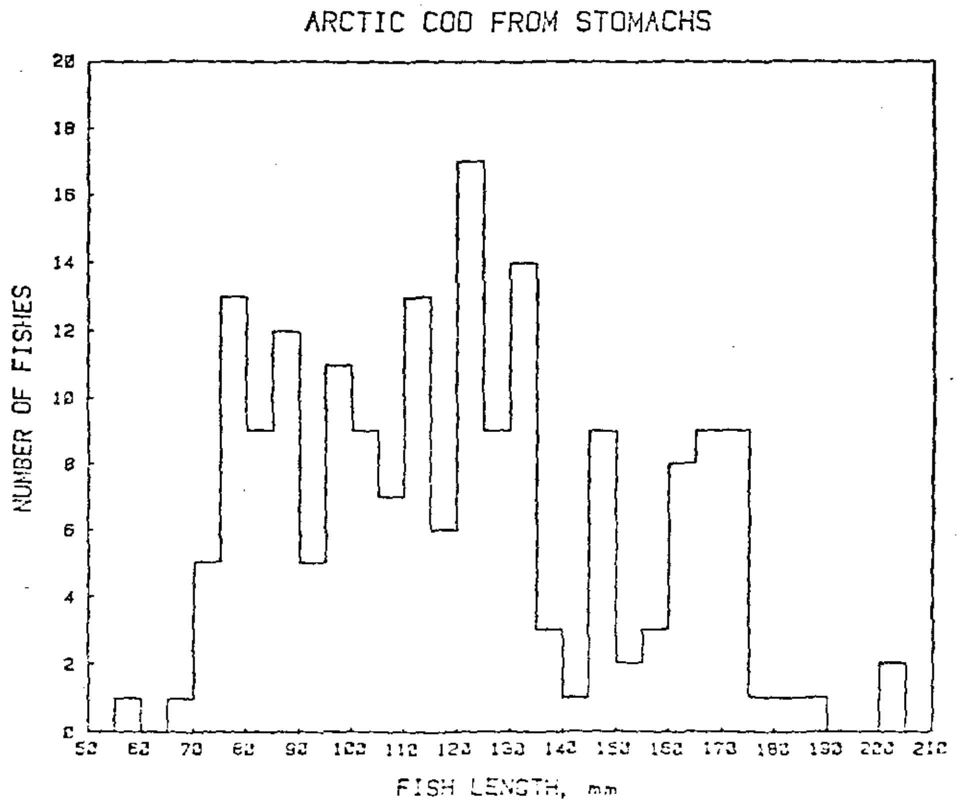
ARCTIC COD FROM STOMACHS

Figure 7. Length distribution of arctic cod measured from otter trawls and estimated from otoliths in ringed seals collected at Beaufort Lagoon, September 1980.

seasons (McLaren 1958; Johnson et al. 1966). In addition, daily caloric requirements vary greatly with age of the seal (Parsons 1977). Expressed as a percent of body weight, the average daily food consumption for prey of average caloric value ranges from about 9% in pups to 3% in adults (see Lowry et al. 1980). We will assume 6% of the body weight per day as the average daily consumption. This value can be adjusted to reflect monthly changes in food consumption by considering the ratio of observed stomach contents volume in a given month to the average stomach volume for all months combined. Such calculations suggest the following feeding rates (expressed as percent of total body weight per day): November to March - 8.4%; April to June - 1.9%; July - 4.1%; August and September - 5.6%; and October - 7.4%.

B. Seabirds

A considerable quantity of information exists with which to make an approximation of the composition of the diet of seabirds in the study area. Relevant published data will be discussed below. However, although we will estimate and use values for the average composition of the diet for the entire Alaskan Beaufort Sea for the entire summer period, significant regional and temporal differences in feeding may occur which combined with the distribution of collections of samples may greatly influence our estimates.

Data on diet of seabirds in the study area have been collected during 1976-79 by Divoky (1979 and in prep.) and summarized in qualitative fashion in Schamel (1978). We have used those sources where possible, supplemented with other relevant data from arctic and subarctic localities (Uspenskiy 1959; Swartz 1966; Divoky 1976 and pers. comm.; Bradstreet 1980; Hunt et al., in press) to derive the diet composition summarized in Table 15. In general, arctic cod are a major food of most species, comprising as much as 90% of the overall diet. Primary consumers of copepods are phalaropes and Sabine's gulls. Euphausiids are commonly eaten by several species and when they wash up in abundance on beaches they can dominate the diet of species such as terns and gulls (Divoky 1980). Hyperiid amphipods are only occasionally found in seabird stomachs, which is perhaps an indication of their patchy distribution. In areas of high hyperiid abundance they probably comprise significant proportions of the diet of some bird species; however, the low values indicated in Table 15 may be realistic for the study area as a whole.

Estimates of daily food consumption of seabirds range from 15 to 40% of total body weight (Swartz 1966; Livingston 1980; Hunt et al., in press). The value for a particular species will obviously vary with individual size, activity, time of year, and availability of food. We will use 25% of the total body weight as an estimate of daily food consumption for all species in the study area.

Table 15. Estimated composition of the diet of seabirds in the study area.

	Percent of Prey Category in Diet				
Bird Species/Group	Copepod	Euphausiid	Hyperiid Amphiphod	Arctic Cod	Other
Black-legged kittiwake	--	2	1	90	7
Glaucous gull	--	9	1	50	40
Ivory gull	--	10	--	80	10
Ross' gull	--	40	--	40	20
Sabine's gull	13	10	--	10	67
Arctic tern	--	18	2	40	40
Jaegers	--	--	--	40	60
Black guillemot	--	--	--	80	20
Thick-billed murre	--	2	2	90	6
Loons	--	--	--	50	50
Phalaropes	90	--	--	--	10

C. Arctic Cod

Arctic cod are a very adaptable species whose diet includes many types of prey, including benthic organisms, planktonic organisms, and species associated with the under surface of ice. Lowry and Frost (1981a) reported on the contents of 157 arctic cod stomachs collected in the northeastern Chukchi and Beaufort Seas in August and September 1977 in waters 40-400 m deep. Based on rank order of importance in stomachs and frequency of occurrence, calanoid copepods (primarily Calanus hyperboreus and C. glacialis) and Apherusa glacialis were the major foods, followed by hyperiid amphipods, mysids, chaetognaths, euphausiids, and shrimps. Similar summer foods have been reported from the eastern Canadian Arctic (Bohn and McElroy 1976), Barents Sea (Hognestad 1968), and the Siberian Arctic (Moskalenko 1964). In very nearshore waters of the central Beaufort, Craig and Haldorson (1981) found the principal summer foods to be mysids, amphipods, and copepods, while in winter samples mysids were the overwhelmingly dominant food.

During field work conducted at Beaufort Lagoon in September 1980 we obtained and examined stomach contents from 91 arctic cod, 86 of which contained recognizable food remains. Over 90% of the food was comprised of crustaceans (Table 16). The contribution of the major prey items to the overall diet expressed as percent of total weight of stomach contents was: copepod - 56%; gammarid amphipod (principally Apherusa glacialis) - 20%; euphausiids - 8%; mysids - 6%; larval fishes (principally arctic cod) - 5%; polychaetes - 4%; and hyperiid amphipods (Parathemisto libellula) - 1%. Vertical plankton tows were done at each location where cod were collected (Table 17). Rank order of abundance of crustacean species eaten by cod and caught by plankton tows is compared in Table 18. Apherusa glacialis, Mysis litoralis, and Thysanoessa raschii were much more common in cod than in plankton tows. This is probably due to selection of large organisms by cod and the ability of large mobile species to avoid the plankton net. The rank order of abundance of copepod species was generally similar in cod and tows, while the very small barnacle larvae were caught more commonly by plankton tows than by cod.

Unfortunately, no data are available on winter foods of arctic cod in offshore waters. Composition of the diet during winter could change in response to seasonality of prey populations, and feeding intensity may be reduced in conjunction with spawning activities. Rather than speculate on the possible winter diet of cod in the study area, we will assume that the overall annual diet composition is like that we observed at Beaufort Lagoon with one exception. Since it is unlikely that arctic cod could support an overall 5% rate of cannibalism and since all cod found in stomachs of other cod were very small juveniles which grow rapidly to a size at which they may escape this cannibalism, we feel that the overall magnitude of cannibalism is exaggerated in the Beaufort Lagoon samples. We will use the following values for the overall annual diet composition: copepod - 56%; euphausiid - 8%; hyperiid amphipod - 1%; arctic cod - 1%, and other organisms - 34%.

Table 16. Stomach contents of arctic cod collected near Beaufort Lagoon, September 1980.

Species or Tax Code	Tot Wgt (g)	% Wgt	Tot #	% #	# of Ocurr.	Freq of Occur.
Unid Harpactacoid copepod	.00	.0	1	.0	1	1.2
Limnocalanus grimaldi	.00	.0	26	.2	5	5.8
Derjuginia tolli	.11	1.3	3373	28.2	25	29.1
Pseudocalanus	1.72	20.3	8132	68.1	59	68.6
Calanus glacialis	.00	.0	16	.1	3	3.5
Calanus hyperboreus	.02	.2	4	.0	2	2.3
Calanus sp.	.00	.0	3	.0	3	3.5
Unid Calanoid copepod	2.85	33.7	179	1.5	36	41.9
COPEPODS	4.70	55.6	11734	98.2	72	83.7
Mysis littoralis	.49	5.8	33	.3	25	29.1
MYSIDS	.49	5.8	33	.3	25	29.1
Monoculodes zernovi	.00	.0	1	.0	1	1.2
Monoculodes longirostris	.00	.0	1	.0	1	1.2
Acanth. behringiensis	.05	.6	2	.0	2	2.3
Apherusa glacialis	1.20	14.2	120	1.0	35	40.7
Acanthonotozoma sp.	.05	.6	1	.0	1	1.2
Unid Gammarid	.36	4.3	21	.2	16	18.6
GAMMARIDS	1.66	19.6	146	1.2	51	59.3
Thysanoessa raschii	.65	7.7	19	.2	3	3.5
EUPHAUSIIDS	.65	7.7	19	.2	3	3.5
Brachyuran crab	.00	.0	2	.0	2	2.3
Pagurid zoea	.00	.0	1	.0	1	1.2
Hippolytid zoea	.00	.0	1	.0	1	1.2
Parathemisto libellula	.10	1.2	1	.0	1	1.2
Barnacle cyprid	.00	.0	10	.1	4	4.7
Unid Crustacean	.09	1.1	0	.0	3	3.5
Polychaete	.31	3.7	1	.0	1	1.2
Unid Invert	.02	.2	0	.0	1	1.2
OTHER	.52	6.1	16	.1	11	12.8
TOTAL INVERTEBRATE	8.02	94.8	11948	100.0	86	100.0
Fish (larval)	.44	5.2	12	100.0	8	9.3
TOTAL FISHES	.44	5.2	12	100.0	8	9.3

TOTAL WGT (g) 8.46
MEAN WGT (g) .10 (empties not included)

TOTAL FISHES 91
W/FOOD 86
EMPTIES 5

MALES 45
FEMALES 44
UNKNOWN SEX 2

DATE RANGE 904 - 917

Table 17. Organisms identified in vertical plankton tow samples taken near otter trawl stations at which arctic cod were collected. For copepods, age class 0 indicates nauplius larvae, 1-5 indicate copepodite stages I-V, and 9 indicates adults.

VERTICAL ZOOPLANKTON TOW ANALYSIS

Tow #:	Date range:
VPT-10A-80	800904-800908
VPT-11A-80	
VPT-12-80	
VPT-13-80	
VPT-14-80	
VPT-15-80	
VPT-16A-80	
VPT-17-80	
VPT-18-80	
VPT-19A-80	

Avg water depth: 18.2m   Avg tow depth: 18.2m   Avg surf temp: - deg C

Avg net diameter: .500m   Avg mesh size: 505 microns

Total # tows selected: 16   # Replicates: 6

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Perigonimus yoldiarcticae	all	.3	.070	0.000	.392
Rathkea octopunctata	all	31.7	8.869	0.000	24.669
Bougainvillia super.	all	.1	.018	0.000	.131
Obelia longissima	all	.1	.035	0.000	.340
Aglantha digitali	all	.6	.158	0.000	.784
Aeginopsis laurentii	all	2.3	.630	0.000	1.959
Cyanea capillata	all	.5	.145	0.000	.821
Beroe sp.	all	.8	.210	0.000	1.114
Polychaete	all	.1	.035	0.000	.261
Clione limacina	all	.1	.018	0.000	.131
Calanus	0	2.8	.788	0.000	5.877
Calanus	1	.2	.053	0.000	.392
Calanus	2	14.9	4.181	0.000	16.062
Calanus hyperboreus	3	7.4	2.063	.318	6.791
Calanus hyperboreus	4	3.1	.873	0.000	2.464
Calanus hyperboreus	5	.2	.053	0.000	.340
Calanus hyperboreus	9	.1	.018	0.000	.131
Calanus glacialis	3	10.2	2.856	0.000	14.784
Calanus glacialis	4	2.3	.658	0.000	2.220
Calanus glacialis	5	5.8	1.620	0.000	10.316
Calanus glacialis	9	.2	.053	0.000	.679
Pseudocalanus	2	.4	.105	0.000	1.019
Pseudocalanus	3	.1	.018	0.000	.340
Pseudocalanus	5	25.8	7.213	.392	25.465
Pseudocalanus	9	104.7	29.313	.522	260.760
Derjuginia tolli	9	58.4	16.355	.340	78.025
Metridia sp.	5	.3	.070	0.000	.392
Limnocalanus grimaldi	9	16.2	4.538	.261	10.865
Acartia clausi	9	1.0	.280	0.000	3.056
Acartia longiremus	5	.1	.018	0.000	.255
Acartia longiremus	9	.1	.035	0.000	1.019
Harpactacoid copepod	9	.1	.018	0.000	.340
Barnacle cyprid	all	29.8	8.332	0.000	27.554
Mysis litoralis	all	2.1	.595	0.000	7.470
Cumacean	all	.4	.110	0.000	.821
Lamprops sp.	all	.1	.018	0.000	.340
Rhachotropis sp.	all	.1	.018	0.000	.131
Rozinante fragilis	all	.1	.018	0.000	.340
Monoculoides sp.	all	.1	.018	0.000	.340
Hyperia sp.	all	.1	.018	0.000	.340
Hyperia medusarum	all	.1	.035	0.000	.392
Hyperoche medusarum	all	.1	.018	0.000	.131
Parathemisto abyssorum	all	.1	.018	0.000	.131
Hippolytid zoea	all	.1	.035	0.000	.159
Crangonidae zoea	all	.1	.018	0.000	.131
Pagurid zoea	all	.9	.263	0.000	1.019
Oregoninae zoea	all	.4	.123	0.000	.764
Sagitta elegans	all	1.5	.420	0.000	2.089
Oikopleura sp.	all	11.9	3.343	0.000	14.365
Fritillaria borealis	all	1.6	.438	0.000	1.959
Gadidae larvae	all	.3	.088	0.000	.522
Liparid	all	.2	.053	.679	1.175

Table 18. Rank order of abundance of crustaceans in arctic cod stomachs and vertical plankton tows.

	In Cod	In Tows
Pseudocalanus sp.	1	1
Derjuginia tolli	2	2
Apherusa glacialis	3	not present
Mysis litoralis	4	8
Limnocalanus grimaldi	5	6
Thysanoessa raschii	6	not present
Calanus glacialis	7	4
Barnacle larvae	8	3
Calanus hyperboreus	9	7
Calanus sp.	10	5

Craig and Haldorson (1981) estimated based on feeding periodicity and gastric clearance rate that arctic cod in summer consume about 6% of their body weight per day. In our arctic cod samples collected at Beaufort Lagoon, the weight of stomach contents exceeded 5% of the total weight of the fish in only five instances. The maximum quantity of food in a single stomach (2.03 g) was 9.8% of the weight of the fish. We consider 6% of the body weight per day to be a reasonable estimate of the average daily food consumption of arctic cod.

VI. Trophic Interactions Among Major Vertebrate Consumers

Using the data and assumptions presented in Sections IV and V, an estimate of the amount of each major prey category eaten annually by each major vertebrate consumer can be easily and directly calculated.

For the individual species or species groups of seabirds, quantities of prey consumed were calculated based on the diet composition given in Table 15, biomass values from Table 8, a feeding rate of 25% of total body weight per day, and a residence time of 90 days for all species except ivory and Ross' gulls, for which a 30-day residence time was assumed. Results of calculations (Table 19) indicate that phalaropes are the major consumers of copepods; gulls and terns are the major consumers of euphausiids, and loons, jaegers, terns, and gulls are the major consumers of arctic cod. In total the seabirds we considered are estimated to consume about 3,546 t of food annually, comprised of about 7% copepods, 2% euphausiids, 44% arctic cod, and 46% other organisms.

Available data indicate seasonal fluctuations in abundance, diet composition, and feeding rate of ringed seals. Therefore, we will calculate quantities of each prey type consumed each month using the assumptions summarized in Table 20. Calculations indicate (Table 21) that large quantities of arctic cod are consumed during the months of August through March, while consumption of euphausiids and hyperiid amphipods is greatest in July to October. Overall, arctic cod comprise about 55% of the total food consumed by ringed seals annually, while euphausiids and hyperiid amphipods comprise about 10% and 18%, respectively.

For bowhead and belukha whales and arctic cod, available data are not adequate to describe seasonality of abundance or food habits. Calculations for these consumers will be based on estimated average values for the entire feeding season (Table 22). Results of calculations for those species, along with total values for seabirds as a group and total annual values for ringed seals are shown in Table 23. These vertebrate species in aggregate consume an estimated 2 million metric tons of food annually in the study area, comprised of approximately 54% copepod, 9% euphausiid, 1% hyperiid, 2% arctic cod, and 34% other organisms. Arctic cod are by far the major consumers of copepods and are estimated to eat over 1 million metric tons annually. Bowhead whales are estimated to eat less than 1% of the total amount of copepod biomass consumed annually by these species of predators. Arctic cod and bowheads are the major

Table 19. Estimated quantities of food (t) consumed by seabirds in the study area.

	Quantity of Prey Category Consumed				
Bird Species/Group	Copepod	Euphausiid	Hyperiid Amphipod	Arctic Cod	Other
Black-legged kittiwake	--	0.9	0.4	40.5	3.2
Glaucous gull	--	17.0	1.9	94.5	75.6
Ivory gull	--	0.3	--	2.4	0.3
Ross' gull	--	6.0	--	6.0	3.0
Sabine's gull	17.6	13.5	--	13.5	90.4
Arctic tern	--	48.6	5.4	108.0	108.0
Jaegers	--	--	--	135.0	202.5
Black guillemot	--	--	--	7.2	1.8
Thick-billed murre	--	0.4	0.4	20.2	1.4
Loons	--	--	--	1125.0	1125.0
Phalaropes	243.0	--	--	--	27.0
Total	260.6	86.7	8.1	1552.3	1638.2

Table 20. Assumptions used in calculating foods consumed by ringed seals in the study area.

	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct
Biomass (t)	1372	1372	1372	1372	1372	1372	1372	1372	2744	2744	2744	2744
Daily consumption rate (% of body weight)	8.4	8.4	8.4	8.4	8.4	1.9	1.9	1.9	4.1	5.6	5.6	7.4
No. of days	30	31	31	28	31	30	31	30	31	31	30	31
Composition of diet (%)												
Arctic cod	81	81	81	81	81	6	6	6	18	30	30	56
Euphausiid	--	--	--	--	--	20	20	20	20	21	21	10
Hyperiid amphipod	4	4	4	4	4	--	--	--	22	44	44	24
Other	14	14	14	14	14	74	74	74	40	5	5	10

Table 21. Estimated quantities of food (t) consumed by ringed seals in the study area.

Prey Category	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Total
Arctic cod	2800	2894	2894	2614	2894	47	48	47	628	1429	1383	3525	23,203
Euphausiid	--	--	--	--	--	156	162	156	698	1000	968	629	3,769
Hyperiid amphipod	138	143	143	129	143	--	--	--	767	2096	2028	1511	7,098
Other	484	500	500	452	500	579	598	579	1395	238	230	629	6,684

Table 22. Assumptions used in computation of food consumption by bowhead and belukha whales and arctic cod in the study area.

Consumer Species	No. Individuals	Average Individual Wt. (t)	Total Estimated Biomass (t)	Residence Time in Area (days)	Daily Feeding Rate (% of total body wt.)	Percent of Prey Category in Diet				
						Copepod	Euphausiid	Hyperiid Amphipod	Arctic Cod	Other
Bowhead whale	2264	15.9	36,000	25	3.0	30	65	1	--	4
Belukha whale	6000	0.8	4,800	30	5.1	--	--	--	80	20
Arctic cod	--	--	85,890	365	6.0	56	8	1	1	34

Table 23. Total quantities of prey (t) eaten annually by major vertebrate consumers in the study area. The percent of the total for each prey eaten by each consumer is given in parentheses.

Consumer Species/ Group	Prey Category					Total
	Copepod	Euphausiid	Hyperiid Amphipod	Arctic Cod	Other	
Bowhead whale	8,100 (0.8)	17,550 (10.2)	270 (1.0)	--	1,080 (0.2)	27,000
Belukha whale	--	--	--	5,875 (12.3)	1,469 (0.2)	7,344
Ringed seal	--	3,769 (2.2)	7,098 (27.2)	21,203 (44.7)	6,684 (1.0)	38,754
Seabirds	261 (<0.1)	87 (0.1)	8 (<0.1)	1,552 (3.3)	1,638 (0.3)	3,546
Arctic cod	1,053,355 (99.2)	150,479 (87.5)	18,810 (71.8)	18,810 (39.7)	639,537 (98.3)	1,880,991
Total	1,061,716	171,885	26,186	47,440	650,408	

consumers of euphausiids, with cod estimated to consume about eight times the quantity eaten by bowheads. Largest amounts of hyperiid amphipods are eaten by arctic cod and ringed seals. Major consumers of arctic cod, in decreasing order of estimated amounts eaten annually, were ringed seals, arctic cod, belukha whales, and seabirds.

VII. Biology of Major Prey Species

A. Euphausiids

Euphausiids, pelagic shrimp-like crustaceans commonly referred to as "krill," occur in large swarms in neritic oceanic waters of all oceans of the world. They have been described as "second in importance only to the copepods as basic animal food in the sea" (Boden et al. 1955). Two species, Thysanoessa raschii and T. inermis, predominate over the shelf and slope of the Beaufort Sea and the Arctic Ocean, although few are found in the eastern Beaufort Sea or at far northern latitudes (Geiger et al. 1968).

Both species are present in the North Atlantic and the North Pacific, and are most abundant over or near the shelf in relatively shallow nearshore waters. Thysanoessa raschii is usually found in slightly shallower water (usually less than 200 m deep) than T. inermis (up to 300 m deep) and is the more abundant of the two in the Pacific sector and at more northern latitudes (Einarsson 1945; Berkes 1976). Distribution of both extends from the neritic waters of British Columbia and Alaska north through the Bering and Chukchi Seas to the nearshore waters of the Alaskan arctic coast (Boden et al. 1955). Geiger et al. (1968) suggested a distribution discontinuity through the Canadian Archipelago, as did Dunbar (1964, cited in Geiger et al. 1968).

Information on the vertical distribution of T. inermis and T. raschii specific to the Beaufort Sea is unavailable. However, in the North Atlantic, where they have been studied in considerable detail, the vertical distribution of the two species is similar. In the Barents Sea and the Firth of Clyde, Scotland, eggs and larvae are present in near-surface waters during summer and descend to lower levels during the fall as they reach late larval stages (8-12 mm) (Macdonald 1928; Drobysheva 1957). The adults are "denizens of the bottom strata" (Einarsson 1945), usually occurring at depths greater than 100 m or in shallower waters within a few meters of the bottom (Macdonald 1928; Einarsson 1945; Drobysheva 1957). Diurnal migrations from the bottom during the day to the surface at night have been reported throughout the North Atlantic. In far northern waters diurnal migrations occur only during spring and fall when a light-dark regime occurs (Drobysheva 1957). In the Gulf of St. Lawrence T. inermis has a somewhat broader vertical distribution than T. raschii; it is found from 0 to 70 m at night and 100 to 300 m during the day, whereas T. raschii is most abundant from 100 to 200 m during the day and in the upper 20 m at night (Berkes 1976). Animals within the layers become more concentrated as they approach the surface (Sameoto 1976a).

Seasonal differences in the vertical distribution of adults vary somewhat geographically. In the Barents Sea, Einarsson (1945) found adult *T. inermis* near the surface in December-January, in the middle and surface layers from February until April, and near the bottom in August. In the Firth of Clyde adults apparently move to deeper water in winter, where densities are four to five times greater than in summer (Mauchline 1966). Macdonald (1928) believed that adults were more concentrated after, rather than during, the spawning period.

Abundance of euphausiids is difficult to quantify. Since they are rapid swimmers and avoid nets, quantitative estimates produced by standard zooplankton sampling techniques greatly underestimate total biomass. At best, such estimates may indicate relative abundance. The use of sonar in the North Atlantic has established that "aggregation, both vertical and horizontal, on scales varying from meters to kilometers, is the rule rather than the exception" (Brodie et al. 1978). By standard techniques, biomass estimates for euphausiids in northern waters are well below 1.0 g/m^3. Brodie et al. (1978) cited 0.1 g/m^3 for Nova Scotian waters. Berkes (1977) found densities of 96 adults/1000 m^3 in the Gulf of St. Lawrence, or about 0.01 g/m^3. Horner (1981) reported maximum concentrations of *T. raschii* off Demarcation Point of 510/1000 m^3 (approximately 0.05 g/m^3) and of *T. inermis* off Barter Island of 100/1000 m^3 (about 0.01 g/m^3). Redburn (1974) caught a maximum of 93 *T. raschii* (juveniles)/100 m^3. In contrast, estimates derived from echo sounding are several orders of magnitude greater, in the range of 1 to 10 to 10 g/m^2 (Cushing and Richardson 1956 and Barry 1966, both cited in Brodie et al. 1978). Brodie et al. (1978) located layers of *Meganyctiphanes norvegica* 5-20 m thick and extending horizontally 300-400 m in which they estimated a biomass of 8-26 g/m^3.

The exact time of spawning for *T. inermis* and *T. raschii* in the Beaufort Sea is unknown; however, throughout their range they are spring-summer spawners. Eggs are released just before or during the spring phytoplankton bloom in relatively shallow coastal waters (Drobysheva 1957; Berkes 1976). Spawning occurs later in cold northern waters, and within the same geographical area may be delayed by several months in cold-water years (Einarsson 1945; Drobysheva 1957). *Thysanoessa raschii* is the only northern euphausiid known to spawn at temperatures below 0°C, sometimes at the ice edge. In the Barents Sea and waters off Greenland and Iceland, spawning begins in early May and is over by June (Einarsson 1945; Drobysheva 1957). Redburn (1974), working off Point Barrow, did not catch spawning adults but reported abundant *Thysanoessa* larvae in late June and again in late July and early August, and suggested that the two peaks correspond to the spawning periods of the two species. Berkes (1976) indicated that *T. inermis* spawned slightly earlier and over a shorter time span than *T. raschii*, and suggested that relative survival of the two species in a particular year is related to the nature of the phytoplankton blooms. In years following a well-developed spring bloom, *T. inermis* predominates; in years when the spring bloom fails to develop or is very late, *T. raschii*, which spawns over a prolonged period, is more successful.

The eggs develop through several larval stages: nauplius larvae, calyptopis larvae, furcilia larvae, and cyrtopia larvae (Macdonald 1928). Development to the adolescent "fry" stage requires about 2 months in the Firth of Clyde and probably somewhat longer in more northern waters (Mauchline 1966). Thysanoessa raschii grows somewhat slower and matures slightly later than T. inermis.

Individuals of T. inermis and T. raschii mature in 1 year in the southern parts of their range (Iceland, English Channel, Firth of Clyde, and Gulf of St. Lawrence), but require 2 years farther north in Greenland and in the Barents Sea (Einarrson 1945; Mauchline 1966; Berkes 1976). Many adults probably live to spawn twice, the first time at 2 years (about 22 mm long) and the second at 3 years (28 mm long). Berkes (1976) suggested that T. inermis is the more long-lived of the two, based on the relative abundance of larger size classes.

Thysanoessa euphausiids eat a variety of foods. They are not strictly herbivorous, but also feed on crustaceans (especially copepodites), dinoflagellates, eggs, tintinnids, and detrital materials found in surface muds which are resuspended by beating pleopods (Mauchline 1966; Berkes 1976). In the Gulf of St. Lawrence, Berkes (1976) found feeding intensity to be greatest in August and least in winter. Food is obtained by filtering water through a "basket" formed by thoracic appendages which are covered with long plumose setules spaced 6-9 microns apart (Berkes 1976). The setules of T. raschii are spaced slightly closer together than those of T. inermis, suggesting that, although dietary overlap is considerable, T. raschii can utilize somewhat smaller food particles than T. inermis. Lasker (1966) found that in Euphausia pacifica filtering rate is dependent on the density of prey down to a minimum concentration when filtering ceases.

Euphausiids are major prey of many vertebrate consumers in the Beaufort Sea. They are eaten by seabirds, including phalaropes, arctic terns, black-legged kittiwakes, Sabine's gulls, oldsquaws, glaucous gulls, and Ross' gulls (Divoky 1979). In offshore waters they are occasionally eaten by arctic cod. During August-September they are eaten by ringed seals and bowhead whales. They are an important intermediate link between phytoplankton and microcrustaceans and higher trophic levels. Sameoto (1976b) estimated that in regions of the Gulf of St. Lawrence with high euphausiid biomass they could consume as much as 29% of the total primary production in September and up to 60% in December. Lasker (1966) suggested that in another northern euphausiid, Euphausia pacifica, almost 30% of the total carbon ingested throughout its life span may be available to other organisms in the food chain. Of that 30% about 9% is due to eggs, 6-11% to molts, and the remainder, about 10%, to growth. Over the lifetime of an adult Thysanoessa about seven times its body mass is returned to the food chain as molts (Sameoto 1976b). Since marine mammals, birds, and fishes eat the euphausiids themselves, not eggs and molts, they have available to them approximately 10% of the total carbon ingested by the euphausiids.

Energetic values for euphausiids vary somewhat by species and by season. Lipid levels in *T. raschii* (and presumably *T. inermis*) are high in the fall (up to 9-12% of wet weight) and decrease in winter, reaching minimum levels in January to March (Mauchline 1966; Ackman et al. (1970). The lipids of euphausiids are not stored in lipid sacs or globules as they are in copepods, and are mostly phospholipids rather than triglycerides. In general, triglycerides are storage products, whereas phospholipids are characteristic of cellular organization. The predominance of phospholipids suggests that *Thysanoessa* makes it through the winter by reduced metabolism and/or utilization of body proteins and carbohydrates (Ackman et al. 1970).

Parsons (1977) estimated the caloric value of *Thysanoessa* to be 665 cal/g wet weight. Nishiyama (1977) presented considerably higher values of 1,173-1,204 cal/g wet weight (5,414-5,554 cal/g ash-free dry weight), as did Sameoto (1976b) who reported 4,910 cal/g dry weight for *T. inermis* and 4,950 cal/g dry weight for *T. raschii*. Based on Sameoto's data, an adult *Thysanoessa* weighing 0.1 g (the average size of euphausiids found in the seal and bowhead stomachs we examined) has an energy value of about 88 cal.

B. Hyperiid Amphipods

Two species of pelagic hyperiid amphipods are abundant in the Beaufort Sea: *Parathemisto libellula* and *P. abyssorum*. *Parathemisto libellula* is a circumpolar arctic species, indicative of cold arctic waters, although it is also present in subarctic regions. It is distributed from the surface to 2,500 m but frequently swarms near the surface in very large numbers (Dunbar 1942, 1946). It is positively phototropic, and Dunbar (1942) suggested that the deep purple pigmentation, similar to that of the pteropod *Limacina* which also swarms close to the surface, may be an adaptation to bright light.

Parathemisto abyssorum, also circumpolar in distribution, is more typically subarctic, but is also found in the Arctic Basin (Grainger 1962). In Wellington Channel in the Canadian Arctic, Bain et al. (1977) found *P. abyssorum* mostly deeper than 50 m.

Information on the abundance of *Parathemisto* in the Beaufort Sea is very general. Like euphausiids, they are highly mobile and difficult to sample with traditional plankton nets. MacGinitie (1955) noted that *P. libellula* was extremely abundant near Barrow, while Redburn (1974) found them to be less common than gammarid amphipods, reaching maximum concentrations under the ice in spring and early summer. Horner (1981) reported that *P. libellula* and *P. abyssorum* were present at about 75% of the stations she sampled in the Beaufort Sea in August-September 1977-79. They were most abundant (7,970/1,000 m^3) near Harrison Bay in September 1977, where Lowry et al. (1980) collected ringed seals eating large volumes of *P. libellula*. Virtually nothing is known about the temperature and salinity requirements of either species, except that both are found in cold arctic and subarctic waters. Little is known about seasonal changes in distribution and abundance. Griffiths and Dillinger (1981) sampled in the Beaufort Sea in Simpson Lagoon and off shore from Pingok Island in July-September; they caught no *P. libellula* in July and small numbers in August. In September this species made up 25-50% of all amphipods caught inside the lagoon and more than 80% of those caught outside the lagoon.

Female *Parathemisto* carry eggs and brood young in an abdominal pouch. In southeastern Alaska, *P. libellula* carry the eggs and early juveniles for 3 to 8 weeks (Wing 1976). In the eastern Canadian Arctic, Dunbar (1946, 1957) found mature females in late January through April and small juveniles until early August from which he concluded that release of young from brood pouches started by February and continued until June or July. Spawning occurs over a similar period in *P. abyssorum*, from February until early August (Bowman 1960; Hoffer 1972). Peak release of young in both species apparently occurs during the spring phytoplankton bloom. Young *P. libellula* are released at a length of 2-3 mm and spend the first few months near the surface. Growth is slow in northern waters where individuals of both species require 18 months to 2 years to mature (at about 25-45 mm length) (Dunbar 1957; Hoffer 1972). In Baffin Bay during summer, the size distribution of the *P. libellula* population is clearly bimodal, consisting of immatures (<20 mm) and adults (>20 m) (Dunbar 1957).

Hyperiid amphipods are generally considered carnivorous, although some vegetable matter is consumed by both young and adults. Dunbar (1946) reported that in August *P. libellula* ate small crustaceans and plankton, including all stages of copepods, decapod larvae, ostracods, and vegetable material. Some cannibalism has been documented. Dunbar suggested that young released during winter when phytoplankton is scarce probably consume detritus.

Parathemisto is eaten by a variety of arctic fishes, birds, and mammals. Dunbar (1957) considered that *P. libellula* "forms the most important link in the food chain between the copepods and other smaller planktonic forms on the one hand, and the vertebrates on the other, and in fact it takes the place, in cold water, of the euphausiids in this respect." Mohr and Geiger (1968) stated that "*Parathemisto* apparently serves as a "krill" for the bowhead and gray whales in the waters north of Alaska." Although we cannot verify the statement of Mohr and Geiger, large numbers of *P. libellula* are present in the Beaufort Sea in at least September through November and are consumed in quantity by ringed seals at that time (Lowry et al. 1980). Oldsquaws and glaucous gulls feeding in Simpson Lagoon and seaward of Pingok Island in 1977 and 1978 had also eaten *Parathemisto* (Johnson and Richardson 1981). Craig and Haldorson (1981) reported that *Parathemisto* was never a major food of lagoon fishes, and Frost and Lowry (unpubl.) found that of 19 species or species groups of offshore demersal fishes only leatherfin lumpsuckers (*Eumicrotremis derjugini*) ate these hyperiids. Johnson and Richardson (1981) found large numbers of hyperiids washed up on the beaches near Simpson Lagoon in September 1977.

Nishiyama (1977) reported the caloric value of *P. libellula* collected in the Bering Sea as 652 cal/g wet weight (4,458 cal/g ash-free dry weight or 3,415 cal/g dry weight). Griffiths and Dillinger (1981) reported a considerably higher value of 6,300 cal/g ash-free dry weight in the Beaufort Sea. *Parathemisto* accumulates storage lipids; lipid levels are higher in fall than in winter when food is scarce. Triglycerides are the main storage product and comprise 12-56% of the total lipids (Lee 1975).

C. Mysids

Several species of mysids occur in the Beaufort Sea, but only one, *Mysis litoralis*, is an important prey species of birds and marine mammals. (The taxonomy of this and another species, *M. oculata*, is somewhat confused. For the purposes of this report we refer to the *M. litoralis* - *M. oculata* group as *M. litoralis*.) *Mysis litoralis* is a circumpolar arctic and subarctic species ranging from 55-82°N latitude, including waters of the west coast of Greenland, western North America, Baffin Island, and the Beaufort Sea (Banner 1954; Holmquist 1958). It is euryhaline and most abundant in shallow neritic waters where it is littoral-nektonic rather than benthonic (Dunbar 1942; Geiger 1969). Along the Beaufort Sea coast, Griffiths and Dillinger (1981) found juveniles to be abundant inside lagoons and older, mature animals to be more common several kilometers outside the barrier islands. Crane (1974) also encountered high concentrations of *Mysis* in samples from the Beaufort Sea off Simpson Lagoon. He estimated a standing stock of 28 mg C/m^2. Horner (1981) caught *M. litoralis* at about 20% of all stations sampled in the Beaufort Sea.

Life history information is available for the Alaska Beaufort Sea coast (Griffiths and Dillinger 1981). Spawning occurs in late September and October. The females brood an average of 50 young over the winter and release them in spring at a length of 2-4 mm. Growth of juveniles is rapid during July-August; by the end of the open water season first-year individuals measure 10-12 mm. Individuals do not mature until fall of the following year when they reach 16-18 mm; many live to produce a second brood in the fall of their third year when they have grown to 25-35 mm. Geiger (1969) also reported a 2-year life cycle off the Siberian coast, with maturity occurring at about 20 mm.

The food habits of mysids have been little studied. In Sanguenay Fjord, Quebec, *Mysis* ate a variety of phytoplankton, zooplankton, and detritus (DeLadurantaye and Lacroix 1980). Mysids are eaten by many fishes, birds, and marine mammals. Of the offshore demersal fishes, sculpins especially feed on *Mysis* (Frost et al. 1978). Ross' gulls, common eiders, Sabine's gulls, arctic terns, oldsquaws, phalaropes, and glaucous gulls eat substantial quantities of mysids (Divoky 1977; Johnson and Richardson 1981).

Caloric value of mysids varies according to age and reproductive status. Griffiths and Dillinger (1981) reported a value of 5,470 cal/g ash-free dry weight for a sample of *Mysis litoralis* of unknown age and sex. Clutter and Theilacker (1971) reported similar values for another mysid, *Metamysidopsis elongata*: adult males and non-gravid females were 5,100-5,200 cal/g ash-free dry weight, and gravid females were 5,700 cal/g ash-free dry weight. They found lipids to comprise an average of 9-11% of dry weight, except in brooding females where lipids were about 19%. In working out energy budgets for *Metamysidopsis* they determined that about 19-29% of the calories ingested over the life of an individual is available for transfer to the rest of the trophic web.

D. Copepods

In the Arctic, copepods as a group are the dominant component of the zooplankton throughout most of the year. According to Hopkins (1969, cited in Bain et al. 1977), copepods comprise over 80% of the zooplankton biomass in arctic waters. In the Canadian Archipelago near Resolute, 72-98% of the total zooplankton biomass in the upper 25 m was copepods (Bain et al. 1977). At Beaufort Sea stations east of Harrison Bay, copepods made up more than 50% of the zooplankton at most stations and sometimes as much as 90% (Horner 1981). They comprised a much larger proportion of the zooplankton east of Harrison Bay than west of there to Barrow. Diatom abundance was correspondingly higher at easternmost stations, whereas flagellates were the dominant phytoplankters to the west. Grainger (1965) described what he considered a widespread, truly arctic group of zooplankton species occurring throughout surface waters of the Arctic Ocean, the eastern Canadian Archipelago, and Baffin Bay. Eight species of copepods are included in that group: *Calanus hyperboreus*, *C. glacialis*, *Pseudocalanus minutus*, *Microcalanus pygmaeus*, *Pareuchaeta glacialis*, *Metridia longa*, *Oithona similis*, and *Oncaea borealis*. Most of those eight were reported as abundant in the central and western Beaufort Sea (English and Horner 1977) and in the eastern Beaufort and Amundsen Gulf (Grainger and Grohe 1975; Griffiths 1981). In Grainger's (1965) samples those eight made up 99% of the total number of copepods in the upper 50 m of water and 95% of those from depths of 50-300 m. Johnson (1956) found *C. hyperboreus*, *M. longa*, and *P. minutus* to be the most abundant species in the Beaufort Sea. Horner (1981) reported that *C. hyperboreus*, *C. glacialis*, and *M. longa* were generally most abundant, with *C. glacialis* dominant in the western area and *C. hyperboreus* and *M. longa* most numerous to the east.

Copepod life cycles are generally similar to those of other pelagic crustaceans. Females are usually more abundant than males, and immature individuals are far more abundant than adults. Eggs are released directly into the water and hatch into nauplius larvae which develop, in a brief period lasting only hours to days, through six stages to become copepodite larvae. Larvae then pass through five copepodite stages, each resulting in the addition of abdominal segments and/or swimming legs, finally reaching the adult stage which is reproductively fully developed (Brodskii 1950). The time required to complete a generation varies from as little as a few weeks in warm southern waters to as much as 2 years in the high Arctic.

Most, though not all, copepods are herbivorous filter feeders. They swim in a vertical position, anterior end up, creating a swimming vortex by rapidly rotating mouth parts. *Calanus* copepods can probably filter particles as small as 3-4 microns, but prefer those of larger size (Vyshkvartzeva 1977). Foods frequently eaten include diatoms, flagellates, small crustaceans, radiolaria, infusoria, bacteria, and crustacean (including other copepods) eggs and larvae (Brodskii 1950; Vyshkvartzeva 1977). They can also utilize detritus, but with reduced assimilation efficiency (Vyshkvartzeva 1977).

In the Arctic where primary production occurs for only a few months of the year the primarily herbivorous copepods must be able to live for long periods with little or no food. As an adaptation to such a life style they store large quantities of lipids as oil droplets or globules. Fat reserves are greater in fall than in winter and make up 15-20% of total body weight (Brodskii 1950), possibly as much as 20-42% (Vyshkvartzeva 1977). Caloric values vary accordingly, since the energy value of fat is about 9,500 cal/g, considerably higher than that of whole organisms (Laurence 1976). Laurence (1976) presented an average value for eight copepod species of 5,252 ± 182 cal/g dry weight (5,626 cal/g ash-free dry weight). *C. finmarchicus* (closely related to *C. glacialis*) was somewhat higher in calories (6,425 cal/g dry weight) than *Pseudocalanus* (5,071 cal/g dry weight). Nishiyama (1977) reported similar values: 5,512 cal/g ash-free dry weight for copepods in general and 5,400-5,700 for two *Calanus* species.

Calanus hyperboreus is a dominant copepod of the Arctic Basin, occurring from the surface to at least 400 m deep in all arctic seas (Brodskii 1950; English and Horner 1977), including the waters off the coast of Ireland, the east and west coasts of Greenland, Baffin Bay, the American Atlantic coast south to Cape Cod, the European Atlantic including the French and Norwegian coasts, and the Bering, Chukchi, and Beaufort Seas (Fontaine 1955). It is the most abundant species of copepod in much of the Beaufort Sea, including Amundsen Gulf, waters north and east of Banks Island, and the southern Beaufort Sea (Johnson 1956; Mohammed and Grainger 1974; Griffiths 1981). Off Barter Island in 1972, *C. hyperboreus*, mostly adult females and stage V's, made up 60% of all copepods (English and Horner 1977). In August-September 1976, English and Horner (1977) caught mostly stage I-IV's but no V's and no adult females. Griffiths (1981) caught mostly stage IV's in Amundsen Gulf. In the central Beaufort, *C. hyperboreus* was more abundant from 10-20 m deep than in the upper 10 m of the water column and was most abundant over depths greater than 100 m (English and Horner 1977).

Calanus hyperboreus breeds in the absence or scarcity of phytoplankton, independent of the spring and summer blooms (Grainger 1965). In Ungava Bay peak spawning probably occurs in February-March (Fontaine 1955). Grainger (1965) reported finding stage I copepodites in all months of the year, with a peak in June, which suggests peak spawning in April or May. Grainger (1959), working at Igloolik caught nauplii in late May, stage I copepodites in June, II's in late June, III's at the end of

July, IV's in late August, and adults in early fall and winter. Some overwinter as stage III's and may become adults the following July. Adult females are 7-10 mm in length and weigh about 3.7 mg; adult males are 5-7 mm. Copepodite stage V's weight about 1.6 mg (Brodskii 1950; Conover 1960).

Calanus hyperboreus is mostly herbivorous, although when food is scarce it will eat its own eggs (Conover 1960). Lipids are stored as wax esters, rather than triglycerides. The degree of saturation of those lipids indicates that feeding takes place in summer but not in winter (Lee 1975).

Calanus glacialis is characteristic of cold arctic surface waters, with an overall distribution similar to that of C. hyperboreus. It usually occurs in the upper 300 m at salinities greater than 20 ppt (Grainger 1975). It is one of the three most abundant copepods throughout much of the Arctic (Grainger 1962; Bain et. al. 1977; English and Horner 1977; Griffiths 1981). Off northern Alaska, English and Horner (1977) found C. glacialis to be more abundant west of Harrison Bay than to the east. During August-September they caught C. glacialis throughout the water column. Maclellan (1967) found none at depths less than 100 m from October-February off west Greenland and suggested that stages IV, V, and adults migrate to deep water in winter and to surface waters by mid-March.

Spawning in C. glacialis is thought to coincide with peak phytoplankton abundance; if the phytoplankton bloom is prolonged, so is the spawning period (Grainger 1965; Maclellan 1967). Grainger (1959) suggested that C. glacialis spawn in June-July. Horner (1981) caught females with eggs in August-September 1977. Most samples collected in the Beaufort Sea during August-September contained stages III-V, with some adult females (Griffiths 1981; Horner 1981). Grainger (1965) reported that nauplii from eggs spawned in June-July reached stage I by late July-early August, II in early September, and overwintered as III's or IV's. He suggested that the many stage III's, IV's, and V's caught in June-July are from the previous year's spawn, and probably don't reproduce until the following year at age 2. In C. finmarchicus, the "Atlantic version" of C. glacialis, nauplii produced early in the season when phytoplankton is most abundant reach greater size at corresponding stages than do nauplii produced in fall. They require only 6 weeks to become copepodite V's and 7 or 8 months until they breed, whereas the later nauplii overwinter as copepodites III or IV, do not reach adulthood until the following winter, and breed at 19-20 months of age. Off west Greenland the life cycle apparently requires only 1 year (Maclellan 1967).

Calanus glacialis is primarily an herbivore; it eats mostly diatoms (Bain et al. 1977).

In the Arctic the genus Pseudocalanus is represented by several species. However, there is sufficient taxonomic confusion over the validity of those species that, for the purposes of this report, we have grouped them as Pseudocalanus sp. Members of this group have wide temperature and salinity tolerances. They are found in both oceanic waters and near shore in the Arctic and sub-Arctic, including the Arctic Ocean; the coasts of Greenland, Iceland, Norway, and Alaska; the North Sea; the American Atlantic; and Baffin Bay (Fontaine 1955). It is the most abundant copepod group in much of the Canadian Arctic and at some locations in the Beaufort Sea (Grainger 1962 and 1965; Bain et al. 1977; Tarbox et al. 1979).

Pseudocalanus spawns throughout the summer, with a peak during the main phytoplankton bloom (Fontaine 1955; Grainger 1959, 1965). At Igloolik Grainger (1959) found ovigerous females from April to August. Horner (1981) caught adult females near shore between Harrison Bay and Demarcation Point in August and early September 1977-78. In Amundsen Gulf during August 1980, Griffiths (1981) reported mostly adults and stage V's.

At Igloolik copepodite stage I's are present in mid-June; II's, III's, and IV's in early, mid-, and late July; and V's in late August, for a total development time of about 14 weeks (Grainger 1959). Development is faster at higher temperatures and when phytoplankton is more abundant. Hatching occurs in 10-11 days at 0°C and 2-3 days at 11°C (McLaren et al. 1968). Depending on when they were spawned and local conditions, some individuals reach maturity in less than a year while some require longer. Size of adult males is 1-2 mm; females are slightly larger (Brodskii 1950; Tarbox et al. 1979).

Pseudocalanus is primarily an herbivore but can also utilize detritus (Bain et al. 1977; Poulet 1977). Copepodites and adults can utilize the same particles within the size range 1.5-144.0 microns; however, copepodites feed most efficiently on small particles (<10 microns), whereas adults prefer larger particles (Poulet 1977).

Copepods of the genus Acartia are found in neritic surface waters. Grainger (1965) considered them coastal in the southern Beaufort Sea and Amundsen Gulf. They are most common at depths of less than 20 m, usually in the upper 5-10 m of the water column. They eat primarily diatoms (Conover 1960). Adults are about 1 mm in length (Tarbox et al. 1979).

Metridia longa is characteristic of deep offshore waters. They are found near the surface (upper 50 m) in November-March and deeper (175-300 m) during the summer (Grainger 1959; English and Horner 1977). It is an arctic form, widely distributed in the Arctic Ocean and its epicontinental seas, east and west Greenland, Iceland, Norway, Spitzbergen, and the eastern Chukchi Sea (Brodskii 1950; Fontaine 1955). Like C. hyperboreus, the time of breeding for Metridia is not completely dependent on the phytoplankton bloom. Breeding occurs over an extended period and the development of young apparently continues through winter. Most spawning probably takes place from March-July in deep water (Grainger 1965). Adults are about 4 mm in length (Brodskii 1950).

Derjuginia tolli[1] is a neritic species often associated with brackish waters (Brodskii 1950). It is found in all marginal seas of the Polar Basin and is widely distributed in the southern Beaufort Sea (English and Horner 1977; Tarbox et al. 1979; Griffiths 1981). No adult females were caught by either Griffiths or English and Horner during August. Adults are 2.0-2.5 mm in length (Brodskii 1950).

E. Gammarid Amphipods

Many species of gammarid amphipods are abundant in the Beaufort Sea (Frost et al. 1978). We will discuss only one species, Apherusa glacialis, which is a pelagic and ice-associated form of considerable importance in the diet of fishes and seabirds. Apherusa glacialis is a circumpolar arctic and subarctic species usually found in the upper 200 or 300 m of water (Shoemaker 1955; Grainger 1959; Tencati and Leung 1970), often in association with sea ice surfaces. Juveniles are abundant in the upper 50 m in areas where breeding occurs. Apherusa is probably more abundant than indicated by plankton tows, since it is a common food of seabirds and arctic cod (Divoky 1976; Bain et al. 1977; Frost and Lowry, this report), even in areas where fewer or none are caught in tows.

In the Arctic Basin, spawning probably occurs during winter. Grainger (1959) reported catching females in November that had recently liberated young. Tencati and Leung (1970) suggested that spawning occurs in January-February in the Arctic Basin. By June juveniles are 6-8 mm; final adult size is 7-11 mm (Shoemaker 1955; Grainger 1959).

Apherusa, like other arctic crustaceans, stores lipids (primarily triglycerides) for the winter period of reduced food availability (Lee 1975).

VIII. Discussion and Conclusions

A. Foods and Feeding of Bowhead Whales

Based on the examinations of bowhead stomach contents we have conducted and other published observations, a reasonable assessment of the foods utilized by bowheads in the Alaskan Beaufort Sea can be made. Dominant prey are euphausiids, principally Thysanoessa raschii, and calanoid copepods, primarily of the genus Calanus. Although a variety of other planktonic and benthic organisms has been recorded from bowhead gastrointestinal tracts (Table 11), organisms other than copepods and euphausiids have not occurred in significant quantities. This is consistent with observations of the morphology of bowhead baleen, the

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[1] A recent publication (Mapkhaceva 1980) has suggested that the name of Derjuginia tolli be changed to Jaschnovia tolli.

long, fine nature of which suggests adaptation to feeding on small pelagic crustaceans (Tomilin 1957; Nemoto 1970). The occasional occurrence of benthic organisms in bowhead stomachs has led some investigators (e.g., Mitchell 1975; Griffiths 1981) to consider benthos as an important food source. Observations of bowheads surfacing with mud streaming from their mouths have also been considered evidence of feeding of benthos (Wursig et al. 1981). We discount the presumed importance of benthos in the bowhead diet for two reasons. First, the feeding apparatus of bowheads shows no specializations for bottom feeding, and in fact the bowhead appears to be the most specialized of all baleen whales for straining small zooplankton from the water column. Secondly, our observations (Section III) indicate that in at least some circumstances copepods are concentrated in dense layers within a few meters of the bottom. We think that both the presence of epifaunal benthic species in stomachs and the mud seen in the presence of feeding whales are adequately explained by whales feeding close to the bottom, eating primarily copepods and perhaps euphausiids which are also known to concentrate just off the bottom (Einarsson 1945; Mauchline 1966). Griffiths (1981) also speculated that hyrodozoans, which are abundant in the Beaufort Sea, could be a major food for bowheads. However, hydrozoans have not occurred in any of the stomach samples we examined, and it seems unlikely to us that baleen specialized to catch small hard-bodied crustaceans would also efficiently capture large soft-bodied organisms. We therefore agree with Tomilin (1957) that organisms such as ctenophores and hydrozoans are consumed only incidentally.

Little is known of the feeding behavior of bowheads. Undoubtedly sensory mechanisms are used to detect appropriate types and quantities of prey. The excellent observations of Watkins and Schevill (1976, 1979) indicate that right whales (Eubalaena glacialis) feed on patches and bands of concentrated plankton, sometimes at the surface and sometimes at greater depths. They stated that "These whales usually turned away from sparse patches towards areas of denser material, turning within the patch (as much as 90° or more) to maintain courses that were well within heavy concentrations of plankton." Wursig et al. (1981) observed and described bowheads engaged in what they termed bottom feeding, water column feeding, and skim feeding. These may correspond to feeding on plankton concentrations which are near the bottom, in midwater, and near the surface, respectively, although Wursig et al. (1981) did not see dense patches of plankton in the vicinity of skim feeding whales. Griffiths (1981), however, as part of the same study found that copepod biomass was significantly higher where whales were seen than at other stations.

Limital concentrations of prey for efficient feeding by bowheads have not been determined. Experiments conducted by Braithwaite (1980 and pers. comm.) indicate that bowhead baleen can filter Artemia at 96-98% efficiency over a fairly wide range of prey sizes and concentrations. The lower limit of prey abundance at which bowheads might seek more favorable feeding grounds is not known. Our observations (Section V, Appendix II) and those of Durham (1972) indicate that at times, perhaps especially during the spring migration, bowheads ingest food when neither long, fine nature of which suggests adaptation to feeding on small pelagic crustaceans (Tomilin 1957; Nemoto 1970). The occasional occurrence of benthic organisms in bowhead stomachs has led some investigators (e.g., Mitchell 1975; Griffiths 1981) to consider benthos as an important food source. Observations of bowheads surfacing with mud streaming from their mouths have also been considered evidence of feeding of benthos (Wursig et al. 1981). We discount the presumed importance of benthos in the bowhead diet for two reasons. First, the feeding apparatus of bowheads shows no specializations for bottom feeding, and in fact the bowhead appears to be the most specialized of all baleen whales for straining small zooplankton from the water column. Secondly, our observations (Section III) indicate that in at least some circumstances copepods are concentrated in dense layers within a few meters of the bottom. We think that both the presence of epifaunal benthic species in stomachs and the mud seen in the presence of feeding whales are adequately explained by whales feeding close to the bottom, eating primarily copepods and perhaps euphausiids which are also known to concentrate just off the bottom (Einarsson 1945; Mauchline 1966). Griffiths (1981) also speculated that hydrozoans, which are abundant in the Beaufort Sea, could be a major food for bowheads. However, hydrozoans have not occurred in any of the stomach samples we examined, and it seems unlikely to us that baleen specialized to catch small hard-bodied crustaceans would also efficiently capture large soft-bodied organisms. We therefore agree with Tomilin (1957) that organisms such as ctenophores and hydrozoans are consumed only incidentally.

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There are no direct observations of feeding of bowheads on the wintering grounds. Bowheads are extremely "fat" whales and based on comparisons with other species (Brodie 1975, 1980) it would be expected that they would feed extensively during a short summer season and fast the remainder of the year. Since primary production is low during the period when bowheads are on the wintering grounds in the Bering Sea and since the species of copepods eaten by right whales descend to deep water during that time (Nemoto 1970), we speculate that little if any feeding occurs during winter. Although small amounts of copepods, euphausiids, and other organisms sometimes occur in the stomachs of whales taken during spring, migrating and mating are the primary activities and foods consumed during the spring migration are likely to be of little overall significance. Bowheads probably derive the bulk of their annual nutrition during summer and early fall in the Beaufort and Chukchi Seas. We estimated (Section IV) that bowheads spend about 105 days feeding in the Canadian sector of the Beaufort, 25 days in the Alaskan Beaufort, and 30 days in the Chukchi. If the rate of feeding in each of the three areas is similar, they would contribute 66%, 16%, and 18%, respectively, of the annual foods eaten by bowheads.

Based on available information three areas can be delimited as regularly important feeding grounds. These are: 1) the southeastern Beaufort Sea and western Amundsen Gulf, particularly in the vicinity of the Tuktoyaktuk and Bathurst Peninsulas (Fraker and Bockstoce 1980, Wursig et al. 1981); 2) the area between Barter Island and the U.S.-Canada demarcation line (Ljungblad et al. 1980, Lowry and Burns 1980); and 3) the area between Point Barrow and Lonely (Braham and Krogman 1977; Lowry et al. 1978). It is possible that significant feeding occurs throughout the Alaskan Beaufort Sea; however, it is very unlikely that stomach contents samples will become available to confirm the possibility.

B. Trophic Interactions Among Major Vertebrate Consumers

We have assessed the quantities of food eaten annually by major vertebrate consumers in the Alaskan Beaufort Sea based on the best available estimates of population biomasses, residence times, diet composition, and feeding rates. Four major prey groups--copepods, euphausiids, hyperiid amphipods, and arctic cod--were considered as they are of particular importance in the trophic structure of the pelagic food web in the area (Frost 1978). Obviously, we have not modeled or simulated the structure of the pelagic food web of the Beaufort Sea. For example, we did not consider consumption of copepods by ctenophores, hydrozoans, pteropods, and chaetognaths, or competition for phytoplankton between copepods, larvaceans, euphausiids, and meroplankton. In addition, interactions such as predation on larval fishes by hyperiid amphipods and consumption of copepod eggs and larvae by older copepods were not dealt with. Available data and theory do not, in our opinion, allow such a model at the present time.

Nonetheless, it is possible in a very broad sense to estimate the zooplankton biomass available to consumers as a fraction of phytoplankton productivity. In Section III we estimated total annual primary production over the continental shelf of the Alaskan Beaufort Sea to be 3-44 million t (wet weight) per year. At a conservative conversion efficiency of 10% (Gulland 1974) that would produce 0.3-4.4 million t of zooplankton per year. Of that amount about 50-90% is copepods (Horner 1981). In Section V we estimated that vertebrate consumers eat approximately 1.3 million t of zooplankton and nekton annually. Thus, if the species we considered in this report represent most of the annual zooplankton consumption, it would seem that in "good" years of high primary productivity food is probably not limiting. However, in years of poor primary productivity due to heavy ice or a combination of other factors (for example, 1978, as discussed in Horner 1981), it is possible that food may indeed be limiting. Our estimate of vertebrate consumption exceeds the minimum zooplankton production estimate by a factor of four.

Several studies have compared the measured abundance of prey with the estimated food requirements of large whales (Brodie et al. 1978; Brodie 1980; Griffiths 1981). All concluded that traditional methods for estimating zooplankton abundance do not give a true picture of the actual availability of food. Brodie et al. (1978), working off Nova Scotia, found that the average euphausiid density as measured by plankton tows was 200 times too low to meet the food requirements of fin whales. They concluded that "whales must feed on euphausiid densities far greater than the average indicated by net samples" and that "aggregation of zooplankton must, therefore, be the general rule." Griffiths (1981) sampled zooplankton in Amundsen Gulf and found that biomass estimates were several times too low for a bowhead to obtain an adequate daily ration. He too concluded that "it would appear that bowheads must concentrate their feeding in areas where zooplankton biomass is somewhat greater than average." Brodie et al. (1978) suggested that minimum densities in prey patches must be about 20 g/m^3 for fin whales; Brodie (1980) suggested a similar density of 30 g/m^3 for bowheads. The inadequacy of existing data on prey availability and the evidence for concentrated prey patches are further reinforced by the fact that whales are only one of many consumers utilizing the zooplankton resource.

We estimate that the vertebrate consumers we considered eat about 2.0 million t of food annually in the study area. The distribution of the total among consumer groups was: seabirds - 0.2%, belukha whales - 0.4%, bowhead whales - 1.4%, ringed seals - 2.1%, and arctic cod - 96.0%. If only zooplankton and nekton (copepods, euphausiids, and hyperiid amphipods) are considered, approximately 1.3 million t are consumed annually, with the following distribution among consumers: seabirds - <0.1%, bowhead whales - 2.0%, ringed seals - 2.1%, and arctic cod - 95.8%. The small amount consumed annually by seabirds is due to a combination of their small total biomass and short residence time in the area. Belukha whales comprise a substantial biomass but were considered to feed in the study area for a short period of time. The estimated biomass of ringed seals in the area was less than that of belukhas, even during the summer period of maximum seal numbers. However, since they reside and feed in the area throughout the year, their total estimated annual food consumption was considerably greater than that of seabirds or belukhas. Bowheads were estimated to comprise a biomass more than 13 times as great as the maximum for ringed seals. The comparatively small amount of food estimated to be consumed annually by bowheads is due to the assumption of a short feeding period in the study area and a comparatively small daily food ration. Due to their year-round residence and large population size, calculations indicate that arctic cod are the major vertebrate consumer in the study area.

Based on our calculations, arctic cod are by far the major consumers of copepods, euphausiids, and hyperiid amphipods (Figure 8). Ringed seals consume a considerable amount of hyperiid amphipods, while both bowheads and ringed seals consume a significant portion of the total amount of euphausiids eaten by all vertebrate consumers. Arctic cod are eaten in quantity by all consumers except bowheads. Based on the assumptions we used, most of the predation on arctic cod is by ringed seals and arctic cod.

Our study did not include Amundsen Gulf and the Canadian sector of the Beaufort Sea, areas where bowheads feed for approximately 3-1/2 months. Based on data available on the fauna of that region (Galbraith and Fraser 1974; Barry 1976; Blood 1977; Stirling et al. 1977), we suspect that the situation in those areas is similar to that in the Alaskan sector of the Beaufort Sea. However, since bowheads feed there for a considerably longer time than in the Alaskan Beaufort, their relative importance as a consumer would be correspondingly greater.

The possible significance of our results depends on the competitive relationships among the consumer species and the relationship between total annual production and consumption. The latter question, that of food limitation, cannot at present be answered directly due to the complexity of even comparatively simple pelagic food webs and the lack of rigorous data on inter-species interactions. However, indirect evidence, primarily from other areas, strongly suggests that food limitation may be a common occurrence. This evidence takes two complementary forms. The first includes cases where reduction in the population size of a consumer species results in increased productivity of populations of that and/or trophically competing species (Mitchell 1975; Laws 1977; Hempel 1978). The second includes circumstances in which a reduction of prey populations has caused reductions in size or productivity of predator populations (e.g., Schaeffer 1970). In the case of bowheads the reduction in abundance caused by commercial whaling may have allowed an increase in populations of ringed seals, belukhas, seabirds, or arctic cod. If populations of seals and arctic cod were affected in a similar manner, increases in their populations may have been comparatively slight since arctic cod are the major prey of ringed seals. However, if ringed seal numbers in the

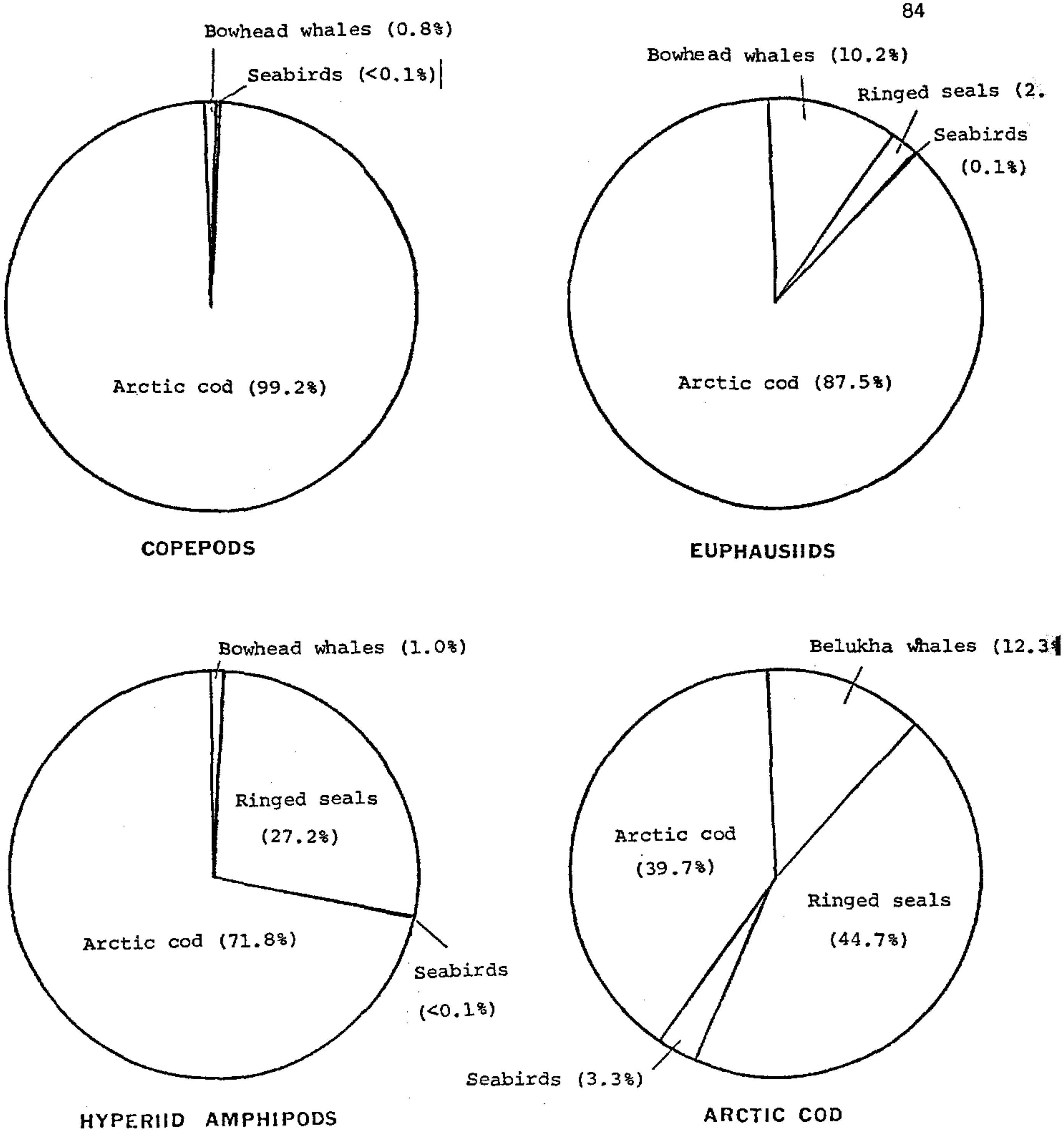

Figure 8. Pie diagrams representing the proportion of the total amount of copepods, euphausiids, hyperiid amphipods, and arctic cod consumed annually in the study area by each of the major groups of vertebrate consumers.

Beaufort are limited by predation (from foxes, polar bears, or humans) or some other non-trophic factor, arctic cod populations may have increased greatly with the demise of bowheads. Belukhas obtain much of their annual nutrition in areas other than the Beaufort Sea, and the effect of an increase in arctic cod abundance there would probably have only a slight impact on their population size or productivity. Seabirds may have increased in numbers in response to an increase in arctic cod and plankton; however, even at present their impact on the overall trophic system of the Beaufort appears comparatively slight. The magnitude of annular and longer term fluctuations in production of food in the Beaufort is not known. Considering the effects of sea ice cover and characteristics on primary productivity (see Section III) and the well-documented annual variability in ice characteristics in the Beaufort, considerable variation in annual levels of production seems likely. Stirling et al. (1977) documented a substantial decline in numbers and productivity of ringed seals in the eastern Beaufort Sea from 1974 to 1975 which they correlated with heavy ice conditions which might have reduced primary productivity. Of perhaps greater significance are long-term changes in ice conditions. Results of compilations (summarized in Shapiro and Barry 1978) show more open water in August and September since 1940 than between 1860 and 1919 but an increasing frequency of heavy ice seasons since about 1953.

If food is limiting in the Beaufort Sea then competition between consumers must occur. However, the mechanisms by which such competition is mediated and its possible effects on populations of the various consumers can at present only be speculated upon. It is critical to realize that the greatest competition will occur among individuals of the same species since they will have nearly identical requirements and responses. Unfortunately, very few data are available on the functional response of individual and population parameters to variations in food availability, particularly for large marine vertebrate species. Increased productivity of harp seals (Phoca groenlandica) and antarctic baleen whales and seals has occurred in response to presumed increases in food availability (Sergeant 1973; Laws 1977). However, changes in food availability in those circumstances have not been measured directly and correlated with observed responses in consumer populations. Decreased productivity of seabird populations has been recorded in years of presumed (but incompletely documented) food limitation (Divoky 1980; Drury et al. 1980). Fishes, which can be maintained with comparative ease in captive situations, are more suited for experiments on feeding ecology. However, most studies (e.g., Brocksen et al. 1968) have dealt with the effects of food ration on growth rates, although some have investigated the effects on reproductive performance (Scott 1962; Wootton 1973). The study of Sealy (1980) measured reproductive responses of northern orioles (Icterus galbula) to changes in food availability.

The results of two or more species feeding on shared prey resources are probably divisible into two major categories. First, the combined predation on prey populations may reduce overall standing stock, and, if predation exceeds the sustainable yield, productivity may be reduced. Overgrazing could result in decreased prey stocks in succeeding years.

The probability of such occurring in the Beaufort Sea and the characteristics of possible prey population declines and recoveries depend on the biological characteristics of the prey species. Secondly, the proximate effect of any predation is the removal of prey from the environment, making them unavailable to other consumers. The effect on consumers relates to their feeding mode, particularly the relationship between efficiency of food procurement and abundance and distribution patterns of prey. In the Beaufort Sea arctic cod and ringed seals probably feed mostly by selection of individual prey, although when ringed seals consume euphausiids, mysids, and hyperiid amphipods it is likely that more than one is captured with each "bite" (Lowry et al. 1980). Bowheads filter large volumes of water, retaining those organisms which are caught by the baleen. Although this process is not highly selective, the whales undoubtedly choose areas where they feed based on a perception of prey in the water column. One might speculate that bowheads would be the most effective consumer at low prey densities, although they could easily take advantage of patches of appropriate prey. Ringed seals may require greater densities of euphausiids than bowheads for effective feeding, although they may be able to exploit smaller, more local patches.

A predator has a number of options if prey species populations are not available at appropriate densities. An obvious option is to feed on something else, provided that an alternative appropriate prey is available. Arctic cod are capable of feeding on benthic organisms as well as on zooplankton and nekton (Craig and Haldorson 1981; Lowry and Frost 1981a). Although ringed seals also feed on benthos, it appears that they catch less food when feeding on benthic organisms as compared to nekton and arctic cod (Lowry et al. 1980). The availability and suitability of alternate prey for bowheads are poorly known. Predators may also seek better feeding areas if they encounter circumstances of inadequate available prey. Schools of arctic cod show great mobility (Craig and Haldorson 1981), and ringed seals appear to localize in areas of abundant prey (Frost and Lowry, *in prep. and unpubl.*). Based on commercial whaling records (Dahlheim et al. 1980) the summer feeding grounds of the bowhead once extended over much of the Bering, Chukchi, and Beaufort Seas.

If a predator does not locate and consume an adequate quantity of prey during a particular year there are several possible effects. Most drastic and least likely, the animal could die from starvation. Reduced vitality could, however, result in increased chances of mortality from disease, predation, or physical stress. More likely, an immature predator would experience a reduced growth rate, while mature individuals probably sacrifice reproductive output. Arctic marine mammals carry a considerable mass of blubber which, in addition to its insulative value, provides a large, portable food reserve. Individuals would therefore be expected to experience little stress from a single year of inadequate feeding. However, since they usually give birth to one large young which is nurtured at considerable energetic expense to the mother, reproductive output in the following year would likely be lessened. In addition, a reduced growth rate of subadults would cause delayed maturation (Laws

1959) and reduced population productivity. Being reproductively conservative, seal and whale populations would respond slowly to an increase in available forage.

In contrast, arctic cod, while they produce few eggs in comparison with other cods (Svetovidov 1948), have a large reproductive potential and might respond effectively to favorable feeding conditions. Growth rates of arctic cod vary among areas and years (Lowry and Frost 1981a) and since reproductive output in fishes is generally correlated with size (Serobaba 1971) this may be a mechanism by which food availability regulates arctic cod populations. Cannabalism and predation may also be important factors regulating arctic cod numbers. Food limitation causes decreased nesting and fledging success in seabirds (Divoky 1980; Drury et al. 1980). Since foraging of breeding birds is restricted to an area surrounding the nest, very local conditions are likely to be of great importance in regulating production.

Unfortunately, the results of this study and the information summarized in this report do not conclusively indicate whether competition for food is affecting populations of consumers, particularly bowhead whales, in the Beaufort Sea. Available information does suggest that competition and food limitation are very real possibilities. Further studies are needed before the ecology of the Beaufort Sea and the quantitative interactions among major vertebrate consumers are adequately understood. We suggest four major topics for future studies.

1. More refined estimates of total annual primary production are needed. Of particular interest are the effects of variations in ice conditions and other factors on production, as well as the magnitude of annual and longer term variations in production.

2. Interactions between consumers and producers as well as among the various consumer species need to be investigated. The proportion of primary production which is converted to prey usable by vertebrate consumers is of major importance, as are the responses of herbivore populations to fluctuations in their food supply.

3. Further studies of foods of major vertebrate consumers are needed. Particularly needed are data on winter foods of arctic cod and summer foods of ringed seals. Observations of foods of cod and seals in the vicinity of feeding bowheads would be of great value.

4. Information on the responses of vertebrate consumer populations to fluctuations in their food supply is urgently needed. Although it is probably impossible to obtain such information for bowhead whales, it may be possible to gather such data for ringed seals and arctic cod.

IX. Summary

1. A three-part study was conducted to examine trophic interactions among major vertebrate consumers, particularly bowhead whales, in the Alaskan Beaufort Sea. Major parts of the study were: 1) a synthesis of all available data on foods and feeding of bowhead whales, 2) field studies in the eastern portion of the Alaskan Beaufort Sea during September 1980 to examine foods utilized by ringed seals and arctic cod in an area where bowheads were known to feed, and 3) an assessment of the kinds and quantities of prey required on an annual basis to support populations of bowheads and their potential trophic competitors.

2. The study area, which was defined as the continental shelf of the Alaskan Beaufort Sea, is influenced primarily by arctic surface waters which move east to west with the Beaufort Gyre. Bering Sea water penetrates eastward from Point Barrow as a relatively warm subsurface layer. Upwelling, which occurs in the eastern portion of the study area, brings nutrient-rich waters on to the shelf. Primary productivity is limited by low light levels during much of the year and by nutrient availability during and after summer phytoplankton blooms. Ice covers nearshore areas completely for most of the year. Areas of open water occur during July-September. The temporal and geographic extent of open water varies greatly from year to year which probably causes major variations in the total annual primary production of the area.

3. Copepods and euphausiids convert primary production to a form that can be utilized by vertebrate consumers. Few data are available on the abundance of copepods and euphausiids in the study area. Based on our sampling, copepods sometimes occur in dense layers near the bottom, especially in water depths of 20 to 30 m. Abundance of copepods varied vertically in the water column, geographically both with depth and station location, and from day to day at the same station.

4. Three marine mammal species were considered to be major consumers in the study area. Bowhead whales were considered to feed in the area for 25 days during their fall migration (September-October). It was estimated that the population of 2,264 whales comprised a biomass of 36,000 t. They were estimated to consume 3% of their body weight per day, consisting of 30% copepod, 65% euphausiid, 1% hyperiid amphipod, and 4% other organisms. Belukha whales were estimated to feed in the area for 30 days in September. The population of 6,000 was estimated to weigh 4,800 t. They were estimated to consume 5.1% of their body weight per day, consisting of 80% arctic cod and 20% other organisms. The abundance, diet composition, and food consumption rate of ringed seals vary seasonally. The population was estimated as 80,000 seals (2,744 t) during summer and 40,000 seals (1,372 t) during

winter. Arctic cod are the primary ringed seal food in November-March. In April-June benthic crustaceans are the principal prey. In August-September, hyperiid amphipods, euphausiids, and arctic cod are all significant food items. The feeding rate (expressed as a percent of total body weight per day) was estimated to vary from a low of 1.9% in April-June to 8.4% in November-March.

5. Approximately 11 species (or species groups) of seabirds forage in the study area on organisms connected to the pelagic food web. In aggregate these seabird species were estimated to number 435,000 individuals, weighing a total of 159.2 t. Arctic cod comprise a major portion of the diet of gulls, terns, guillemots, jaegers, murres, and loons. Copepods are principally eaten by phalaropes and to a lesser extent Sabine's gulls. Euphausiids are eaten mostly by gulls and terns. Seabirds were estimated to consume 25% of their body weight daily.

6. Arctic cod is the only species of fish which is abundant in the study area and feeds primarily on organisms connected to the pelagic food web. The biomass of arctic cod was estimated to be 85,890 t. Arctic cod were considered to consume 6% of their body weight per day, comprised of 56% copepod, 8% euphausiid, 1% hyperiid amphipod, 1% arctic cod, and 34% other organisms.

7. In aggregate the vertebrate consumers considered were estimated to eat about 2 million metric tons of food annually in the study area, comprised of about 54% copepod, 9% euphausiid, 1% hyperiid amphipod, 2% arctic cod, and 34% other organisms. Of the total amount of copepods eaten, arctic cod were estimated to consume 99.2% and bowheads 0.8%. Of euphausiids, 87.5% was estimated to be consumed by arctic cod, 10.2% by bowheads, 2.2% by ringed seals, and 0.1% by seabirds. Of the estimated total hyperiid amphipod biomass eaten, arctic cod were estimated to consume 71.8%, ringed seals 27.2%, and bowheads 1.0%. Major consumers of arctic cod were ringed seals (44.7%), arctic cod (39.7%), belukha whales (12.3%), and seabirds (3.3%).

8. Some features of the biology of major prey species are discussed. Most species are comparatively long-lived and require more than one year to reach maturity and reproduce. Reproductive events for most species are linked in some manner to seasonal phytoplankton availability. Energy is stored as lipids and used to survive the winter period of reduced food availability. Caloric values of whole prey organisms are generally highest in the fall after the period of summer feeding and lipid accumulation.

9. In the Alaskan Beaufort Sea, and probably in other areas as well, the dominant prey of bowheads are euphausiids, principally *Thysanoessa raschii*, and copepods of the genus *Calanus*. It is speculated that little significant feeding occurs in wintering

areas or during the spring migration. Three areas can presently be identified as regularly important summer-fall feeding grounds: 1) the southeastern Beaufort Sea and western Amundsen Gulf, 2) the area between Barter Island and the U.S.-Canada demarcation line, and 3) the area between Point Barrow and Lonely in the western Beaufort Sea.

10. It is not possible at present to determine with certainty whether competition for food is affecting the recovery of the Bering-Chukchi-Beaufort stock of bowhead whales. Available data indicate that in heavy ice years production may be only one-fourth as great as the estimated quantity of food required by vertebrate consumers. Most of the food consumed is eaten by arctic cod whose numbers may be controlled by food limitation, predation, or cannibalism. If food is limiting, the effect on the population of each consumer species will depend on many poorly understood relationships and factors. Further studies are needed in order to understand the magnitude and effects of competition for food among vertebrate consumers in the Beaufort Sea.

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Appendix I. Organisms identified in vertical plankton tows done near Beaufort Lagoon, September 1980. For copepods, age class 0 indicates nauplius larvae, 1-5 indicate copepodite stages I-V, and 9 indicates adults. Station locations are shown in Figure 4.

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 1 - STATION A - 10 SEPTEMBER 1980

Tow #: VPT-21-80 Date: 800910 Time: 1355 Location: 695430N 1421612W

Water depth: 5m Tow depth: 5m Surf temp: - deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	9.0	9.167	9.167	9.167
Aeginopsis laurentii	all	1.0	1.019	1.019	1.019
Calanus hyperboreus	3	2.0	2.037	2.037	2.037
Calanus glacialis	3	2.0	2.037	2.037	2.037
Calanus glacialis	5	1.0	1.019	1.019	1.019
Pseudocalanus	5	11.0	11.205	11.205	11.205
Pseudocalanus	9	30.0	30.558	30.558	30.558
Limnocalanus grimaldi	9	1.0	1.019	1.019	1.019
Oregoninae zoea	all	2.0	2.037	2.037	2.037

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 1 - STATION B - 10 SEPTEMBER 1980

Tow #: VPT-22-80 Date: 800910 Time: 1408 Location: 695518N 1421454W

Water depth: 10m Tow depth: 10m Surf temp: - deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	49.0	24.956	24.956	24.956
Aeginopsis laurentii	all	2.0	1.019	1.019	1.019
Cyanea capillata	all	2.0	1.019	1.019	1.019
Calanus	2	3.0	1.528	1.528	1.528
Pseudocalanus	5	7.0	3.565	3.565	3.565
Pseudocalanus	9	1.0	.509	.509	.509
Derjuginia tolli	9	2.0	1.019	1.019	1.019
Limnocalanus grimaldi	9	4.0	2.037	2.037	2.037
Acartia clausi	9	3.0	1.528	1.528	1.528
Barnacle cyprid	all	3.0	1.528	1.528	1.528
Pagurid zoea	all	1.0	.509	.509	.509

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V E R T I C A L   Z O O P L A N K T O N   T O W   A N A L Y S I S

TRANSECT 1 - STATION C - 10 SEPTEMBER 1980

Tow #:       VPT-23-80    Date: 800910    Time: 1421    Location: 695636N 1421236W

Water depth:    15m    Tow depth:    15m    Surf temp: - deg C

Net diameter:  .500m    Mesh size: 505 microns

Total # tows selected: 1    # Replicates: 0

Species or tax code        Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
------------------------------------------------------------------------------------------------------

Rathkea octopunctata          all          11.0          3.735           3.735           3.735
Aeginopsis laurentii          all           1.0           .340            .340            .340
Cyanea capillata              all           1.0           .340            .340            .340

Calanus                        2            1.0           .340            .340            .340
Calanus hyperboreus            3            2.0           .679            .679            .679
Calanus hyperboreus            9            3.0          1.019           1.019           1.019
Pseudocalanus                  5           12.0          4.074           4.074           4.074
Pseudocalanus                  9            1.0           .340            .340            .340
Derjuginia tolli               9            5.0          1.698           1.698           1.698
Limnocalanus grimaldi          9            7.0          2.377           2.377           2.377

Barnacle cyprid               all           1.0           .340            .340            .340
Mysis litoralis               all           1.0           .340            .340            .340

Pagurid zoea                  all           1.0           .340            .340            .340
Oregoninae zoea               all           1.0           .340            .340            .340

Fish larvae                   all           1.0           .340            .340            .340
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VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 1 - STATION D - 10 SEPTEMBER 1980

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Tow #:        VPT-24-80    Date: 800910    Time: 1540    Location: 695812N 1420000W

Water depth:    20m    Tow depth:    20m    Surf temp: - deg C

Net diameter:  .500m    Mesh size: 505 microns

Total # tows selected: 1     # Replicates: 0

Species or tax code         Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
---------------------------------------------------------------------------------------------------

Perigonimus yoldiarcticae    all           5.0          1.273           1.273           1.273
Rathkea octopunctata         all          25.0          6.366           6.366           6.366
Obelia longissima            all           1.0           .255            .255            .255
Aeginopsis laurentii         all           4.0          1.019           1.019           1.019

Calanus                       2            1.0           .255            .255            .255
Calanus                       3            2.0           .509            .509            .509
Calanus hyperboreus           4            1.0           .255            .255            .255
Calanus hyperboreus           5            1.0           .255            .255            .255
Calanus glacialis             4            2.0           .509            .509            .509
Pseudocalanus                 1            2.0           .509            .509            .509
Pseudocalanus                 2            2.0           .509            .509            .509
Pseudocalanus                 5            6.0          1.528           1.528           1.528
Pseudocalanus                 9          278.0         70.792          70.283          70.792
Derjuginia tolli              9            2.0           .509            .509            .509
Limnocalanus grimaldi         9            6.0          1.528           1.528           1.528
Acartia longiremus            9            1.0           .255            .255            .255

Barnacle cyprid              all          14.0          3.565           3.565           3.565
Mysis litoralis              all          25.0          6.366           6.366           6.366

Monoculoides sp.             all           1.0           .255            .255            .255

Hyperia galba                all           1.0           .255            .255            .255

Pagurid zoea                 all           3.0           .764            .764            .764
Oregoninae zoea              all           2.0           .509            .509            .509
```

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 1 - STATION E - 10 SEPTEMBER 1980

Tow #: VPT-25-80 Date: 800910 Time: 1600 Location: 695930N 1420736W

Water depth: 25m Tow depth: 25m Surf temp: - deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Perigonimus yoldiarcticae	all	1.0	.204	.204	.204
Rathkea octopunctata	all	26.7	5.432	5.432	5.432
Beroe sp.	all	1.0	.204	.204	.204
Calanus	3	9.0	1.833	1.833	1.833
Calanus glacialis	9	6.0	1.222	1.222	1.222
Pseudocalanus	5	66.7	13.581	13.581	13.581
Pseudocalanus	9	506.7	103.217	100.501	103.217
Derjuginia tolli	9	1253.3	255.327	255.327	255.327
Barnacle cyprid	all	13.3	2.716	2.716	2.716
Apherusa glacialis	all	1.0	.204	.204	.204
Hyperia galba	all	1.0	.204	.204	.204
Pagurid zoea	all	2.0	.407	.407	.407
Oregoninae zoea	all	2.0	.407	.407	.407
Sagitta elegans	all	2.0	.407	.407	.407
Fish larvae	all	1.0	.204	.204	.204

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V E R T I C A L   Z O O P L A N K T O N   T O W   A N A L Y S I S

TRANSECT 1 - STATION F - 10 SEPTEMBER 1980

Tow #:      VPT-26A-80    Date: 800910    Time: 1608    Location: 695930N 1420736W

Water depth:    30m    Tow depth:    30m    Surf temp: - deg C

Net diameter:  .500m    Mesh size: 505 microns

Total # tows selected: 2    # Replicates: 1

Species or tax code        Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
----------------------------------------------------------------------------------------------------

Perigonimus yoldiarcticae   all            1.5          .255            .170            .340
Rathkea octopunctata        all           25.5         4.329           3.735           4.923
Obelia longissima           all             .5          .085           0.000            .170
Aeginopsis laurentii        all            2.5          .424            .170            .679
Cyanea capillata            all            1.0          .170           0.000            .340

Calanus                      2             8.0         1.358           1.188           1.528
Calanus                      3             8.0         1.358           2.716           2.716
Calanus hyperboreus          3             2.5          .424            .340            .509
Calanus hyperboreus          4             3.0          .509            .170            .849
Calanus glacialis            0             2.0          .340           0.000            .679
Calanus glacialis            3            15.0         2.546           0.000           5.093
Calanus glacialis            4             6.5         1.103            .679           1.528
Pseudocalanus                5             6.5         1.103            .340           1.867
Pseudocalanus                9            13.0         2.207            .340           4.074
Derjuginia tolli             9           146.5        24.871          17.825          31.916
Metridia sp.                 4              .5          .085           0.000            .170
Limnocalanus grimaldi        9             6.0         1.019            .679           1.358
Acartia longiremus           9              .5          .085           0.000            .170

Barnacle cyprid             all           19.5         3.310           2.207           4.244

Monoculoides sp.            all             .5          .085           0.000            .170

Hyperiid                    all             .5          .085           0.000            .170
Hyperia medusarum           all             .5          .085            .170            .170

Pagurid zoea                all            3.0          .509            .509            .509
Oregoninae zoea             all             .5          .085           0.000            .170

Sagitta elegans             all            3.0          .509            .170            .849

                                                                        .170            .340
```

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 1 - STATION G - 10 SEPTEMBER 1980

Tow #: VPT-27-80 Date: 800910 Time: 1623 Location: 700324N 1420106W

Water depth: 35m Tow depth: 35m Surf temp: - deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	77.0	11.205	11.205	11.205
Aeginopsis laurentii	all	6.0	.873	.873	.873
Cyanea capillata	all	1.0	.146	.146	.146
Beroe sp.	all	4.0	.582	.582	.582
Calanus	2	16.0	2.328	2.328	2.328
Calanus	3	43.0	6.257	6.257	6.257
Calanus hyperboreus	5	1.0	.146	.146	.146
Calanus glacialis	4	21.0	3.056	3.056	3.056
Calanus glacialis	5	24.0	3.492	3.492	3.492
Pseudocalanus	1	1.0	.146	.146	.146
Pseudocalanus	5	1.0	.146	.146	.146
Pseudocalanus	9	4.0	.582	.582	.582
Derjuginia tolli	9	10.0	1.455	1.455	1.455
Euchaeta glacialis	5	1.0	.146	.146	.146
Limnocalanus grimaldi	9	1.0	.146	.146	.146
Eurytemora sp.	5	1.0	.146	.146	.146
Barnacle cyprid	all	52.0	7.567	7.567	7.567
Pagurid zoea	all	4.0	.582	.582	.582
Oregoninae zoea	all	1.0	.146	.146	.146
Sagitta elegans	all	1.0	.146	.146	.146
Oikopleura sp.	all	11.0	1.601	1.601	1.601
Gadidae larvae	all	1.0	.146	.146	.146

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V E R T I C A L   Z O O P L A N K T O N   T O W   A N A L Y S I S

TRANSECT 1 - STATION H - 10 SEPTEMBER 1980

Tow #:        VPT-28-80    Date: 800910    Time: 1635    Location: 700536N 1415718W

Water depth:    40m    Tow depth:    40m    Surf temp: - deg C

Net diameter:  .500m    Mesh size: 505 microns

Total # tows selected: 1    # Replicates: 0

Species or tax code        Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
-----------------------------------------------------------------------------------------------------

Rathkea octopunctata          all          42.0          5.348           5.348           5.348
Obelia longissima             all           1.0           .127            .127            .127
Aeginopsis laurentii          all           2.0           .255            .255            .255

Polychaete                    all           1.0           .127            .127            .127

Calanus                        1            2.0           .255            .255            .255
Calanus                        2          104.0         13.242          13.242          13.242
Calanus                        3           71.0          9.040           9.040           9.040
Calanus hyperboreus            3            1.0           .127            .127            .127
Calanus hyperboreus            4            5.0           .637            .637            .637
Calanus glacialis              4           22.0          2.801           2.801           2.801
Calanus glacialis              9           20.0          2.546           2.546           2.546
Pseudocalanus                  5           14.0          1.783           1.783           1.783
Pseudocalanus                  9           20.0          2.546           2.419           2.546
DerJuginia tolli               9           19.0          2.419           2.419           2.419

Barnacle cyprid               all          77.0          9.804           9.804           9.804

Pagurid zoea                  all           1.0           .127            .127            .127
Oregoninae zoea               all           1.0           .127            .127            .127

Sagitta elegans               all           7.0           .891            .891            .891

Oikopleura sp.                all          16.0          2.037           2.037           2.037
Fritillaria borealis          all           8.0          1.019           1.019           1.019
```

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 1 - STATION I - 10 SEPTEMBER 1980

Tow #: VPT-29-80 Date: 800910 Time: 1645 Location: 700706N 1415442W

Water depth: 45m Tow depth: 45m Surf temp: - deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	10.0	1.132	1.132	1.132
Aglantha digitali	all	5.0	.566	.566	.566
Aeginopsis laurentii	all	3.0	.340	.340	.340
Cyanea capillata	all	1.0	.113	.113	.113
Polychaete	all	5.0	.566	.566	.566
Copepod	0	5.0	.566	.566	.566
Calanus	2	55.0	6.225	6.225	6.225
Calanus	3	125.0	14.147	14.147	14.147
Calanus hyperboreus	4	5.0	.566	.566	.566
Calanus glacialis	4	95.0	10.752	10.752	10.752
Calanus glacialis	5	50.0	5.659	5.659	5.659
Pseudocalanus	1	5.0	.566	.566	.566
Pseudocalanus	5	20.0	2.264	2.264	2.264
Pseudocalanus	9	45.0	5.093	5.093	5.093
Barnacle cyprid	all	75.0	8.488	8.488	8.488
Lysianassidae	all	1.0	.113	.113	.113
Hyperoche medusarum	all	1.0	.113	.113	.113
Thysanoessa raschii	all	1.0	.113	.113	.113
Crangonidae zoea	all	1.0	.113	.113	.113
Pagurid zoea	all	10.0	1.132	1.132	1.132
Sagitta elegans	all	16.0	1.811	1.811	1.811
Oikopleura sp.	all	116.0	13.128	13.128	13.128
Fritillaria borealis	all	5.0	.566	.566	.566

```
V E R T I C A L   Z O O P L A N K T O N   T O W   A N A L Y S I S

TRANSECT 2 - STATION A - 14 SEPTEMBER 1980

       Tow #:          Date range:
      VPT-39-80       800914-800914
      VPT-40-80

Avg water depth: 5m    Avg tow depth: 5m    Avg surf temp: - deg C

Avg net diameter: .500m    Avg mesh size: 505 microns

Total # tows selected: 2    # Replicates: 0

Species or tax code       Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
-----------------------------------------------------------------------------------------------


Perigonimus yoldiarcticae    all              .5             .509           0.000           1.019
Rathkea octopunctata         all             6.7            6.791           0.000          13.581
Aglantha digitali            all              .5             .509           0.000           1.019

Calanus hyperboreus           4               .5             .509           0.000           1.019
Calanus hyperboreus           9               .5             .509           0.000           1.019
Calanus glacialis             3             25.5           26.009          13.581          38.437
Calanus glacialis             5              1.0            1.019           0.000           2.037
Pseudocalanus                 4              6.7            6.791           0.000          13.581
Pseudocalanus                 5           1321.4         1345.950        1154.400        1537.500
Pseudocalanus                 9           4472.6         4555.730          19.219        5458.120
Derjuginia tolli              9              6.7            6.791           0.000          13.581
Limnocalanus grimaldi         9            727.7          741.202         271.625        1210.780
Acartia clausi                9              9.4            9.609           0.000          19.219
Acartia longiremus            9              6.7            6.791           0.000          13.581

Mysis litoralis              all              .5             .509           0.000           1.019

Hyperia galba                all              .5             .509           0.000           1.019

Pagurid zoea                 all             1.0            1.019           0.000           2.037

Sagitta elegans              all             1.0            1.019           0.000           2.037

Fish larvae                  all              .5             .509           0.000           1.019
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VERTICAL ZOOPLANKTON TOW ANALYSIS

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TRANSECT 2 - STATION B - 14 SEPTEMBER 1980

Tow #:      VPT-38-80    Date: 800914    Time: 1521    Location: 695518N 1421454W

Water depth:    10m    Tow depth:    10m    Surf temp:  -.5 deg C

Net diameter:  .500m    Mesh size: 505 microns

Total # tows selected: 1     # Replicates: 0

Species or tax code      Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
-------------------------------------------------------------------------------------------------

Perigonimus yoldiarcticae   all           1.0            .509            .509            .509
Aglantha digitali           all           1.0            .509            .509            .509
Aeginopsis laurentii        all           1.0            .509            .509            .509
Cyanea capillata            all           1.0            .509            .509            .509

Calanus hyperboreus          3            3.0           1.528           1.528           1.528
Calanus hyperboreus          5            1.0            .509            .509            .509
Calanus glacialis            3           33.3          16.977          16.977          16.977
Calanus glacialis            4           19.0           9.677           9.677           9.677
Calanus glacialis            5           22.0          11.205          11.205          11.205
Pseudocalanus                5          200.0         101.859         101.859         101.859
Pseudocalanus                9          853.3         434.599          10.186         434.599
Limnocalanus grimaldi        9           20.0          10.186          10.186          10.186

Barnacle cyprid             all          26.7          13.581          13.581          13.581

Thysanoessa longipes        all           1.0            .509            .509            .509
Hippolytid zoea             all           1.0            .509            .509            .509
Pagurid zoea                all           2.0           1.019           1.019           1.019

Sagitta elegans             all           9.0           4.584           4.584           4.584

Oikopleura sp.              all           5.0           2.546           2.546           2.546
Fritillaria borealis        all          13.3           6.791           6.791           6.791
```

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 2 - STATION C - 14 SEPTEMBER 1980

Tow #: VPT-37-80 Date: 800914 Time: 1507 Location: 695636N 1421236W

Water depth: 15m Tow depth: 15m Surf temp: -.2 deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	4.0	1.358	1.358	1.358
Aglantha digitali	all	1.0	.340	.340	.340
Aeginopsis laurentii	all	1.0	.340	.340	.340
Calanus	2	5.0	1.698	1.698	1.698
Calanus hyperboreus	3	1.0	.340	.340	.340
Calanus hyperboreus	4	2.0	.679	.679	.679
Calanus glacialis	3	10.0	3.395	3.395	3.395
Calanus glacialis	4	10.0	3.395	3.395	3.395
Calanus glacialis	5	23.0	7.809	7.809	7.809
Pseudocalanus	5	28.0	9.507	9.507	9.507
Pseudocalanus	9	9.0	3.056	3.056	3.056
Derjuginia tolli	9	2.0	.679	.679	.679
Metridia sp.	9	1.0	.340	.340	.340
Limnocalanus grimaldi	9	1.0	.340	.340	.340
Barnacle cyprid	all	18.0	6.112	6.112	6.112
Hippolytid zoea	all	1.0	.340	.340	.340
Pagurid zoea	all	1.0	.340	.340	.340
Oregoninae zoea	all	1.0	.340	.340	.340
Sagitta elegans	all	12.0	4.074	4.074	4.074
Oikopleura sp.	all	13.0	4.414	4.414	4.414
Fritillaria borealis	all	1.0	.340	.340	.340

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 2 - STATION D - 14 SEPTEMBER 1980

Tow #: VPT-36-80 Date: 800914 Time: 1452 Location: 695812N 1420000W

Water depth: 20m Tow depth: 20m Surf temp: -.5 deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	1.0	.255	.255	.255
Aglantha digitali	all	1.0	.255	.255	.255
Beroe sp.	all	1.0	.255	.255	.255
Polychaete	all	1.0	.255	.255	.255
Gastropod	all	2.0	.509	.509	.509
Calanus	2	2.0	.509	.509	.509
Calanus hyperboreus	0	1.0	.255	.255	.255
Calanus hyperboreus	9	1.0	.255	.255	.255
Calanus glacialis	3	9.0	2.292	2.292	2.292
Calanus glacialis	4	17.0	4.329	4.329	4.329
Calanus glacialis	5	48.0	12.223	12.223	12.223
Pseudocalanus	5	38.0	9.677	9.677	9.677
Pseudocalanus	9	9.0	2.292	2.292	2.292
Derjuginia tolli	9	1.0	.255	.255	.255
Euchaeta sp.	9	1.0	.255	.255	.255
Metridia sp.	5	1.0	.255	.255	.255
Limnocalanus grimaldi	9	8.0	2.037	2.037	2.037
Barnacle cyprid	all	19.0	4.838	4.838	4.838
Euphausiid larvae	all	3.0	.764	.764	.764
Sagitta elegans	all	14.0	3.565	3.565	3.565
Oikopleura sp.	all	43.0	10.950	10.950	10.950
Fritillaria borealis	all	1.0	.255	.255	.255

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 2 - STATION E - 14 SEPTEMBER 1980

Tow #: VPT-35-80 Date: 800914 Time: 1418 Location: 695930N 1420736W

Water depth: 25m Tow depth: 25m Surf temp: -1 deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	29.0	5.908	5.908	5.908
Corymorpha flammea	all	1.0	.204	.204	.204
Aglantha digitali	all	9.0	1.833	1.833	1.833
Aeginopsis laurentii	all	4.0	.815	.815	.815
Beroe sp.	all	1.0	.204	.204	.204
Polychaete	all	1.0	.204	.204	.204
Calanus	2	24.0	4.889	4.889	4.889
Calanus hyperboreus	3	4.0	.815	.815	.815
Calanus hyperboreus	4	2.0	.407	.407	.407
Calanus hyperboreus	5	6.0	1.222	1.222	1.222
Calanus hyperboreus	9	2.0	.407	.407	.407
Calanus glacialis	3	21.0	4.278	4.278	4.278
Calanus glacialis	4	22.0	4.482	4.482	4.482
Calanus glacialis	5	82.0	16.705	16.705	16.705
Calanus glacialis	9	1.0	.204	.204	.204
Pseudocalanus	5	31.0	6.315	6.315	6.315
Pseudocalanus	9	7.0	1.426	1.426	1.426
Derjuginia tolli	9	1.0	.204	.204	.204
Limnocalanus grimaldi	9	13.0	2.648	2.648	2.648
Barnacle cyprid	all	35.0	7.130	7.130	7.130
Onisimus glacialis	all	1.0	.204	.204	.204
Hyperia galba	all	1.0	.204	.204	.204
Euphausiid larvae	all	1.0	.204	.204	.204
Thysanoessa longipes	all	1.0	.204	.204	.204
Thysanoessa raschii	all	1.0	.204	.204	.204
Pagurid zoea	all	1.0	.204	.204	.204
Oregoninae zoea	all	1.0	.204	.204	.204
Sagitta elegans	all	23.0	4.686	4.686	4.686
Oikopleura sp.	all	59.0	12.019	12.019	12.019
Fritillaria borealis	all	12.0	2.445	2.445	2.445
5130010102	all	1.0	.204	.204	.204

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V E R T I C A L   Z O O P L A N K T O N   T O W   A N A L Y S I S

TRANSECT 2 - STATION F - 14 SEPTEMBER 1980

Tow #:       VPT-34-80    Date: 800914    Time: 1320    Location: 700100N 1420506W

Water depth:    30m    Tow depth:    30m    Surf temp:    -1 deg C

Net diameter:  .500m    Mesh size: 505 microns

Total # tows selected: 1    # Replicates: 0

Species or tax code        Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
-------------------------------------------------------------------------------------------------

Perigonimus yoldiarcticae     all          1.0            .170            .170            .170
Rathkea octopunctata          all         17.0           2.886           2.886           2.886
Aglantha digitali             all          6.0           1.019           1.019           1.019
Aeginopsis laurentii          all          3.0            .509            .509            .509
Cyanea capillata              all          2.0            .340            .340            .340

Polychaete                    all          3.0            .509            .509            .509

Calanus                        2          21.0           3.565           3.565           3.565
Calanus hyperboreus            3           8.0           1.358           1.358           1.358
Calanus hyperboreus            4          13.0           2.207           2.207           2.207
Calanus hyperboreus            5           7.0           1.188           1.188           1.188
Calanus hyperboreus            9           2.0            .340            .340            .340
Calanus glacialis              3          27.0           4.584           4.584           4.584
Calanus glacialis              4          28.0           4.753           4.753           4.753
Calanus glacialis              5          71.0          12.053          12.053          12.053
Pseudocalanus                  5          19.0           3.226           3.226           3.226
Pseudocalanus                  9           6.0           1.019           1.019           1.019
Derjuginia tolli               9           1.0            .170            .170            .170
Metridia sp.                   9          20.0           3.395           3.226           3.395

Barnacle cyprid               all         44.0           7.470           7.470           7.470

Hippolytid zoea               all          1.0            .170            .170            .170
Pagurid zoea                  all          2.0            .340            .340            .340

Sagitta elegans               all         18.0           3.056           3.056           3.056

Oikopleura sp.                all        110.0          18.674          18.674          18.674
Fritillaria borealis          all          3.0            .509            .509            .509

Gadidae larvae                all          1.0            .170            .170            .170
```

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 3 - STATION A - 17 SEPTEMBER 1980

Tow #: VPT-47-80 Date: 800917 Time: 1810 Location: 695454N 1421642W

Water depth: 5m Tow depth: 5m Surf temp: -2 deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Cyanea capillata	all	1.0	1.019	1.019	1.019
Calanus	2	4.0	4.074	4.074	4.074
Calanus hyperboreus	3	1.0	1.019	1.019	1.019
Calanus glacialis	4	1.0	1.019	1.019	1.019
Pseudocalanus	2	2.0	2.037	2.037	2.037
Pseudocalanus	3	1.0	1.019	1.019	1.019
Pseudocalanus	4	7.0	7.130	7.130	7.130
Pseudocalanus	5	45.0	45.837	45.837	45.837
Pseudocalanus	9	818.0	833.209	7.130	833.209
Derjuginia tolli	9	1.0	1.019	1.019	1.019
Limnocalanus grimaldi	9	9.0	9.167	9.167	9.167
Acartia clausi	9	3.0	3.056	3.056	3.056
Barnacle cyprid	all	1.0	1.019	1.019	1.019
Fritillaria borealis	all	2.0	2.037	1.019	2.037

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 3 - STATION B - 17 SEPTEMBER 1980

Tow #: VPT-46-80 Date: 800917 Time: 1801 Location: 695518N 1421454W

Water depth: 10m Tow depth: 10m Surf temp: - deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Calanus	2	14.1	7.173	7.173	7.173
Calanus	3	14.1	7.173	7.173	7.173
Pseudocalanus	3	14.1	7.173	7.173	7.173
Pseudocalanus	5	408.5	208.022	208.022	208.022
Pseudocalanus	9	2957.8	1506.370	7.173	1506.370
Limnocalanus grimaldi	9	70.4	35.866	35.866	35.866
Mysis litoralis	all	1.0	.509	.509	.509
Oikopleura sp.	all	1.0	.509	.509	.509

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 3 - STATION C - 17 SEPTEMBER 1980

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Tow #:        VPT-41-80    Date: 800917    Time: 1110    Location: 695636N 1421236W

Water depth:    15m    Tow depth:    15m    Surf temp:    -1 deg C

Net diameter:  .500m    Mesh size: 505 microns

Total # tows selected: 1    # Replicates: 0

Species or tax code        Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
-------------------------------------------------------------------------------------------------

Perigonimus yoldiarcticae    all            1.0           .340            .340            .340
Rathkea octopunctata         all           14.1          4.782           4.782           4.782

Calanus                       2            70.4         23.911          23.911          23.911
Pseudocalanus                 5            70.4         23.911          23.911          23.911
Pseudocalanus                 9          1450.7        492.559         492.559         492.559
Derjuginia tolli              9            42.3         14.346          14.346          14.346
Limnocalanus grimaldi         9            42.3         14.346          14.346          14.346

Pagurid zoea                 all            2.0           .679            .679            .679

Oikopleura sp.               all            2.0           .679            .679            .679
Fritillaria borealis         all           70.4         23.911          23.911          23.911
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VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 3 - STATION D - 17 SEPTEMBER 1980

Tow #: VPT-42-80 Date: 800917 Time: 1247 Location: 695812N 1420000W

Water depth: 20m Tow depth: 20m Surf temp: -2 deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Perigonimus yoldiarcticae	all	2.0	.509	.509	.509
Rathkea octopunctata	all	5.0	1.273	1.273	1.273
Aglantha digitali	all	2.0	.509	.509	.509
Calanus	2	9.0	2.292	2.292	2.292
Calanus hyperboreus	4	1.0	.255	.255	.255
Calanus glacialis	3	10.0	2.546	2.546	2.546
Calanus glacialis	4	7.0	1.783	1.783	1.783
Calanus glacialis	5	9.0	2.292	2.292	2.292
Pseudocalanus	2	5.0	1.273	1.273	1.273
Pseudocalanus	5	41.0	10.441	10.441	10.441
Pseudocalanus	9	32.0	8.149	.764	8.149
Limnocalanus grimaldi	9	3.0	.764	.764	.764
Acartia longiremus	9	1.0	.255	.255	.255
Barnacle cyprid	all	4.0	1.019	1.019	1.019
Mysis litoralis	all	4.0	1.019	1.019	1.019
Pagurid zoea	all	2.0	.509	.509	.509
Oikopleura sp.	all	6.0	1.528	1.528	1.528
Fritillaria borealis	all	20.0	5.093	5.093	5.093
Gadidae larvae	all	2.0	.509	.509	.509

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 3 - STATION E - 17 SEPTEMBER 1980

Tow #: VPT-44-80 Date: 800917 Time: 1539 Location: 695930N 1420736W

Water depth: 25m Tow depth: 25m Surf temp: - deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	24.0	4.889	4.889	4.889
Aglantha digitali	all	4.0	.815	.815	.815
Beroe sp.	all	1.0	.204	.204	.204
Polychaete	all	1.0	.204	.204	.204
Calanus	2	34.0	6.926	6.926	6.926
Calanus hyperboreus	3	1.0	.204	.204	.204
Calanus hyperboreus	4	2.0	.407	.407	.407
Calanus glacialis	0	16.0	3.260	3.260	3.260
Calanus glacialis	3	18.0	3.667	3.667	3.667
Calanus glacialis	5	54.0	11.001	11.001	11.001
Calanus glacialis	9	1.0	.204	.204	.204
Pseudocalanus	5	32.0	6.519	6.519	6.519
Pseudocalanus	9	3.0	.611	.611	.611
Derjuginia tolli	9	2.0	.407	.407	.407
Limnocalanus grimaldi	9	3.0	.611	.611	.611
Barnacle cyprid	all	26.0	5.297	5.297	5.297
Apherusa glacialis	all	1.0	.204	.204	.204
Sagitta elegans	all	1.0	.204	.204	.204
Oikopleura sp.	all	28.0	5.704	5.704	5.704
Fritillaria borealis	all	8.0	1.630	1.630	1.630
Gadidae larvae	all	1.0	.204	.204	.204

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V E R T I C A L   Z O O P L A N K T O N   T O W   A N A L Y S I S

TRANSECT 3 - STATION F - 17 SEPTEMBER 1980

Tow #:        VPT-45-80    Date: 800917    Time: 1603    Location: 700100N 1420506W

Water depth:    30m    Tow depth:    30m    Surf temp: - deg C

Net diameter:  .500m    Mesh size: 505 microns

Total # tows selected: 1     # Replicates: 0

Species or tax code        Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
--------------------------------------------------------------------------------------------------

Rathkea octopunctata          all           5.0            .849            .849            .849

Calanus                        2           13.0           2.207           2.207           2.207
Calanus                        3           16.0           2.716           2.716           2.716
Calanus glacialis              4           18.0           3.056           3.056           3.056
Calanus glacialis              5           35.0           5.942           5.942           5.942
Pseudocalanus                  5           21.0           3.565           3.565           3.565
Pseudocalanus                  9            3.0            .509            .170            .509
Limnocalanus grimaldi          9            2.0            .340            .340            .340

Barnacle cyprid               all          14.0           2.377           2.377           2.377

Oregoninae zoea               all           1.0            .170            .170            .170

Sagitta elegans               all           2.0            .340            .340            .340

Oikopleura sp.                all          27.0           4.584           4.584           4.584
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VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 4 - STATION J - 12 SEPTEMBER 1980

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Tow #:        VPT-33-80     Date: 800912     Time: 1450     Location: 694806N 1414642W

Water depth:      5m     Tow depth:      5m     Surf temp:    -1 deg C

Net diameter:  .500m     Mesh size: 505 microns

Total # tows selected: 1     # Replicates: 0

Species or tax code         Age class    Avg # found    Avg #/cubic m    Min #/cubic m    Max #/cubic m
---------------------------------------------------------------------------------------------------------

Rathkea octopunctata           all           1.0            1.019            1.019            1.019
Aeginopsis laurentii           all           1.0            1.019            1.019            1.019

Calanus                         2            5.0            5.093            5.093            5.093
Pseudocalanus                   5            7.0            7.130            7.130            7.130
Pseudocalanus                   9           70.0           71.301            2.037           71.301
Limnocalanus grimaldi           9            6.0            6.112            6.112            6.112
Acartia clausi                  9            2.0            2.037            2.037            2.037

Barnacle cyprid                all           1.0            1.019            1.019            1.019

Pagurid zoea                   all           1.0            1.019            1.019            1.019
Oregoninae zoea                all           1.0            1.019            1.019            1.019
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VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 4 - STATION K - 12 SEPTEMBER 1980

Tow #: VPT-32-80   Date: 800912   Time: 1440   Location: 694836N 1414600W

Water depth: 10m   Tow depth: 10m   Surf temp: -.7 deg C

Net diameter: .500m   Mesh size: 505 microns

Total # tows selected: 1   # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	3.0	1.528	1.528	1.528
Aeginopsis laurentii	all	1.0	.509	.509	.509
Calanus	2	19.0	9.677	9.677	9.677
Calanus hyperboreus	3	1.0	.509	.509	.509
Calanus hyperboreus	4	1.0	.509	.509	.509
Calanus glacialis	3	3.0	1.528	1.528	1.528
Calanus glacialis	4	1.0	.509	.509	.509
Pseudocalanus	3	1.0	.509	.509	.509
Pseudocalanus	5	20.0	10.186	10.186	10.186
Pseudocalanus	9	575.0	292.845	5.602	292.845
Derjuginia tolli	9	1.0	.509	.509	.509
Limnocalanus grimaldi	9	43.0	21.900	21.900	21.900
Acartia clausi	9	1.0	.509	.509	.509
Barnacle cyprid	all	4.0	2.037	2.037	2.037
Pagurid zoea	all	2.0	1.019	1.019	1.019

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 4 - STATION L - 12 SEPTEMBER 1980

Tow #: VPT-31-80 Date: 800912 Time: 1430 Location: 694906N 1414512W

Water depth: 15m Tow depth: 15m Surf temp: -1 deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	11.0	3.735	3.735	3.735
Obelia longissima	all	1.0	.340	.340	.340
Aeginopsis laurentii	all	3.0	1.019	1.019	1.019
Calanus	2	17.0	5.772	5.772	5.772
Calanus hyperboreus	3	2.0	.679	.679	.679
Calanus glacialis	3	1.0	.340	.340	.340
Calanus glacialis	4	1.0	.340	.340	.340
Pseudocalanus	5	15.0	5.093	5.093	5.093
Pseudocalanus	9	15.0	5.093	5.093	5.093
Derjuginia tolli	9	6.0	2.037	2.037	2.037
Metridia sp.	5	1.0	.340	.340	.340
Limnocalanus grimaldi	9	7.0	2.377	2.377	2.377
Acartia clausi	9	2.0	.679	.679	.679
Barnacle cyprid	all	6.0	2.037	2.037	2.037
Hippolytid zoea	all	1.0	.340	.340	.340
Pagurid zoea	all	1.0	.340	.340	.340
Fish larvae	all	1.0	.340	.340	.340

VERTICAL ZOOPLANKTON TOW ANALYSIS

TRANSECT 4 - STATION M - 12 SEPTEMBER 1980

Tow #: VPT-30-80 Date: 800912 Time: 1350 Location: 695030N 141431BW

Water depth: 20m Tow depth: 20m Surf temp: - deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 1 # Replicates: 0

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	11.0	2.801	2.801	2.801
Aglantha digitali	all	1.0	.255	.255	.255
Aeginopsis laurentii	all	2.0	.509	.509	.509
Limacina helicina	all	1.0	.255	.255	.255
Calanus	1	1.0	.255	.255	.255
Calanus	2	37.0	9.422	9.422	9.422
Calanus hyperboreus	3	2.0	.509	.509	.509
Calanus hyperboreus	4	1.0	.255	.255	.255
Calanus glacialis	3	11.0	2.801	2.801	2.801
Pseudocalanus	5	42.0	10.695	10.695	10.695
Pseudocalanus	9	7.0	1.783	1.783	1.783
Derjuginia tolli	9	38.0	9.677	9.677	9.677
Limnocalanus grimaldi	9	7.0	1.783	1.783	1.783
Acartia clausi	9	1.0	.255	.255	.255
Barnacle cyprid	all	7.0	1.783	1.783	1.783
Fritillaria borealis	all	4.0	1.019	1.019	1.019

VERTICAL ZOOPLANKTON TOW ANALYSIS

WHALE SIGHTING 1 - STATION W1 - 9 SEPTEMBER 1980

Tow #: VPT-20A-80 Date: 800909 Time: 1223 Location: 700036N 1420548W

Water depth: 28m Tow depth: 28m Surf temp: - deg C

Net diameter: .500m Mesh size: 505 microns

Total # tows selected: 3 # Replicates: 2

Species or tax code	Age class	Avg # found	Avg #/cubic m	Min #/cubic m	Max #/cubic m
Rathkea octopunctata	all	43.3	7.882	0.000	12.732
Aeginopsis laurentii	all	.3	.061	0.000	.182
Beroe sp.	all	3.3	.606	0.000	1.819
Calanus	2	6.7	1.213	0.000	3.638
Calanus	3	3.3	.606	0.000	1.819
Pseudocalanus	5	16.7	3.032	0.000	5.457
Pseudocalanus	9	890.0	161.883	80.032	312.853
DerJuginia tolli	9	2306.7	419.563	152.789	807.598
Limnocalanus grimaldi	9	20.0	3.638	0.000	7.276
Barnacle cyprid	all	40.0	7.276	3.638	10.913
Mysis litoralis	all	.3	.061	0.000	.182
Hippolytid zoea	all	.3	.061	0.000	.182
Pagurid zoea	all	5.3	.970	0.000	1.819
Oregoninae zoea	all	1.0	.182	0.000	.546

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VERTICAL ZOOPLANKTON TOW ANALYSIS

WHALE SIGHTING 2 - STATION W2

Tow #:      VPT-43A-80     Date: 800917     Time: 1423     Location: 695900N 1420818W

Water depth:    23m     Tow depth:    23m     Surf temp:   -2 deg C

Net diameter:  .500m     Mesh size: 505 microns

Total # tows selected: 3     # Replicates: 2

Species or tax code       Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
-----------------------------------------------------------------------------------------------

Rathkea octopunctata         all         16.0          3.543           2.657           4.650
Aglantha digitali            all          3.3           .738            .443           1.771
Aeginopsis laurentii         all          2.0           .443            .221            .664
Cyanea capillata             all           .3           .074           0.000            .221

Polychaete                   all           .3           .074           0.000            .221
Gastropod                    all           .3           .074           0.000            .221

Calanus                      1             .7           .148           0.000            .443
Calanus                      2           11.7          2.583           1.993           3.321
Calanus                      3            4.7          1.033           0.000           3.100
Calanus hyperboreus          3            1.3           .295           0.000            .886
Calanus hyperboreus          4            1.0           .221            .221            .443
Calanus glacialis            3           11.3          2.510           0.000           4.207
Calanus glacialis            4           10.0          2.214            .886           3.764
Calanus glacialis            5           37.0          8.193           5.757          10.186
Calanus glacialis            9             .3           .074           0.000            .221
Pseudocalanus                5           70.3         15.574          11.072          22.143
Pseudocalanus                9           22.0          4.872            .886           7.086
DerJuginia tolli             9           41.7          9.226            .443          26.793
Limnocalanus grimaldi        9            1.0           .221           0.000            .443
Eurytemora herdmani          9             .3           .074           0.000            .221

Barnacle cyprid              all          5.3          1.181           1.107           1.329
Cumacean                     all           .3           .074           0.000            .221

Hippolytid zoea              all           .3           .074           0.000            .221
Pagurid zoea                 all          3.0           .664            .221           1.550

Sagitta elegans              all         10.7          2.362           1.771           2.879

Oikopleura sp.               all         23.3          5.167           4.429           6.422
Fritillaria borealis         all         10.3          2.288           1.550           3.100

Gadidae larvae               all          1.0           .221            .221            .443
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VERTICAL ZOOPLANKTON TOW ANALYSIS

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WHALE SIGHTING 3 - STATION W3

      Tow #:          Date range:
    VPT-48A-80      800918-800918
    VPT-49A-80

Avg water depth: 20.5m    Avg tow depth: 20.5m    Avg surf temp: -2.5 deg C

Avg net diameter: .500m    Avg mesh size: 505 microns

Total # tows selected: 4    # Replicates: 2

Species or tax code       Age class   Avg # found   Avg #/cubic m   Min #/cubic m   Max #/cubic m
-----------------------------------------------------------------------------------------------


Rathkea octopunctata         all          8.8          2.174           1.455           2.910
Obelia longissima            all           .3           .062           0.000            .243
Aglantha digitali            all          1.0           .248           0.000            .485
Aeginopsis laurentii         all           .8           .186           0.000            .485
Cyanea capillata             all           .3           .062           0.000            .243

Beroe sp.                    all           .8           .186           0.000            .485

Calanus                       1            .3           .062           0.000            .243
Calanus                       2          15.5          3.851           1.783           5.335
Calanus                       3           5.8          1.429           0.000           5.578
Calanus hyperboreus           3           1.0           .248           0.000            .728
Calanus hyperboreus           4            .8           .186           0.000            .509
Calanus glacialis             3           7.8          1.925           0.000           3.395
Calanus glacialis             4           4.8          1.180            .728           2.183
Calanus glacialis             5          14.5          3.602            .764           6.063
Pseudocalanus                 3            .3           .062           0.000            .243
Pseudocalanus                 5          42.3         10.497           5.821          14.006
Pseudocalanus                 9         101.5         25.216            .728          64.026
Derjuginia tolli              9            .8           .186           0.000            .509
Metridia sp.                  5            .3           .062           0.000            .255
Limnocalanus grimaldi         9           8.8          2.174            .243           5.348
Acartia longiremus            9            .8           .186           0.000            .728

Barnacle cyprid              all         10.0          2.484           1.528           3.880
Mysis litoralis              all           .5           .124           0.000            .485

Pagurid zoea                 all           .5           .124           0.000            .509
Oregoninae zoea              all          1.5           .373           0.000            .764

Sagitta elegans              all          2.0           .497            .243            .970

Oikopleura sp.               all          6.8          1.677            .255           2.910
Fritillaria borealis         all         10.5          2.609            .970           4.329
```

Appendix II. Description of bowhead whale prey samples examined. Samples were collected from the stomach unless noted otherwise.

Samples from Whales Taken at Barrow

4388 - Sample collected by Floyd Durham, spring 1969. Sex and exact collection date not known. Sample contained about 50 ml of mostly digested material, including numerous euphausiid fragments and no identifiable remains of other organisms. Both *Thysanoessa inermis* and *T. raschii* appeared to be present.

76-B-6F - Female - 16.0 m long - taken 10 September 1976, about 10 miles north of Point Barrow. Reported to be an Ingutuk. Sample consisted of mostly *T. raschii* (17.0 ml), small amounts of *Parathemisto libellula* (0.4 ml) and *Rozinante fragilis* (0.1 ml), and a small pebble.

76-B-7F - Female - 14.3 m long - taken 20 September 1976, 15-20 miles north of Point Barrow. Total volume of contents estimated as 30 gallons. Sample of 33.0 ml was comprised mostly of *T. raschii* (28.6 ml). Remainder of sample consisted of hyperiid and gammarid amphipods and a partial shrimp carapace.

77-B-5 - Male - 10.6 m long - taken 5 May 1977 at 1600 hrs local time. Sample of about 20 ml consisted mostly of copepods. Numbers of each copepod species counted were: *Metridia longa* - 1,892; *Calanus glacialis* - 411; *Euchaeta glacialis* - 40, and *Pseudocalanus* sp. - 2. Also occurring were one *T. raschii*, one *Parathemisto abyssorum*, six pteropod molluscs (*Limacina helicina*), three ostracods, and a fish scale.

79-B-3 - Male - 8.3 m long - taken 27 May 1979, reported to be an Ingutuk. Sample from colon consisted of one small clam, *Nuculana* sp., perhaps *N. radiata*. Shell was 2.1 cm long, empty, and had a hole indicating that it had been drilled by a predator and was probably empty when eaten. Two other clams were reported to be in the gastrointestinal tract of this whale.

80-B-3 - Male - 8.5 m long - taken 25 May 1980 at 0630 hrs local time. Contents were noted as a few invertebrates in lining of stomach. Sample consisted of: euphausiids (*T. raschii* and *T. inermis*) - 1.6 ml; copepods - 0.8 ml; *Neomysis rayi* - 0.5 ml; *Hyperia galba* - 0.1 ml; and a pebble, 0.6 cm in diameter - 0.3 ml. Numbers of each copepod species were: *C. hyperboreus* - 16, *C. cristatus* - 1, *E. glacialis* - 10, and *Chiridius obtusifrons* - 2.

80-B-5 - Male - 10.4 m long - taken 25 May 1980 at 0616 hrs local time. Stomach contents estimated as 1 liter, mixed with partially congealed blood. Sample was comprised of several thousand *T. raschii* (70.0 ml), 16 *N. rayi* (2.8 ml), and a pebble 1.5 cm in diameter (0.6 ml). Euphausiids in sample were small; abdomen and uropods combined mostly less than 1.0 cm long, some as long as 1.7 cm.

80-B-9 - Female - 13.7 m long - taken 27 May 1980 at 1800 hrs local time. Stomach contents noted as about 10 gallons of water and 2 liters of euphausiids. Sample consisted of euphausiids (mostly *T. raschii*, few *T. inermis*) - 128.0 ml, mysids (44 *N. rayi* and a fragment of *Mysis litoralis*) - 7.5 ml; copepods (30 *E. glacialis*, 29 *C. hyperboreus*, 20 *C. glacialis*, and 10 *C. obtusifrons*) - 2.0 ml; hyperiid amphipods (mostly *H. galba*) - 1.4 ml; and six *Anonyx nugax* - 0.8 ml. An additional two *A. nugax* were found in the baleen of this whale.

Samples from Whales Taken at Kaktovik

79-KK-1 - Male - 12.7 m long - killed 20 September 1979 at 1400 hrs local time about 20 miles east of Kaktovik. Whale was recovered as a stinker on 22 September 1979. Total stomach contents estimated as 12 gallons. Contents partially digested. Sample consisted of: copepods (all identifiable were *C. hyperboreus*) - 2,400.0 ml; gammarid amphipods - 3.0 ml, a small (1.2 cm total length) crangonid shrimp - 0.2 ml; fragments of two hyperiid amphipods - <0.1 ml; and two tiny (largest 4.8 mm) pebbles - 3.0 ml).

79-KK-2 - Female - 10.5 m long - taken 6 October 1979. Total contents estimated as 5 gallons. Sample consisted of: copepods - 540.0 ml; euphausiids (*T. raschii*) - 1.8 ml; *M. litoralis* - 1.6 ml; hyperiid amphipods - 0.8 ml; gammarid amphipods - 0.6 ml; a vertebral fragment from *Boreogadus saida* - 0.4 ml, and a fragment of a shrimp - <0.1 ml. Numbers of each copepod species counted in a subsample were: *C. hyperboreus* - 1,000; *C.* sp. - 200; *Heterorhabdus* sp. - 3; and *Metridia lucens* - 2.

79-KK-3 - Male - 10.3 m long - taken 8 October 1979. Total contents estimated as 5-7 gallons. Sample consisted of: *T. raschii* (estimated 2,955 individuals) - 271.0 ml; copepods (all identifiable were *C. hyperboreus*) - 93.5 ml; *M. litoralis* (estimated 296 individuals) - 28.0 ml; hyperiid amphipods (estimated 140 *P. abyssorum* and 2 *P. libellula*) - 2.0 ml; gammarid amphipods (5 individuals, each of a different species) - 1.2 ml; and one *Myoxocephalus quadricornis* (estimated 8.0 cm total length) - 4.0 ml.

79-KK-4 - Male - 10.6 m long - taken 10 October 1979. Total contents estimated as 5 gallons. Sample consisted of: copepods - 116.0 ml; *T. raschii* - 6.5 ml, gammarid amphipods (5 individuals, 4 species) - 3.1 ml; shrimps (2 *Eualus gaimardii*, 1 *Sabinea septemcarinata*) - 3.0 ml; *P. libellula* - 0.5 ml; and unidentifiable fish flesh - 2.2 ml. Numbers of each copepod species counted in a subsample were: *C. hyperboreus* (mostly copepodite stage IV) - 160; *C.* sp. - 6; *C. finmarchicus* (adult female) - 1; *C. obtusifrons* - 1; *Heterorhabdus* sp. (copepodite V, male) - 1; and *M. lucens* (adult male) - 1.

79-KK-5 - Male - 10.6 m long - taken 11 October 1979 at 1740 hrs local time. Total contents estimated as at least 10 gallons. Quantitative sample consisted of: euphausiids (mostly *T. raschii*, at least 1 *T.*

inermis) - 350.4 ml; copepods (all identifiable were C. hyperboreus) - 0.1 ml; Saduria entomon (1 individual, 6.0 cm total length) - 4.0 ml; M. litoralis (30 individuals) - 3.0 cm; one Atylus carinatus - 0.2 ml; and two pebbles (5.0 and 9.0 mm) - 0.2 ml. An additional qualitative sample was taken, comprising primarily large, conspicuous items. In addition to items identical to those in the quantitative sample, this sample contained 1 P. libellula, 10 gammarid amphipods belonging to three species, and 6 small fishes (1 B. saida, 2 M. quadricornis, and 3 Pungitius pungitius).

80-KK-1 - Male - 9.1-10.7 m long - taken 14 September 1980 at about 2000 hrs local time several miles east of Kaktovik. Sample was probably from small intestine and was mostly digested. Contents were mostly copepod (probably Calanus) and several gammarid amphipods (Weyprechtia pinguis).

Samples from Whales Taken at Other Localities

78-H-2 - Male - 9.7 m - taken 4 May 1978 at Point Hope. Sample consisted of one intact gammarid amphipod (Ampelisca macrocephala), 2.9 cm total length, weighing 0.2 g.

79-H-3 - Male - 9.1 m long - taken 6 May 1979 at Point Hope. Contents of stomach were one snail (Natica clausa), 3.4 cm high, 2.6 cm in basal diameter, weighing 8.0 g.

80-SH-1 - Male - 10.1 m long - taken 9 May 1980 at 1430 hrs local time near Shaktoolik. Stomach empty; intestine contained only green liquid. Sample from colon contained crustacean fragments, including eyes and antennal scale from a small shrimp.

inermis) - 350.4 ml; copepods (all identifiable were *C. hyperboreus*) - 0.1 ml; *Saduria entomon* (1 individual, 6.0 cm total length) - 4.0 ml; *M. litoralis* (30 individuals) - 3.0 cm; one *Atylus carinatus* - 0.2 ml; and two pebbles (5.0 and 9.0 mm) - 0.2 ml. An additional qualitative sample was taken, comprising primarily large, conspicuous items. In addition to items identical to those in the quantitative sample, this sample contained 1 *P. libellula*, 10 gammarid amphipods belonging to three species, and 6 small fishes (1 *B. saida*, 2 *M. quadricornis*, and 3 *Pungitius pungitius*).

80-KK-1 - Male - 9.1-10.7 m long - taken 14 September 1980 at about 2000 hrs local time several miles east of Kaktovik. Sample was probably from small intestine and was mostly digested. Contents were mostly copepod (probably *Calanus*) and several gammarid amphipods (*Weyprechtia pinguis*).

Samples from Whales Taken at Other Localities

78-H-2 - Male - 9.7 m - taken 4 May 1978 at Point Hope. Sample consisted of one intact gammarid amphipod (*Ampelisca macrocephala*), 2.9 cm total length, weighing 0.2 g.

79-H-3 - Male - 9.1 m long - taken 6 May 1979 at Point Hope. Contents of stomach were one snail (*Natica clausa*), 3.4 cm high, 2.6 cm in basal diameter, weighing 8.0 g.

80-SH-1 - Male - 10.1 m long - taken 9 May 1980 at 1430 hrs local time near Shaktoolik. Stomach empty; intestine contained only green liquid. Sample from colon contained crustacean fragments, including eyes and antennal scale from a small shrimp.

Appendix III. Stomach contents of ringed seals collected in the Alaskan Beaufort Sea, August-September 1980.

RINGED SEAL STOMACH CONTENTS--BEAUFORT LAGOON, SEPTEMBER 1980 20-Apr-81

Species or Tax Code	Tot Vol (ml)	% Vol	Tot #	% #	# of Ocurr.	Freq of Occur.
Mysis sp.	.5	.0	5	10.0	3	18.8
MYSIDS	.5	.0	5	10.0	3	18.8
Acanthostepheia sp.	4.0	.4	5	10.0	1	6.3
Onisimus sp.	2.6	.2	14	28.0	1	6.3
Anonyx sp.	30.0	2.8	0	.0	1	6.3
Melita sp.	.4	.0	1	2.0	1	6.3
Gammarus sp.	2.0	.2	4	8.0	3	18.8
Gammaracanthus sp.	.6	.1	1	2.0	1	6.3
Unidentified Amphipod	1.0	.1	6	12.0	4	25.0
GAMMARID AMPHIPODS	40.6	3.8	31	62.0	6	37.5
Sabinea septemcarinata	.4	.0	1	2.0	1	6.3
Unidentified Shrimp	.4	.0	2	4.0	2	12.5
SHRIMPS	.8	.1	3	6.0	3	18.8
Thysanoessa raschii	289.5	26.9	0	.0	6	37.5
Thysanoessa inermis	177.5	16.5	0	.0	6	37.5
Thysanoessa sp.	.0	.0	2	4.0	1	6.3
EUPHAUSIIDS	467.0	43.5	2	4.0	7	43.8
Parathemisto libellula	.2	.0	1	2.0	1	6.3
Unidentified Hyperiid	.4	.0	2	4.0	2	12.5
Synidotea sp.	1.5	.1	5	10.0	1	6.3
Unidentified Polychaete	70.2	6.5	1	2.0	3	18.8
Unidentified Invertebrate	.3	.0	0	.0	1	6.3
OTHER	72.6	6.8	9	18.0	5	31.3
TOTAL INVERTEBRATE	581.5	54.1	50	100.0	12	75.0
Liparis sp.			1	.3	1	6.3
Gymnocanthus sp.			3	.8	2	12.5
Lycodes sp.			1	.3	1	6.3
Boreogadus saida			371	98.7	15	93.8
Unidentified Fish			0	.0	1	6.3
TOTAL FISHES	492.4	45.8	376	100.0	15	93.8
Rock, Stick, etc.	.7	.1			3	18.8

TOTAL VOL (ml)	1074.6
MEAN VOL (ml)	67.2
# W/FOOD	16
# MALES	6
# FEMALES	10
# EMPTY STOM	0
DATE RANGE	904 - 919

RINGED SEAL STOMACH CONTENTS - PINGOK ISLAND, AUGUST 1980   25-Mar-81

Species or Tax Code	Tot Vol (ml)	% Vol	Tot #	% #	# of Ocurr.	Freq of Occur.
Mysis sp.	5.1	.4			5	62.5
MYSIDS	5.1	.4			5	62.5
Onisimus sp.	.6	.1			1	12.5
Anonyx sp.	1.0	.1			1	12.5
Unidentified Amphipod	.2	.0			2	25.0
GAMMARID AMPHIPODS	1.8	.2			2	25.0
Eualus gaimardii	10.0	.8			3	37.5
SHRIMPS	10.0	.8			3	37.5
Thysanoessa sp.	.0	.0			2	25.0
EUPHAUSIIDS	.0	.0			2	25.0
Unidentified Hyperiid	.4	.0			1	12.5
Unidentified Cumacean	.6	.1			1	12.5
OTHER	1.0	.1			1	12.5
TOTAL INVERTEBRATE	17.9	1.5			7	87.5
Family Cottidae			1	.2	1	12.5
Boreogadus saida			639	99.8	8	100.0
TOTAL FISHES	1173.5	98.1	640	100.0	8	100.0
Rock, Stick, etc.	4.5	.4			1	12.5

TOTAL VOL (ml)	1195.9
MEAN VOL (ml)	149.5
# W/FOOD	8
# MALES	3
# FEMALES	5
# EMPTY STOM	0
DATE RANGE	821 - 901