THE ECOLOGY OF THE INSHORE

MARINE ZOOPLANKTON OF THE CHUKCHI

SEA NEAR POINT BARROW, ALASKA

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A

THESIS

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By

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ABSTRACT

The temporal variability in abundance, composition, and production of an arctic-marine inshore zooplankton community was investigated near Point Barrow, Alaska from May through August, 1972. Significant temporal differences ($\underline{P} < 0.05$) in population abundance over the summer were noted for 29 of 30 species. Changes in community composition resulted from the summer intrusion of Bering Sea water into the study area; southern copepods were observed during July and August. This intrusion imposes a temperature regime favorable for the rapid development and high production of meroplankton, particularly barnacle larvae. The meroplankters were largely responsible for creating a more diverse and productive community than that occurring in the epipelagic zone of the central arctic. Extensive recruitment of meroplankton was correlated with periods of high phytoplankton standing stock.

Community dry weight ranged from 4 to 41 mg/m^3, with the maximum occurring under the ice in late June one week after the phytoplankton bloom.

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CHAPTER 1. INTRODUCTION

Zooplankton organisms play a central role in the economy of the sea through their conversion of phytoplankton energy into protein and lipid stores suitable for the needs of members of higher trophic levels in the oceanic plankton food web. Shoaling fishes, some species of seals, and whales, are either directly or indirectly dependent upon this source of food for their survival. Accordingly, emphasis has been historically directed towards accumulating data on zooplankton with the intent of examining ecological interactions of this energy pool with commercially exploitable pelagic species in the world ocean. The approach taken toward evaluating these interrelationships has been divided among field and laboratory investigations. Baseline data collected in the field is essential for establishing biomass, reproductive periodicity, and the specific composition of the community in question. However, an understanding of the basic energy requirements and physiological processes of the zooplankton consumer organism should also supplement field data in the estimation of secondary production and the efficiency of energy transfer through the food web via the primary consumer level. Such studies of bioenergetics are necessarily conducted in the laboratory under controlled conditions.

Zooplankton field studies in the world ocean date from the mid-1800's and were characteristically descriptive in nature up through the early part of the 20th century; laboratory investigations concerned with the biology of the animal plankton have a more recent history.

Field research in arctic polar regions has long been difficult because of restricted access to many areas and deterents imposed by a harsh climate. These handicaps have been partially overcome through use of air transportation to previously inaccessible ice platforms and ice floes but plankton research in the Arctic Ocean is still conducted almost exclusively on a seasonal basis.

The Arctic Ocean represents a unique marine environment, characterized by its annular ice cover, vertical stability of the water column, and low annual biological productivity. Exceptions to this stable environment are found in the neritic areas of peripheral seas of the arctic, which are ice-free and vertically mixed during short portions of the summer and capable of producing rather high plankton standing stocks. Such a condition exists in the environment investigated by this study, a location where the livelihood of a portion of a large Eskimo community is indirectly dependent upon the high production of zooplankton organisms, manifested in the form of larger stocks of fishes, seals, and whales.

Laboratory research on the feeding biology and energy requirements of grazing zooplankton has historically been conducted in temperate latitudes. Relatively little is known of the bioenergetics and physiology of arctic and subarctic species, with the exception of Conover's work on *Calanus hyperboreus* in the Gulf of Maine (1962, 1966).

1.1 *Historical Arctic Plankton Investigations*

Early studies of the plankton of the Arctic Ocean were conducted either from drifting icebound vessels or seasonally along the ice-free coastlines of the continent. Two expeditions were noteworthy for their contributions to arctic plankton research up to the early 20th century. The pioneering physical and biological oceanographic investigations of the Eurasian basin and perimeter were undertaken from 1893-1896 by the Norwegian North Polar Expedition under the leadership of Fridtjof Nansen. The identifications of the collections of marine planktonic Crustacea from this voyage by G. O. Sars (1900) set a precedent for subsequent investigations into the diversity and general zoogeographical patterns of arctic zooplankton. The collections of the Canadian Arctic Expedition of 1913-1916 resulted in the preliminary description of the planktonic fauna along the arctic coastline of the Northwest Territories and Alaska and a good portion of the western Alaskan coastline. Major groups of plankton reported from the expedition included the hydromedusae and ctenophores (Bigelow, 1920), amphipods (Shoemaker, 1920), copepods (Willey, 1920), and the schizopod crustaceans (Schmitt, 1919). The results from these pioneering descriptive surveys indicated that the primary constituents of the zooplankton of the Arctic Ocean were crustaceans, most particularly the Copepoda.

For the past four decades, major contributions by the USSR, United States, and Canada have broadened our understanding of boreal and arctic zooplankton ecology. The first extensive, systematic studies of the calanoid copepod fauna in the Bering and Chukchi seas were initiated by the Soviet State Hydrological Institute in 1932. The advent of the *Sadko* expedition and the drift of the icebound vessel *Sedov* from 1937-1939 further extended Russian research on plankton biology into the Eurasian basin of the high arctic. The analysis of the *Sedov* collections by Bogorov (1946) corroborated Sars' earlier conclusion that many copepod species found in the central arctic were Atlantic in origin.

The use of air transportation to ice floes and ice islands by the Soviets in the late 1930's added a new dimension to conventional sampling platforms in the arctic. Early Soviet investigations from ice stations North Pole I in 1937, and most notably, North Pole II from 1950-1951, permitted the first long term and deep water collection of the zooplankton in the central arctic. A number of vertically divided hauls down to 3000 m depth were taken from NP II and provided material for the description of 19 additional copepod species not previously recorded. It was concluded that most of these species were endemic to the deeper waters of the basin (Brodskii and Nikitin, 1955).

The cruise of the U.S. Coast Guard Cutter *Chelan* in 1934 represented the initial major American effort toward the collection and study of marine zooplankton in the Bering and Chukchi seas (Johnson, 1934). This and later United States surveys in the vicinity by Johnson (1953) as well as Soviet investigations (Stepanova, 1937) provided much information on the composition and reproductive biology of the native species. The results from these studies also demonstrated the existence of a northward transport of endemic Bering Sea plankton through the Bering Strait and delineated their zones of expatriation in the Chukchi Sea. Subsequent to these investigations, the icebreaker U.S.S. *Burton Island* made an extensive survey of the zooplankton at 106 stations throughout the Beaufort and Chukchi seas during the summers of 1950 and 1951. Johnson (1956) reported on the copepod constituents of the *Burton Island* collections and discussed zoogeographical distributions of selected species in relation to the hydrography of the Beaufort and Chukchi areas. Hand and Kan (1961) provided a description of the hydromedusae and their breeding ranges and also included a discussion of the influence of the hydrography on species distribution.

American oceanographic investigations expanded into the central arctic with the establishment of Station "Bravo" on Fletcher's Ice Island (T-3) during the International Geophysical Year, 1952. The objectives for the research effort at this permanent station were not biological, but rather primarily to collect meteorological data, support geophysical research in the arctic, and establish a base for subsequent biological research. Initial American investigations into the plankton of the high arctic began with the occupation of IGY drift station "Alpha" during 1957-1958. Up to this time, a feature common to most previous plankton research in peripheral seas and the polar basin was an emphasis on systematics and the definition of general zoogeographical patterns. Research on "Alpha" provided continuous and deep water samples down to 2000 m depth from June, 1957 to February, 1958, and expanded upon previous research by emphasizing zooplankton biomass and primary productivity (English, 1961) in addition to systematics (Johnson, 1963).

The occupation of T-3 by the United States for studies of zooplankton biology began in 1958, six years following the establishment of Station "Bravo" on the ice island. The results of these investigations are well reported in the literature, concerned mainly with seasonal variation in biomass, plankton associations with water masses in the central arctic, and seasonal vertical distributions of organisms (Grainger, 1965; Mohr and Geiger, 1968; Hughes, 1968; Hopkins, 1969; Scott, 1969). Supplemental data from the ARLIS series I-IV, in particular ARLIS II from 1964-1965, provided additional information on seasonal changes in zooplankton biomass in the Eurasian basin north of Greenland (Minoda, 1967). Fletcher's Ice Island is the only ice station presently occupied by the United States in the central polar basin.

Knowledge of annual cycles of biomass, population dynamics, and production of the zooplankton communities in neritic areas of the arctic comes principally from research in the Canadian eastern arctic by Grainger (1959, 1962); east Greenland by Digby (1953, 1954); and in the Barents Sea, as reported by Zenkevitch (1963). Extensive studies have not been conducted along the Alaskan arctic coast. Early investigations in the marine environment near Barrow, Alaska adjacent to the Naval Arctic Research Laboratory by MacGinitie (1955) were concerned primarily with the benthos and included only a limited discussion of the macroplankton, this being generally descriptive in nature with some data on reproductive periods and the relative abundances of selected species in the plankton. Johnson (1958) provided data on the qualitative and quantitative composition of the inshore zooplankton community adjacent to NARL for a one month period during the summer of 1957.

1.2 *Laboratory Studies of Zooplankton Feeding Biology*

Since the beginning of this century, much attention has been paid to the feeding biology of grazing zooplankton, most particularly to the copepods of the genus *Calanus*. Early investigations were largely qualitative and included gross examination of gut contents (Dakin, 1908; Esterly, 1916; Lebour, 1922; Marshall, 1924). Later experiments emphasized measurements of filtration rates to determine whether utilization of filtered particulate matter was sufficient to meet the minimal metabolic requirements of the species (Fuller and Clarke, 1936; Harvey, 1937; Gauld, 1951). Recent work has been directed toward measuring growth rates and the effect of food type, developmental stage of the organism, and temperature on growth (Mullin, 1963; Mullin and Brooks, 1967, 1970); the relative grazing rates of nauplii and copepodid stages of copepods has also received attention in the literature recently (Paffenhöfer, 1971).

The research of Marshall and Orr on the calanoid copepod *Calanus finmarchicus* spanned four decades and introduced a high degree of sophistication to feeding studies and proposed the examination of new problems and methods. Marshall and Orr (1955a) were among the first to use radioactive tracers (^{32}P) to study the uptake and assimilation of algae by zooplankton. With the development of the use of ^{14}C by Steemann Nielsen (1952) for the measurement of primary production, a new method was evolved that could be similarly applied to basic research on the consumer level for the measurement of assimilation and ingestion (Marshall and Orr, 1955b).

Lasker (1960) applied ^{14}C techniques to a study of the feeding biology of the Pacific euphausiid, *Euphausia pacifica*, and emphasized assimilation and the daily ration necessary for metabolic maintenance. Lasker also endeavored to estimate secondary production, a subject presently being evaluated (for a review see Mullin, 1969).

The methods developed by Sorokin (1969) allowed for the measurement of the total energy balance of aquatic grazers using radioactive carbon, providing direct measurements of growth, respiration, reproduction, excretion, and egestion through use of ^{14}C.

1.3 Purpose of the Investigation

Quantitative studies of the dynamics of a nearshore zooplankton community along the arctic coast of Alaska are nonexistent. In contrast, the taxonomy and seasonal standing stock of the phytoplankton community in the coastal waters of the Chukchi Sea near Point Barrow have been investigated for eight years (Horner, 1969, personal communication). A logical extension of this research was a study of the animal plankton and its interaction with the phytoplankton community. Such an investigation on the inshore zooplankton community near NARL was initiated in 1972 for a three month period concurrent with investigations on the phytoplankton in the same area by Horner. My research expands upon previous taxonomic work along the Alaskan coastline and provides more ecological data. The following objectives were cited for this study: (1) to quantitatively describe the pattern of temporal variability in species abundance, composition, and standing stock of the inshore zooplankton community in the Point Barrow vicinity during the study period of May 25 through August 29, 1972; (2) to examine relationships between the variability of this community and changes observed in the state of the local hydrography and phytoplankton community; (3) to describe the life histories, associations, and recruitment periods of major zooplankton species; and (4) to investigate trophic interrelationships of the plankton in the laboratory.

A study of the plankton in the Chukchi Sea near Point Barrow was of special interest because of the dynamic state of the hydrography during the summer period and its expected influence on the dynamics of the pelagic community. The coastal oceanic environment of northern Alaska annually experiences two distinctly different hydrographic phases: (1) an open water period from July to September, characterized by extensive mixing of the water column with associated nutrient enrichment and relatively high productivity in the warm surface waters, and (2) an ice cover period from October to June, characterized by uniformly stable hydrographic conditions, low temperatures, reduced light transmission, and low productivity. These fluctuating conditions are unique and in opposition to the relatively uniform oceanographic state and stable plankton community persisting year round throughout the central basin and much of the periphery of the Arctic Ocean.

It was hoped that my research would provide a more complete understanding of the dynamics of the nearshore summer plankton community in the seasonally variable marine environment near Point Barrow, Alaska.

CHAPTER 2. MATERIALS AND METHODS

2.1 *Field Investigations*

The objectives of the field investigation were to describe the pattern of temporal variability in abundance and composition of the summer zooplankton community, to examine the relationship of this variability to the local hydrography, and to study life histories, associations, and periods of recruitment for dominant species. A calendar week was chosen as the time unit for comparisons and statistical testing of variability in species abundance during the summer season.

2.1.1. *Equipment*

The selection of diameter and mesh size of a zooplankton sampling net reflected both a previous knowledge of the minimum size range of dominant zooplankters in the community as well as consideration of which size fraction of the animal community was to be quantitatively examined.

The nets chosen for the majority of the work were of conical design with a 0.75-m diameter opening, tapering approximately 300 cm to a removable polyvinyl chloride collecting cup of 9-cm diameter. The netting was Nitex[1] high-capacity, monofilament nylon cloth with a mesh aperture of 0.308 mm; a short 8-cm nylon collar proceeded the filtration cone for attachment to a galvanized steel ring. A 3:1 open area ratio

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[1] J. J. Ross Mill Furnishing Company, Seattle, Washington 98115

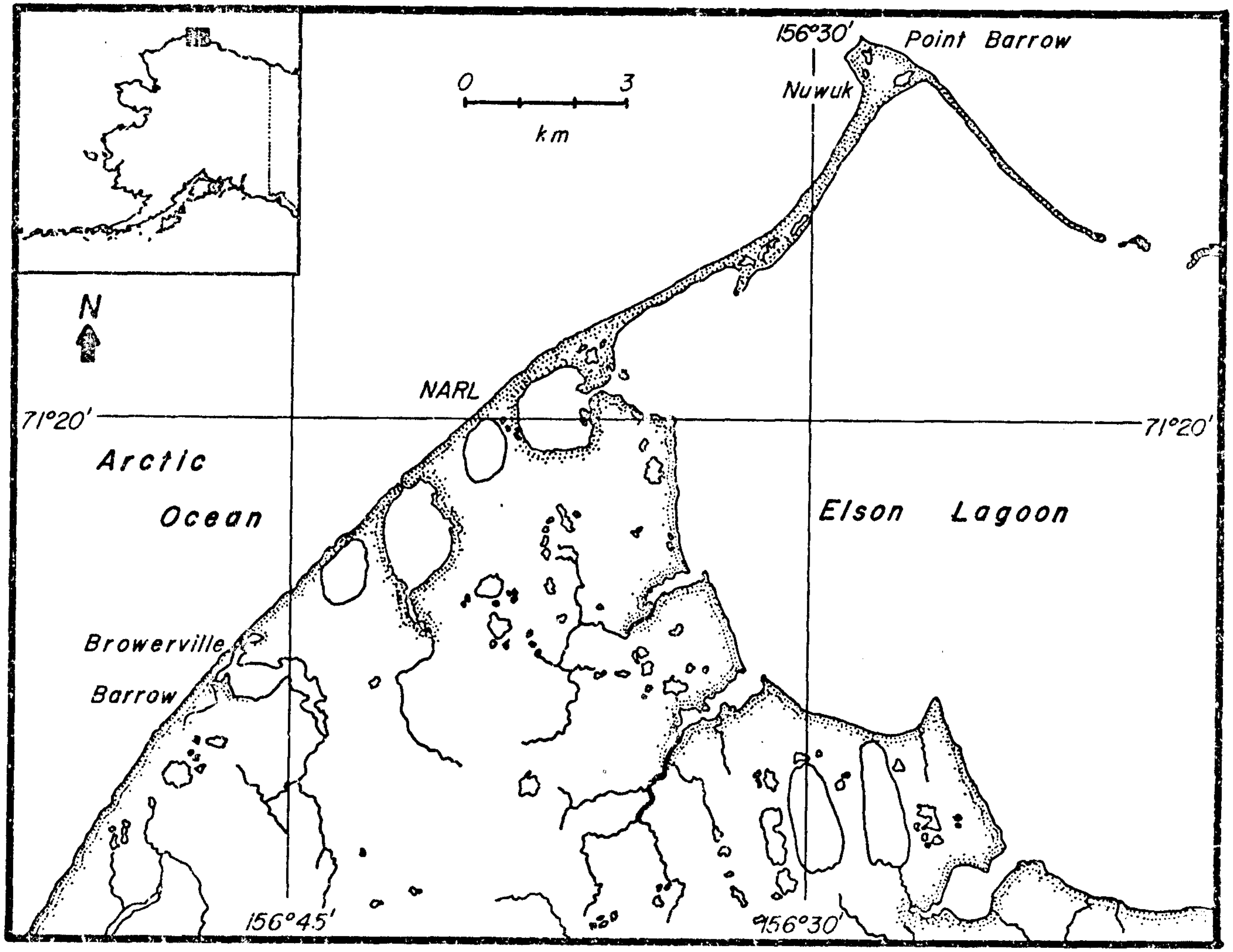
was realized as recommended by UNESCO (1968). In addition, a small number of qualitative samples were obtained during the sampling period with a Nitex 25-cm diameter, 0.046 mm-meshed net. One series of zooplankton samples was taken in February, 1972, with a Nitex 0.50-m diameter, conical net of mesh aperture 0.571 mm borrowed from the Institute of Marine Science, University of Alaska.

2.1.2 Station Locations

The sampling area included the 17 km (ten mile) stretch of coastline from Point Barrow to Barrow Village (Fig. 1). Collections of plankton in February and from May 25 to June 28 were obtained from a single ice station located approximately 1 km north of the NARL airport. Open water sampling was similarly carried out in the vicinity of NARL, roughly 1 to 2 km seaward of the coast in water depths of ten meters or less. Horizontal surface tows were taken 4 km from shore on July 22 and August 3, 4, and 5 at the 30 m depth contour for comparative purposes with the shallower nearshore community. A single sample from a vertical tow was also collected on August 4 at this depth.

A single series of evenly spaced samples was taken along a coastal transect from Point Barrow to Barrow Village on August 19. Three pairs of duplicate samples were collected within two hours for determining whether statistically significant spatial variability in the zooplankton community existed along the coastline at this time. One diel series of hauls was taken on August 28 to determine whether day-night differences in abundance existed for major zooplankters. A listing of sampling effort at the various station locations is included (Table 1).

Figure 1. Map of the northern Alaskan coastline near Point Barrow. Accompanying insert shows the study area in relation to the state



Point Barrow
156°30'
Nuwuk
0
3
km
N
NARL
71°20'
71°20'
Arctic Ocean
Elson Lagoon
Browerville
Barrow
156°45'
156°30'

Table 1. Relative sampling effort at various station locations near Point Barrow, summer 1972. Listed as total number of samples collected

LOCATION				
NARL		Barrow Village	Point Barrow	Outside Pressure Ridge
1 to 2 km seaward	3 to 4 km seaward			
94	6	2	2	2

2.1.3 Zooplankton Sampling Design

The field effort was divided between under-ice and open water sampling. A schedule of two to four sampling days per week was maintained with few exceptions throughout a period from May 25 to August 29, 1972. During this time, 107 samples were collected, the majority between 0900 and 1550 hours.

Shorefast ice was present in the nearshore environment near NARL through June 27. A permanent 1 x 2 m ice hole and wanigan hut were maintained for net sampling and diving purposes approximately 1 km from shore until ice conditions became treacherous. Water depth at this station was 6 m.

Under-ice sampling was accomplished using SCUBA divers or a pulley system. Divers would pull nets out manually to a prearranged distance (usually 17 to 23 m) from the hole where a release was made at mid-depth for retrieval. This operation was duplicated at each sampling date. Care was taken by the divers to avoid filtering water as the net was carried to the release point. The retrieval speed of the net was approximately 0.7 m/sec. The volume of water filtered by this method ranged from 7 to 11 m^3, under the assumption of 100% filtration efficiency.

Retrieved nets were rinsed twice and the sample contents placed in 250 or 500 ml (8 or 16 oz.) jars and returned to the laboratory for preservation in 10% sodium acetate-buffered formalin.

The sampling procedure described above was very demanding of the divers, and an under-ice pulley system was installed on June 20 to relieve the problem. A hole was drilled through the ice 18 m from the ice hole and a small block suspended beneath the ice. Nylon line was run through the pulley and the ends tied off on ice pitons at the diving hole. This method proved to be extremely convenient and excellent replicate hauls could be obtained with little effort.

Ice conditions during breakup prevented sampling from June 29 to July 7. Following this period, a 5-m (16 ft.) aluminum skiff became available for zooplankton sampling.

Consistent towing procedures were followed while operating the skiff. A horizontal tow of about 300 m was chosen, providing a total filtered volume of 130 m^3. It was thought that this distance would be sufficient to provide an adequate sample and would also integrate any small scale patchiness that might exist in the plankton community. Tow distance (300 m), speed (1 m/sec), and methods of rinsing nets were standardized to reduce sampling error. Skiff speed was estimated and adjusted accordingly by measuring the time for a floating object to travel the 5 m distance from the bow to the stern while the net was fishing.

A nylon line of 0.65-cm thickness (1/4 in.) was attached to the net at the middle of the ring crossbar and the net was placed in the water while the skiff was in neutral gear and allowed to sink two or three meters below the surface. Fishing depth was monitored during each tow by measuring the wire angle and the length of line extended. Duplicate hauls were taken on each sampling date and sample contents treated as previously described.

Towing velocity was selected as a compromise between an effort to maximize filtration efficiency and reduce the problem of net avoidance characteristic of certain micronekton at low towing speeds (UNESCO, 1968). Horizontal rather than the more mechanically difficult oblique hauls were used for the open water design because vertical salinity profiles during this period indicated the water column to be homogeneously mixed to the bottom. It was assumed little or no vertical zooplankton stratification existed in the area under these conditions.

2.1.4 Environmental Observations

Water samples were taken concurrently with zooplankton collections for the determination of salinity, nutrient concentrations, and chlorophyll *a* content (See UNESCO, 1966). Samples were consistently collected at the surface during ice cover and also at 1, 3, and 5 m as melting progressed. Open water collections were generally made at 0, 1, 3, and 5 m. A 6-liter PVC Van Dorn bottle (1956) or modified Scott-Richards water sampler were used for all collections. Bottles were lowered to the desired depth and tripped with a brass messenger. A small aliquot of each water sample was removed and placed in a 250 ml squat jar for future phytoplankton identifications and counts (Horner, personal communication). In addition, samples of the larger phytoplankton were collected periodically during the summer with a Nitex net of mesh aperture 0.046 mm. Surface water temperature to the nearest °C and transparency were also recorded on all zooplankton sampling dates. The disappearance of a white 30-cm diameter Secchi disk was noted to increments of 0.5 m.

Phytoplankton primary productivity experiments employing radioactive bicarbonate were also conducted regularly throughout the summer in the inshore waters off NARL (Horner, personal communication).

The general current direction, pack ice movement, wind velocity and direction, and the level of incident radiation were observed regularly in the Barrow area.

2.2 Laboratory Analyses

Zooplankton samples were returned to NARL for identification, counting, length measurements, and dry weight analysis. An occasional examination of gut contents was included for selected species. The analysis of material was completed at the University of Alaska Museum, Aquatic Division. Samples collected in February were only qualitatively examined. Specific identifications were made using the following texts:

Shirley and Leung, 1970 Bigelow, 1920 Naumov, 1969	Hydrozoa
Pettibone, 1954	Polychaeta
Barnard, 1969 Tencati, 1970	Amphipoda
Sars, 1900 Brodskii, 1967 Rose, 1933 Tanaka, 1956 Vidal, 1971 Fulton, 1968	Copepoda
Leung, 1970	Euphausiacea

Dawson, 1971	Chaetognatha
Wimpenny, 1966	Larvacea
Walters, 1955	Pisces

2.2.1 Identification and Enumeration

Each zooplankton sample was poured into a 50 x 75-cm white photographic tray, diluted with water, and evenly distributed and sorted under an overhead light. Larger zooplankton were removed prior to subsampling and individually identified and counted, sized, and placed in vials for future reference. Groups of this type include larger hydromedusae, scyphozoan medusae, pteropods, polychaetes, amphipods, euphausiids, juvenile shrimp, mysids, chaetognaths, and larval and juvenile fishes. Small, rarer specimens were treated similarly.

The remaining, relatively homogeneous sample was placed in a calibrated 1000 ml wide-mouth graduated beaker and diluted to 400 ml in preparation for subsampling. The water height associated with this volume was ideal in minimizing the potential for vertical gradients in plankton concentrations due to settling during the subsampling process.

Subsamples were removed using Hensen-Stempel Pipets[2] equipped with interchangeable sampling spools of 1, 2, 5, or 10 ml. Zooplankters were stirred in a random fashion with precautions taken to avoid introducing localized eddies or pockets of high concentration. Duplicate aliquots were removed in twenty-three cases to determine the error associated with subsampling techniques.

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[2] Wilco Scientific Supply Co., Saginaw, Michigan.

Subsamples were placed in 60 x 15 or 100 x 15-mm Pyrex petri dishes and the organisms identified, counted, and measured under a variable power (0.7 to 6.0X), stereoscopic microscope; a minimum of 100 specimens were examined. The relative abundances of various developmental stages of copepod species were determined by direct counting or roughly estimated as fractions of the total count for the species. Copepod nauplii were not differentiated by stage, but grouped together and counted. Size-frequency relationships for the other zooplankton groups were more easily determined, where direct measurements alone were usually adequate to distinguish life history stages. Chaetognaths were grouped and quantified in size ranges of greater than 30 mm, 20 to 30 mm, 13 to 20 mm, and less than 13 mm to reduce the labor involved in measuring each specimen individually. Size grouping procedures were also followed for some species of hydromedusae and occasionally for the euphausiids. Barnacle nauplii larvae were grouped into sizes of greater than 0.308 mm and less than 0.308 mm for counting.

Total numbers of each species in the sample were determined by multiplying counts in the subsample by the inverse of the aliquant fraction removed. Division by the volume filtered provided the estimate of the number of individuals per cubic meter of water sampled.

2.2.2 *Size of Organisms*

Size measurements were made on all zooplankton in an effort to establish life history stages.

Measurements on all species were made using a calibrated, transparent, millimeter rule. Specimens were placed directly on the ruler and measurements made under the stereomicroscope. Copepods, ostracods, barnacle larvae, and larvaceans were measured to the nearest 0.1 mm; other zooplankton groups were sized to the nearest millimeter. Methods of measurement were consistent with presently acceptable standards. Copepods were sized from the tip of the cephalosome to the end of the caudal rami, euphausiids and mysids from the anterior tip of the carapace to the end of the telson; bell height was determined for hydromedusae and the head length for larvaceans. The diameter of scyphozoans was determined. Chateognaths were measured along the pivotal or central axis. Bent organisms were straightened prior to measurement.

2.2.3 *Dry Weight*

Dry weight analyses were performed on 107 preserved zooplankton samples to examine temporal variability in biomass. The procedure involved dividing the samples into halves using a modified sand splitter (Cooney, 1971). Rarer organisms removed in prior sorting operations for purposes of organizing a museum reference collection were not processed. Large scyphozoan medusae and juvenile fishes were also not considered in dry weight measurements.

Each sample was divided into two parts and after rinsing the splitting apparatus, one half was returned to the original sample jar, preserved in 100% formalin, and stored in the University of

Alaska Museum, Marine Collections. The remaining half-sample was flushed in running tap water for 5 minutes, drained, and poured into a tared, aluminum foil tray. Samples were dried to constant weight at 56°C for 18 to 24 hours (Lovegrove, 1966). Newly removed samples were cooled in a desiccator for 10 minutes and then weighed to the nearest milligram on the Mettler[3] F160N balance.

In addition to total zooplankton biomass, the average individual dry weights were determined for selected developmental stages of the copepods, *Calanus glacialis*, *Pseudocalanus minutus*, *Acartia* sp.; the chaetognath, *Sagitta elegans arctica*; the pteropod, *Limacina helicina*; the hydromedusa, *Aglantha digitale*; and the cirriped, *Balanus* nauplii and cyprid larvae. Fifty individuals of each developmental stage of the Copepoda were selected for weighing. The same number of individuals of the Chaetognatha were chosen in each of the size ranges previously described; a variable number of pteropods and hydromedusae, generally from 15 to 30, were weighed and average values obtained. Five ml aliquots of a sample known to consist predominantly of barnacle larvae were removed for weighing. Organisms were placed in tared, aluminum foil trays of the type used in total dry weight analysis, dried, and weighed on a Mettler Type B6 pan balance to 0.1 mg accuracy. This method provided a fractionation of total dry weight for any given sample into the relative percentages of biomass contributed by the major species.

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[3]Mettler Instrument Corp., San Francisco, California 94119

2.3 *Statistical Procedures*

Statistical analyses were performed to evaluate the variability associated with several levels of sampling and to test differences between means. Three levels of sampling variability were examined: subsampling, field or replication error, and within-week error. Data transformation, one-way analysis of variance, confidence limit estimation, and correlation analysis were techniques employed in the treatment of data. Notation and description of terms follow Snedecor and Cochran (1967).

2.3.1 *Data Transformation*

Counts of all species were recorded as number of individuals per 100 m^3 of water filtered. These data were then transformed into logarithms for one-way analysis of variance (English, 1961). The following transformation was used:

$$X_i = \log_{10} (X_o + 1)$$

where X_i is the transformed variable; and X_o is the original observation. The addition of 1 to the original variable alleviates the problem of taking the logarithm of 0 when organisms are absent in hauls (Taylor, 1953).

Means, sums of squares, and mean squares were obtained using a BMD 01V program for one-way analysis of variance (Dixon, 1965). Computations were made by an IBM 360 computer. The geometric means of original observations were obtained by taking the antilogarithm minus 1 of the transformed means.

2.3.2 *One-Way Analysis of Variance*

A fixed model of a one-way analysis of variance was used to examine the statistical significance of variability in mean abundance for all zooplankton species for the summer period. Variability associated with subsampling techniques, within-day or field methods, and within-week sampling, represented the levels of sampling examined. A weekly interval of 7 days was chosen as the time unit for the statistical analysis of summer population trends for all species. A geometric mean for weekly periods was obtained by averaging the daily means within the week; the daily observations within weeks then formed the basis for testing differences between weekly periods.

The following fixed model was used for the analysis of variance:

$$X_{ij} = \mu + \alpha_i + e_{ij}$$

where X_{ij} is the transformed observation of average numbers of specimens per 100 m^3/day, μ is the overall mean; α_i is the time effect in weeks, $i = 1, 2, 3, \ldots 13$; and e_{ij} is the error term, $j = 1, 2, 3, \ldots n$. Assumptions implicit to the model are: (1) the summation of the treatment effects equal zero ($\Sigma\alpha_i = 0$); and (2) the error terms are normally distributed about a mean of 0 with standard deviation $\delta(e_{ij} = N(0,\delta))$.

2.3.3 *Estimation of Confidence Limits*

Confidence limits were calculated about subsampling, daily, and weekly means to define significant differences in abundances of organisms for the summer. The following equation was used as the model:

$$CL = \overline{X}_{geo} \underset{x}{\div} \text{antilog}\left(t \sqrt{\frac{MSE}{n}}\right)$$

where $\overline{X}_{geo}$ is the weekly geometric mean; *t* is Student's t at P = 0.05 and the degrees of freedom associated with the mean square; MSE is the within-week mean square error; and n is the number of observations contributing to the weekly mean.

2.3.4 *Correlation Analysis*

It was desirable as part of the present study to examine species associations in the zooplankton in relationship to certain major parameters influencing the variability in abundance of organisms with time as well as factors responsible for changes in community composition. To aid in this interpretation, a BMD 02R program for stepwise multiple regression was chosen for the analysis (Dixon, 1965). A correlation matrix was generated for 31 parameters, including 28 zooplankton categories and temperature, salinity, and chlorophyll *a*.

2.4 *Trophic Studies*

As a supplement to field research, the present study included laboratory investigations of the feeding biology and energy budget of selected zooplankton species fed ^{14}C-labelled phytoplankton.

Estimates of filtration and ingestion rates, assimilation efficiency and the relative apportionment of assimilated energy into growth, respiration, and excretion were obtained under varying biological and physical conditions in the laboratory. Energetics were examined on both the community and individual species level of organization.

2.4.1 *Experimental Organisms*

Zooplankters used for the laboratory studies were generally chosen for their numerical dominance in the plankton. These included adult females or stage V copepodids of the copepods *Calanus glacialis*, *Pseudocalanus minutus*, *Acartia* spp., and *Calanus hyperboreus*; a random sample of the zooplankton community of August 28 was used in one experiment, consisting of *Balanus* nauplii and cyprid larvae, echinoderm and polychaete larvae, some juvenile *C. glacialis* and adult *Acartia*, and hydromedusae. Investigations also included the study of the physiology of a Bering Sea expatriate species, *Calanus plumchrus* stage V.

2.4.2 *Algal Culture and Cell Counting Techniques*

All phytoplankton species used in the experiments were common to the Barrow area and included a unialgal, solitary *Chaetoceros* sp., a mixed population of the diatoms *Nitzschia closterium*, *N. seriata*, *Navicula* sp., and a green biflagellated "*Chlamydomonas*-type" alga. Phytoplankton were cultured in 250 ml Erlenmeyer flasks or squat jars, to which were added 40 to 50 ml of Millipore-filtered seawater and 20 ml of half strength Provasoli culture enrichment medium. Solutions were occasionally enriched with 1 drop of $NaSiO_3$. Algae were incubated in culture chambers at 5°C in either continuous or 12-hour daily light cycles. Incident radiation in the culture chambers varied from 2800 to 4800 lux.

Inoculations were made with radioactive carbon in the ratio of 5 to 10 μCi $NaH^{14}CO_3$ per 50 to 70 ml culture solution; the culture flasks were then capped and returned to the chamber for further incubation, usually 2 days to 1 week.

Cultures were prepared for experiments by centrifugation in 50 ml tubes, initially at 2000 rpm for 3 minutes and then at 1500 rpm for an additional 2 to 4 minutes. After decanting and resuspending the cells in double Millipore-filtered seawater, centrifugation was repeated at 1200 rpm for 3 minutes. The "hot" cells were then placed in a 2000 ml beaker and a stock solution prepared by diluting with activity-free filtered seawater to the desired volume. Aliquots of unialgal stock solutions were removed immediately prior to experimentation for establishing initial cell density per unit volume.

A model B Coulter Counter was made available for determining cell concentrations per unit volume of unialgal *Chaetoceros* culture at the beginning and end of the experiments. Five or six replicate counts were taken on 0.5 ml aliquots of *Chaetoceros* culture and the average of these counts used as the cell concentration. Aliquots of double Millipore-filtered seawater were used for establishing background counts.

2.4.3 *Experimental Feeding Procedures*

The mass balance equation for an individual organism established the premise from which the experimental methodology developed. A general form of the equation is as follows:

$$\underset{(I)}{\text{ingestion}} = \underset{(G)}{\text{growth}} + \underset{(RP)}{\text{reproduction}} + \underset{(RS)}{\text{respiration}} + \underset{(E)}{\text{excretion}} + \underset{(F)}{\text{feces}}$$

where G + RP + RS + E = assimilation.

Studies of the energetics of single copepod species involved the use of 250 ml squat jars as feeding containers, to which were added 150 ml of algal culture from a stock solution and 2 to 4 organisms. Community feeding experiments employed 1000 ml wide-mouth beakers as holding vessels and 450 ml of stock culture. Two or three replicate feeding jars or beakers were used in all cases. In addition, a phytoplankton control jar was used in all experiments to account for any possible respiratory, excretory, or photosynthetic activity by the algae during the experimental duration.

All experiments were conducted in culture chambers or in a Gilson respirometer with a water bath at *in situ* temperatures. Feeding jars were gently agitated periodically during the experiment to keep the algal cells in suspension.

The cellular activity and the activity of the filtrate were determined at the beginning of each experiment by filtering aliquots of algal stock solution through a Millipore HA filter (pore size 0.45 μm), and removing 3 ml aliquots of the filtrate. These were added to 10 ml of Aquasol for counting.

After an experimental time period of 4 or 24 hours, the organisms were removed from the feeding jars, rinsed, and placed in 2 ml of Protosol[4] tissue solubilizer and 2 drops of water for a 12 hour dissolution period. Ten ml of Aquasol and 3 ml of water were added to form a thick gel before counting.

Faecal pellets were removed from the feeding jars under a dissecting scope, rinsed, and dissolved in Protosol as described above. Twenty ml aliquots of the cell-filtrate solution were removed from control and feeding jars for establishing cell density of unialgal cultures. The remaining 130 ml of solution were filtered through 0.45 μm Millipore filter paper, to separate the cells (particulate labelled matter) from the filtrate (dissolved labelled matter).

Two methods were employed in the analysis of filtrate activity: the phenethylyamine process and direct volume aliquot method. Both were used to measure the relative amount of assimilated energy diverted into respiration and excretion. The advantage of the phenethylamine method over the direct aliquot measure is that it is possible to differentiate respiratory and excretory losses with the former; the later method measures the composite total activity of respiration and excretion.

The phenethylamine technique used followed the procedures developed by Harrison, Wright, and Morton (1971). The procedure involves capturing liberated $^{14}CO_2$ on phenethylamine-soaked filter paper after acidification with H_2SO_4. Excretory (organic carbon) and respiratory

[4]New England Nuclear West, 200 Professional Building, El Cerrito Plaza South, El Cerrito, California 94530

(inorganic carbon) losses were differentiated by using progressively stronger acids. Filters were added to scintillation cocktails as previously described and counted.

As a check against the efficiency of the phenethylamine process, direct aliquots of filtrate (3 ml) were extracted with volumetric pipets and the radioactivity of both methods compared. The phenethylamine process was abandoned after the first experiment because of the time involved and when it appeared that it considerably underestimated respiration and excretion in comparison to the direct aliquot method. This latter method was used in all other experiments.

All radioactive samples were counted on a Nuclear-Chicago Model 6848 liquid scintillation counter for 10 minutes; extremely "hot" samples were counted at a threshold of 1000 K counts. Quenching was corrected for using the channels ratio method and counting efficiency determined. Absolute disintegrations per minute (DPM) were then calculated by the following formula:

$$DPM = \frac{\text{CPM channel A - CPM background}}{\text{Counting Efficiency}}$$

Equations used for the calculation of filtration rate, total ingested activity, and assimilation and gross growth efficiency are included in Appendix II.

CHAPTER 3. RESULTS

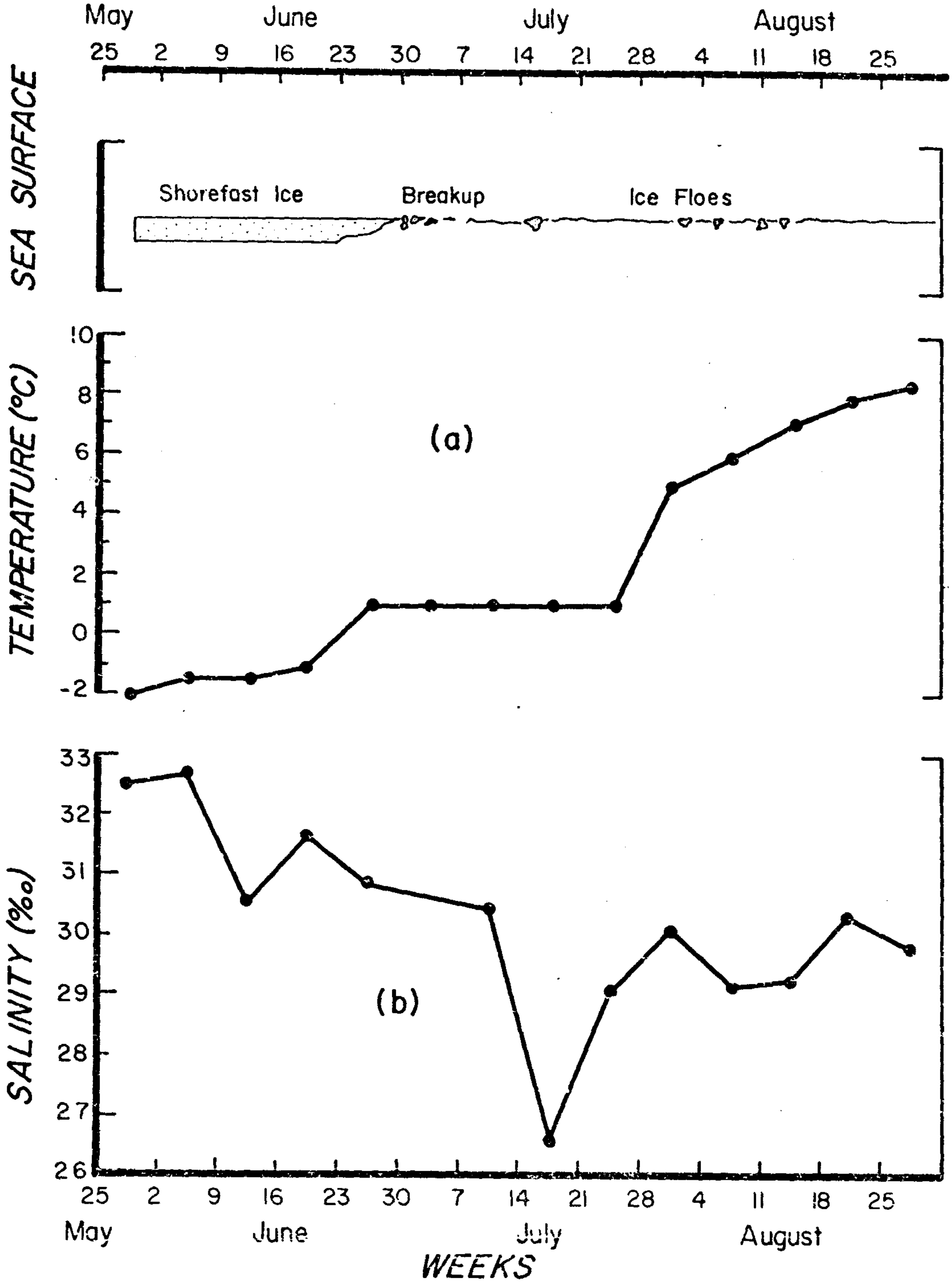
3.1 The Nearshore Hydrography

A dynamic hydrographic regime during the summer season is evidenced by the observed temporal distributions of temperature, salinity, and ice cover (Fig. 2). Surface temperatures increased gradually from a low of -2°C in late May to 1°C the week of June 23. During the period July 21 to August 4, a rapid thermal increase to 6°C was noted, while the surface water maximum, 8.5°C, did not occur until the last week of August. The highest salinity values of the summer, 32.6°/oo, were recorded between June 2 and June 8. A decline in total dissolved salts from 30.4°/oo to 26.6°/oo, occurred from July 7 through July 20, after which an increase to 30.1°/oo was observed the last week of July. Salinities fluctuated between 29.2°/oo and 30.3°/oo for the remainder of the summer.

Following breakup in early July, the inshore open water environment was free of ice with few exceptions. Drift ice usually accompanied a westerly or northwesterly wind and was recorded near shore on the following days: July 19; and August 2, 6, 10, and 12. The permanent ice pack was often times observed on the near horizon, but rarely moved in closer than two miles from shore. Ice conditions hampered the sampling operations only during the breakup period.

The nearshore current direction was generally northeasterly toward Point Barrow from late May to late July. At this time, a complete reversal in direction to the southwest or west occurred, a

Figure 2. Temporal distributions of the state of the sea surface, coincident with (a) surface water temperature, and (b) the average water column salinity, averaged for each of 14 sampling weeks, summer 1972


May
June
July
August
25 2 9 16 23 30 7 14 21 28 4 11 18 25
SEA SURFACE
Shorefast Ice
Breakup
Ice Floes
TEMPERATURE (°C)
10
8
6
4
2
0
-2
(a)
SALINITY (‰)
33
32
31
30
29
28
27
26
(b)
25 2 9 16 23 30 7 14 21 28 4 11 18 25
May
June
July
August
WEEKS

condition that persisted to early August. After August 4, the current showed no consistant directional tendency.

3.2 The Zooplankton Community

Forty-five categories of zooplankton, including 9 phyla and 28 categories identified to species, comprised the inshore community near Point Barrow, Alaska, during the summer, 1972 (Fig. 3). All organisms in my collections were previously reported from the area (Willey, 1920; MacGinitie, 1955; Johnson, 1956, 1958; Hand and Kan, 1961).

3.2.1 Statistical Studies

The results of the statistical studies demonstrated significant differences between weekly mean abundances and in variability associated with sampling levels.

3.2.1.1 Levels of Variability

Estimates of variability from the one-way analysis of variance were used to calculate upper percentage confidence limits about weekly, replication, and subsampling mean abundances for comparison of variability assocated with these sampling levels. The upper percentage confidence limit increased from subsampling, to replication, to the within-week level for 28 of 37 categories of zooplankton examined on these levels (Table 2). In no case did the subsampling error exceed the replication or within-week variability.

Figure 3. Qualitative distribution of the constituents representing the Barrow zooplankton community from May 25 to August 28, 1972

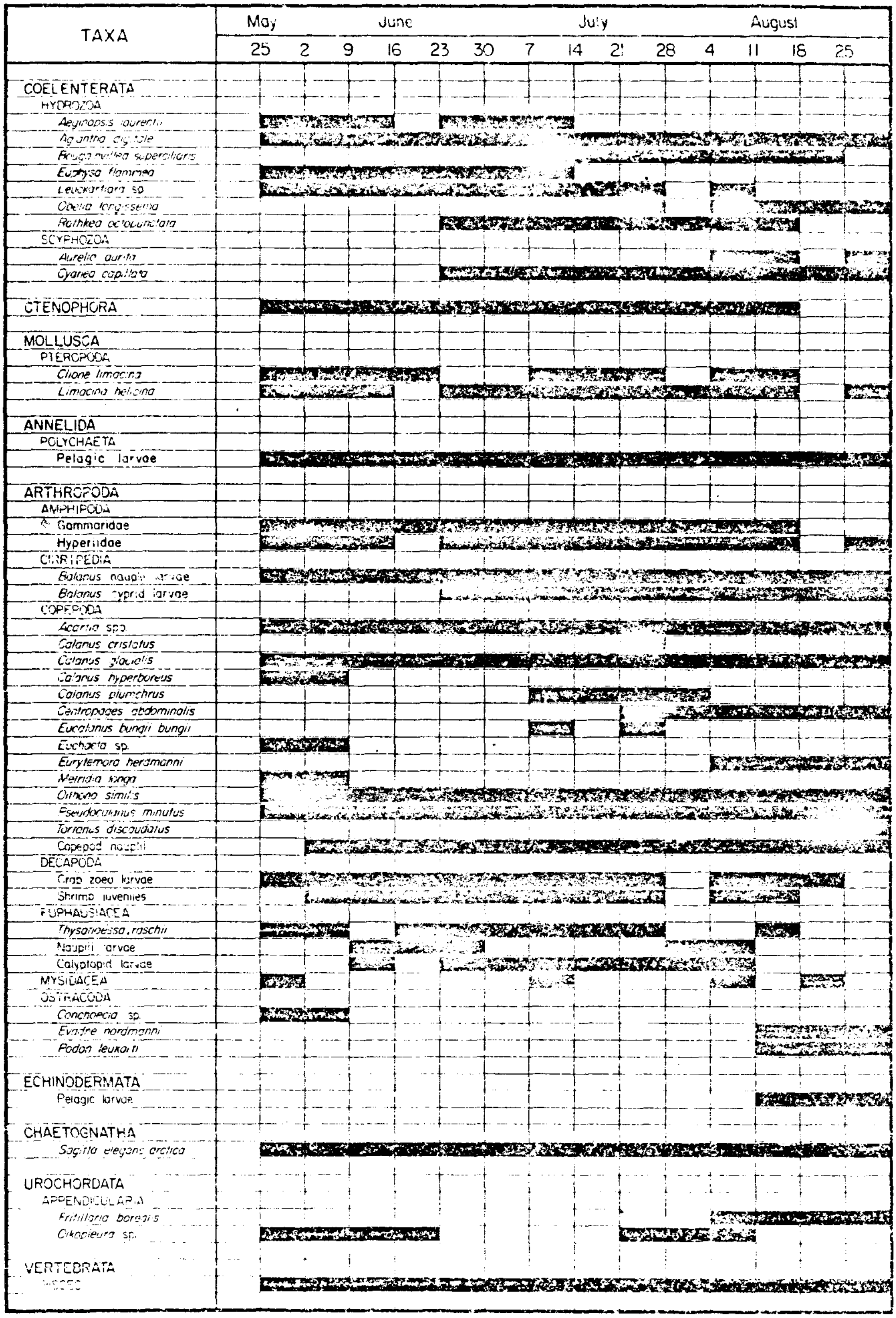

TAXA
May
June
July
August
25
2
9
16
23
30
7
14
21
28
4
11
18
25
COELENTERATA
HYDROZOA
Aeginopsis laurentii
Aglantha digitale
Bougainvillea superciliaris
Euphysa flammea
Leuckartiara sp.
Obelia longissima
Rathkea octopunctata
SCYPHOZOA
Aurelia aurita
Cyanea capillata
CTENOPHORA
MOLLUSCA
PTEROPODA
Clione limacina
Limacina helicina
ANNELIDA
POLYCHAETA
Pelagic larvae
ARTHROPODA
AMPHIPODA
Gammaridae
Hyperiidae
CIRRIPEDIA
Balanus nauplii larvae
Balanus cyprid larvae
COPEPODA
Acartia spp.
Calanus cristatus
Calanus glacialis
Calanus hyperboreus
Calanus plumchrus
Centropages abdominalis
Eucalanus bungii bungii
Euchaeta sp.
Eurytemora herdmanni
Metridia longa
Oithona similis
Pseudocalanus minutus
Tortanus discaudatus
Copepod nauplii
DECAPODA
Crab zoea larvae
Shrimp juveniles
EUPHAUSIACEA
Thysanoessa raschii
Nauplii larvae
Calyptopid larvae
MYSIDACEA
OSTRACODA
Conchoecia sp.
Evadne nordmanni
Podon leukarti
ECHINODERMATA
Pelagic larvae
CHAETOGNATHA
Sagitta elegans arctica
UROCHORDATA
APPENDICULARIA
Fritillaria borealis
Oikopleura sp.
VERTEBRATA

Table 2. Upper percentage confidence limits, P = 0.05, for observations at the subsampling, daily replication, and within-week sampling levels for selected categories of zooplankton

	Percentage Confidence Limits					
Categories	Subsampling	DF[a]	Field Replication	DF[a]	Within-week	DF[a]
Hydrozoa						
Aegiropsis laurentii	-	-	179	10	1,390	5
Aglantha digitale	131	10	580	40	442	24
Bouvainvillea superciliaris	-	-	277	15	240	8
Euphysa flammea	-	-	232	11	339	5
Obelia longissema	-	-	2,471	13	7,280	5
Leuckartiara sp.	-	-	455	22	569	15
Rathkea octopunctata	-	-	638	16	4,677	9
Ctenophora						
Mertensia ovum	-	-	250	15	420	8
Pteropoda						
Clione limacina	-	-	595	15	1,380	5
Limacina helicina	-	-	970	28	1,660	14
Polychaeta						
larvae	128	22	508	41	295	25
Amphipoda						
Gammaridae	-	-	487	29	281	17
Hyperiidae	-	-	364	28	422	15
Cirrepedia						
Balanus nauplii > 308 μm	131	18	270	39	1,320	22
Balanus nauplii < 308 μm	164	17	627	34	7,413	18
Balanus cyprids	136	19	441	31	596	17
Copepoda						
Acartia sp.	170	21	316	40	270	25
Calanus cristatus	-	-	-	-	-	-
C. glacialis	151	18	283	39	379	24
C. hyperboreus	-	-	546	4	584	4
C. plumchrus	-	-	180	10	317	7
Centropages abdominalis	164	10	230	21	259	10
Eucalanus bungii bungii	-	-	-	-	-	-
Euchaeta sp.	-	-	502	3	854	3
Eurytemora herdmanni	-	-	-	-	344	9
Metridia longa	-	-	818	3	2,206	3
Oithona similis	150	19	211	40	264	25
Pseudocalanus minutus	171	21	195	41	225	25
Tortanus discaudatus	-	-	-	-	-	-
copepod nauplii	158	12	556	34	251	21

Table 2 (continued)

Categories	Percentage Confidence Limits					
	Subsampling	DF[a]	Field Replication	DF[a]	Within-week	DF[a]
Decapoda						
Crab zoea larvae	188	10	364	26	295	13
shrimp larvae	-	-	467	18	897	19
Euphausiacea						
Thysanoëssa raschii	-	-	753	14	2,190	6
furcillia larvae	224	10	1,660	6	9,660	3
Ostracoda						
Conchoecia sp.	-	-	222	4	1,259	2
Evadne nordmanni	-	-	229	13	1,660	5
Podon leukarti	-	-	181	13	944	5
Chaetognatha						
Sagitta elegans arctica	167	16	334	41	284	25
Appendicularia						
Oikopleura sp.	-	-	925	9	7,762	2
Fritillaria borealis	-	-	468	18	69,183	7
Pisces	-	-	451	32	344	17

[a] Degrees of freedom corrected for cells containing no organisms.

\- Organisms were not subsampled or were too few in number for statistical analysis.

3.2.1.2 Tests of Hypotheses

The observations within one calendar week provided the basis for testing differences between average weekly abundances for all zooplankton categories during the summer. The null hypothesis of no difference between weekly means was tested using the F-statistic and was rejected for 29 of 30 categories ($\underline{P} < 0.05$; Table 3).

Two additional hypotheses were tested statistically: (1) the effects of sampling location on the average abundance of inshore zooplankton; and (2) the effects of time of day on the average abundance of zooplankton sampled at one location.

The effect of sampling location on zooplankton numbers was of interest in determining whether significant spatial differences existed in the inshore zooplankton community along the Barrow coast. The data from the coastal transect taken on August 19 were used for the analysis. Three pairs of replicate tows were collected within 2 hours, one set each at Barrow Village, NARL, and Point Barrow. The replicates taken at the usual summer sampling site (NARL) were used as the standard to which the other areas were compared. Average abundances were calculated for 9 categories of zooplankton from each set of replicated tows taken at the three areas. Within-week upper and lower confidence limits previously determined for each zooplankton category were applied about the mean abundance of organisms sampled off NARL, the reference location. These limits were then compared with the average abundances for categories from Point Barrow and Barrow Village. If the mean abundance of the zooplankton category

Table 3. Statistical evaluation of the effects of time on the variability of weekly mean population abundance for selected categories of zooplankton from May 25 to August 28, 1972

Zooplankton Category	Statistical Significance: Time[1] F[2]	df
Hydrozoa		
Aglantha digitale	**	12,25
Bougainvillea superciliaris	**	12,25
Leuckartiara sp.	**	12,25
Obelia longissema	**	12,25
Rathkea octopunctata	*	12,25
Pteropoda		
Clione limacina	NS	12,25
Limacina helicina	*	12,25
Polychaeta	**	12,25
Amphipoda		
Gammaridae	**	12,25
Hyperidae	**	12,25
Cirripedia		
Balanus nauplii larvae	**	12,25
Balanus cyprid larvae	**	12,25
Copepoda		
Acartia spp.	**	12,25
Calanus glacialis	**	12,25
Centropages abdominalis	**	12,25
Eurytemora herdmanni	**	12,25
Oithona similis	*	12,25
Pseudocalanus minutus	**	12,25
copepod nauplii	**	12,25
Decapoda		
shrimp juveniles	**	12,25
Chionoecetes zoea larvae	**	12,25
Paralithodes zoea larvae	**	12,25
Euphausiacea		
Thysanoëssa raschii	**	12,25

Table 3 (continued)

Zooplankton Category	Statistical Significance: Time[1] F[2]	df
Ostracoda		
Evadne nordmanni	**	12,25
Podon leukarti	**	12,25
Chaetognatha		
Sagitta elegans arctica	**	12,25
Appendicularia		
Fritillaria borealis	**	12,25
Oikopleura sp.	*	12,25
Pisces	**	12,25
Zooplankton community biomass	*	12,25

1 H_o: $\alpha_i = 0$

2 * = P < 0.05; ** = P < 0.01; NS = not significant (P > 0.05)

tested fell within the limits of the standard interval, no statistically significant spatial difference in abundance was assumed. Means falling outside the limits were considered significant ($\underline{P} < 0.05$).

The results of the analysis indicated the null hypothesis was accepted (i.e., no spatial differences in abundance existed) for 16 of 18 cases (Table 4). Significantly fewer numbers of *Balanus* nauplii were present at Barrow Village relative to NARL on August 19. Also, significantly larger numbers of polychaete larvae existed at Point Barrow.

The test of the effects of the time of day on population abundance for selected categories of zooplankton was conducted similarly to the previous test. Data from a diurnal series of tows taken on August 28 and 29 were used for the analysis. The standard time of day selected to which the data from other times were compared was 1530, since the majority of summer sampling had been conducted nearest to this time. Within-week confidence limits were applied about mean abundances for zooplankton categories sampled at 1530 for comparison with mean numbers at 0930, 2330, and 0630.

The results of the test indicated that the null hypothesis of no diel variation in abundance ($\underline{P} < 0.05$) was accepted for 31 of 36 cases (Table 5). Significant diel differences existed for *Acartia* spp. (higher concentrations at 2330 or 0630), *Oithona similis* (higher concentrations at 0930 and lower concentrations at 0630), and polychaete larvae (higher concentration at 2330).

Table 4. Statistical evaluation of the effects of sampling location on the mean abundance of selected zooplankton categories collected on August 19, 1972

	Statistical Significance		
	Location[1]		
	NARL	Point Barrow	Barrow Village
Zooplankton Category			
Hydrozoa			
Aglantha digitale	-	NS	NS
Polychaeta			
pelagic larvae	-	+*[3]	NS
Cirripedia			
Balanus nauplii larvae	-	NS	-*[4]
Balanus cyprid larvae	-	NS	NS
Copepoda			
Acartia spp.	-	NS[2]	NS
Calanus glacialis	-	NS	NS
Oithona similis	-	NS	NS
Pseudocalanus minutus	-	NS	NS
Ostracoda			
Podon leukarti	-	NS	NS

---

1 H_o: $\beta_i = 0$ (location effect equal zero)

2 NS = not significant ($P > 0.05$)

3 +* = $\underline{P} < 0.05$ of larger numbers of organisms

4 -* = $\underline{P} < 0.05$ of fewer organisms

Table 5. Statistical evaluation of the effects of time of day on the population abundances of zooplankton categories sampled at one location, August 28/29, 1972

Category	Statistical Significance — Time of day[1] 0930	1530	2330	0630
Hydrozoa				
Aglantha digitale	NS	-	NS	NS
Polychaeta				
pelagic larvae	NS	-	+*	NS
Cirripedia				
Balanus nauplii larvae	NS	-	NS	NS
Balanus cyprid larvae	NS	-	NS	NS
Copepoda				
Acartia spp.	NS[2]	-	+*[3]	+*
Calanus glacialis	NS	-	NS	NS
Oithona similis	+*	-	NS	-*[4]
Pseudocalanus minutus	NS	-	NS	NS
Chaetognatha				
Sagitta elegans arctica	NS	-	NS	NS
Appendicularia				
Fritillaria borealis	NS	-	NS	NS

---

1 H_o: $\alpha_i = 0$ (diel effects are zero)

2 NS = not significant ($P > 0.05$)

3 +* = $\underline{P} < 0.05$ of larger numbers

4 -* = $\underline{P} < 0.05$ of smaller numbers at given time

3.2.1.3 *Correlation Analysis*

The results of the correlation determined between selected categories of zooplankton, chlorophyll *a*, surface water temperature, and average salinity in the water column showed a number of species associations among the plankton as well as strong individual affinities to very specific temperature and salinity regimes.

The significance of the simple correlation coefficients (r) of 27 zooplankton categories and community dry weight with surface water temperature, average water column salinity, and chlorophyll *a* were determined for the 14-week summer sampling period (Table 6). Sixteen categories showed significant negative or positive correlations ($P < 0.05$) with temperature and three categories were significantly correlated with salinity. None of the zooplankers tested showed significant correlation with chlorophyll.

The results of the species to species correlation analysis allowed differentiation of the Barrow community into two distinct groupings of associated zooplankton (Table 7). Group 1 consisted of *Pseudocalanus minutus*, *Sagitta elegans arctica*, crab zoea, hyperid and gammarid amphipods, *Leuckartiara* sp., and juvenile shrimp. Group 2 included *Centropages abdominalis*, *Eurytemora herdmanni*, *Evadne nordmanni*, *Podon leukarti*, and *Aglantha digitale*. Several minor subgroups, showing fewer consistant affinities, were also discerned from the results of the analysis. The members within each of the two major groups, in addition to being significantly correlated to one another, also shared a common significant correlation to temperature (see Table 6).

Table 6. Statistical evaluation of the correlation of 27 categories of zooplankton and community dry weight with surface water temperature, average water column salinity, and chlorophyll *a* from May 25 to August 28, 1972

Category	Statistical Significance		
	Temperature	Parameter Salinity	Chlorophyll *a*
Hydrozoa			
Aglantha digitale	+*	NS	NS
Leuckartiara sp.	-*	NS	NS
Rathkea octopunctata	NS	NS	NS
Pteropoda			
Clione limacina	+*	NS	NS
Limacina helicina	NS	NS	NS
Polychaeta larvae	NS	NS	NS
Amphipoda			
Gammaridae	-*	NS	NS
Hyperidae	-*	NS	NS
Cirripedia			
Balanus nauplii > 308 μm	NS	NS	NS
Balanus nauplii < 308 μm	NS	NS	NS
Balanus cyprids	+**	-*	
Copepoda			
Acartia spp.	NS	NS	NS
Calanus glacialis	NS	NS	NS
Centropages abdominalis	+**	NS	NS
Eurytemora herdmanni	+**	NS	NS
Oithona similis	NS	NS	NS
Pseudocalanus minutus	NS	NS	NS
copepod nauplii	NS	NS	NS
Decapoda			
Chionoecetes zoea	-**	NS	NS
Paralithodes zoea	-**	+*	NS
Shrimp juveniles	-*	NS	NS
Euphausiacea			
Thysanoessa raschii	NS	NS	NS

Table 6 (continued)

Category	Temperature	Parameter Salinity	Chlorophyll *a*
	Statistical Significance		
Ostracoda			
Evadne nordmanni	+*	NS	NS
Podon leukarti	+*	NS	NS
Chaetognatha			
Sagitta elegans arctica	-**	+*	NS
Urochordata			
Fritillaria borealis	+**	NS	NS
Pisces	NS	NS	NS
Zooplankton dry weight	NS	NS	NS

---

1 * = P < 0.05

2 ** = P < 0.01

3 NS = not signifcant (P > 0.05)

Table 7. Major groups of associated zooplankton based on category to category correlation

Group 1	*Leuckartiara* sp.	Amphipoda	*Pseudocalanus minutus*	crab zoea	shrimp larvae	*Sagitta elegans*
Leuckartiara	-					
Amphipoda	0.830[1]	-				
Pseudocalanus minutus	0.811	0.765	-			
crab zoea	0.820	0.770	0.910	-		
shrimp larvae	0.625	0.827	0.671	0.797	-	
Sagitta elegans	0.655	0.704	0.776	0.840	0.754	-

Group 2	*Aglantha digitale*	*Centropages abdominalis*	*Eurytemora herdmanni*	*Evadne nordmanni*	*Podon leukarti*
Aglantha digitale	-				
Centropages abdominalis	0.595	-			
Eurytemora herdmanni	0.705	0.787	-		
Evadne nordmanni	0.622	0.555	0.766	-	
Podon leukarti	0.625	0.567	0.794	0.995	-

---

[1] critical r = 0.566 ($\underline{P} < 0.05$); 0.745 ($\underline{P} < 0.01$)

The constituents of group 1 were in greatest abundance in the colder water period of the summer, their population cycles showing a highly negative correlation to temperature as well as a high correlation to one another.

The zooplankton within group 2 all thrived in the warmer waters during August, in positive significant correlation with temperature and to one another.

Calanus glacialis, copepod nauplii, and *Balanus* nauplii represented a fairly well defined third group. The correlation coefficient determined between copepod nauplii and *C. glacialis* was highly significant at 0.790.

Many zooplankton categories showed no consistent associations with either group 1 or 2. Included here are the polychaete larvae, *Thysanoëssa raschii*, and fish larvae. *Limacina helicina* and *Oithona similis* each correlated with only one parameter. *Rathkea octopunctata* was the only organism exhibiting no significant correlation to any physical parameter or biological category.

Zooplankton biomass correlated poorly with chlorophyll *a* concentration (r = 0.084). Figure 9 indicates that the initial summer zooplankton biomass peak at Barrow lagged behind the chlorophyll maximum by approximately two weeks.

Both *Pseudocalanus minutus* and *Sagitta elegans arctica* were closely correlated to total zooplankton biomass during the summer.

3.2.2 *Temporal Distribution and Life History Patterns*

Variability in abundance for all categories of zooplankton was examined during a 14-week sampling period with attention paid to periods of maximal abundance, reproductive periodicity and recruitment, and life histories where possible. Weekly mean abundances for all zooplankton categories are depicted in Table 8. Where mention is made in the text of specific increases or decreases in the concentration of a given category with time, these comments refer only to those trends shown to be statistically significant ($\underline{P} < 0.05$). Major taxa are presented in systematic order with all zooplankton categories listed alphabetically within these taxa.

3.2.2.1 *Hydrozoa*

The Hydrozoa were second only to the Copepoda in the number of species contributed to the Barrow zooplankton community; six species, seven genera, and two unidentified medusae were collected. The taxa included two holoplanktonic species, *Aeginopsis laurentii* and *Aglantha digitale*, while the remaining categories were meroplanktonic, or temporary members of the plankton community.

Aglantha digitale was the only hydrozoan taken in all of the samples; other categories persisted under a wide variety of environmental conditions: (1) exclusively under the ice, (2) in open water only, or (3) intermittently distributed between the ice phase and open water phase of summer.

Table 8. Weekly mean abundances for all categories of zooplankton as numbers/100 m^3, from May 25 to August 28, 1972

CATEGORY	*(4) 5/25	(2) 6/2	(2) 6/9	(2) 6/16	(4) 6/23	6/30	(4) 7/7	(4) 7/14	(2) 7/21	(1) 7/28	(4) 8/4	(4) 8/11	(3) 8/18	(2) 8/25
Hydrozoa														
Aeginopsis laurentii	30	57	4	0	6	-	+	0	0	0	0	0	0	0
Aglantha digitale	55	93	183	174	186	-	16	8	8	266	448	1143	385	1887
Bougainvillea superciliaris	0	0	0	0	0	-	1	1	1	4	+	1	+	0
Euphysa flammea	17	21	2	10	8	-	+	0	0	0	0	0	0	0
Obelia longissima	0	0	0	0	0	-	0	0	164	0	1	13	13	4
Leuckartiara sp.	35	22	32	1	159	-	6	2	2	0	+	0	0	0
Rathkea octopunctata	0	0	0	0	4	-	18	23	1148	90	5	7	0	0
Scyphozoa														
Aurelia aurita	0	0	0	0	0	-	0	0	0	0	+	+	0	+
Cyanea capillata	0	0	0	0	5	-	+	+	4	+	6	5	5	3
Ctenophora														
Beroe cucumis	0	0	0	0	0	-	+	+	+	0	0	0	0	0
Bolinopsis infundibulum	0	0	0	0	+	-	0	0	0	0	0	0	0	0
Mertensia ovum	10	48	18	20	44	-	0	0	+	+	+	0	0	0
Pleurobrachia pileus	0	0	0	0	+	-	+	+	1	+	3	+	0	0
Pteropoda														
Clione limacina	2	3	3	2	0	-	+	+	3	0	+	+	0	0
Limacina helicina	3	9	11	0	2	-	80	23	48	+	4	+	0	22
Polychaeta														
larvae	221	1325	12192	48887	23130	-	5557	1293	5730	114	10494	931	72	172
Amphipoda														
Gammaridae	2	26	68	4	46	-	1	5	2	+	+	+	0	0
Hyperiidae	13	3	6	0	9	-	2	3	3	0	+	+	+	+
Cirripedia														
Balanus nauplii > 308 μm	7	7941	150383	397648	62230	-	35892	3730	12114	246	3793	25050	26424	65705
" " < 308 μm	9	13747	260555	562340	27618	-	27	69	1735	0	208	5157	22264	54777
" cyprids	0	0	0	0	19	-	5750	2264	15630	671	2936	13280	16444	13684

CATEGORY	5/25	6/2	6/9	6/16	6/23	6/30	7/7	7/14	7/21	7/28	8/4	8/11	8/18	8/25
Copepoda														
Acartia sp.	758	398	135	201	492	-	93	170	222	290	145	912	1703	1135
Calanus cristatus	0	0	0	0	0	-	0	0	+	0	0	0	0	0
C. glacialis	9	8	49	634	3736	-	12235	4723	2495	33	121	22	49	55
C. hyperboreus	111	6	0	0	0	-	0	0	0	0	0	0	0	0
C. plumchrus	0	0	0	0	0	-	9	8	6	1	0	0	0	0
Centropages abdominalis	0	0	0	0	0	-	0	0	19	47	32	205	60	47
Eucalanus bungii bungii	0	0	0	0	0	-	1	0	+	0	0	0	0	0
Euchaeta sp.	82	3	0	0	0	-	0	0	0	0	0	0	0	0
Eurytemora herdmanni	0	0	0	0	0	-	0	0	0	0	8	51	73	33
Metridia longa	14	6	0	0	0	-	0	0	0	0	0	0	0	0
Oithona similis	362	301	1225	556	458	-	107	96	76	956	148	471	123	567
Pseudocalanus minutus	37756	22839	27188	17249	15674	-	7405	7891	1143	174	149	325	137	124
Tortanus discaudatus	0	0	0	0	0	-	0	0	0	0	0	0	5	2
copepod nauplii	0	0	1242	582	1080	-	2770	251	75	6	37	25	10	14
Decapoda														
crab zoea larvae	763	2361	1189	2623	3865	-	73	34	98	0	12	+	+	0
shrimp juveniles	0	26	53	203	480	-	1	4	1	0	+	+	0	0
Euphausiacea														
Thysanoessa raschii	1	5	0	2	98	-	1	2	+	0	0	+	0	0
Mysidacea														
Mysis oculata	+	0	0	0	0	-	+	0	0	0	+	0	+	0
Ostracoda														
Conchoecia sp.	25	7	0	0	0	-	0	0	0	0	0	0	0	0
Evadne nordmanni	0	0	0	0	0	-	0	0	0	0	0	8	18	1045
Podon leukarti	0	0	0	0	0	-	0	0	0	0	0	9	45	1325
Echinodermata														
pelagic larvae	0	0	0	0	0	-	0	0	0	0	0	30	50	20000
Chaetognatha														
Sagitta elegans arctica	423	2412	542	1641	1012	-	275	153	220	407	88	46	66	42
Appendicularia														
Oikopleura sp.	8	2	+	2	0	-	0	0	2	+	+	0	0	0
Fritillaria borealis	0	0	0	0	0	-	0	9	0	27319	48	110	163	1110
Pisces	+	6	4	5	93	-	8	8	8	1	+	+	+	2

* = Number of observations contributing to the weekly mean

+ = less than 1 individual/100 m^3

ORDER NARCOMEDUSAE

Aeginopsis laurentii Brant

Fifty-two specimens of *Aeginopsis laurentii* were taken, of which 44 were collected under the ice from May 27 to June 15. Only immature individuals were found in the material, diameters ranging from 3 mm to a 15 mm specimen collected on June 23. The majority of organisms (33) ranged from 6 to 10 mm in diameter. This species disappeared from the plankton after July 10, approximately 10 days after breakup.

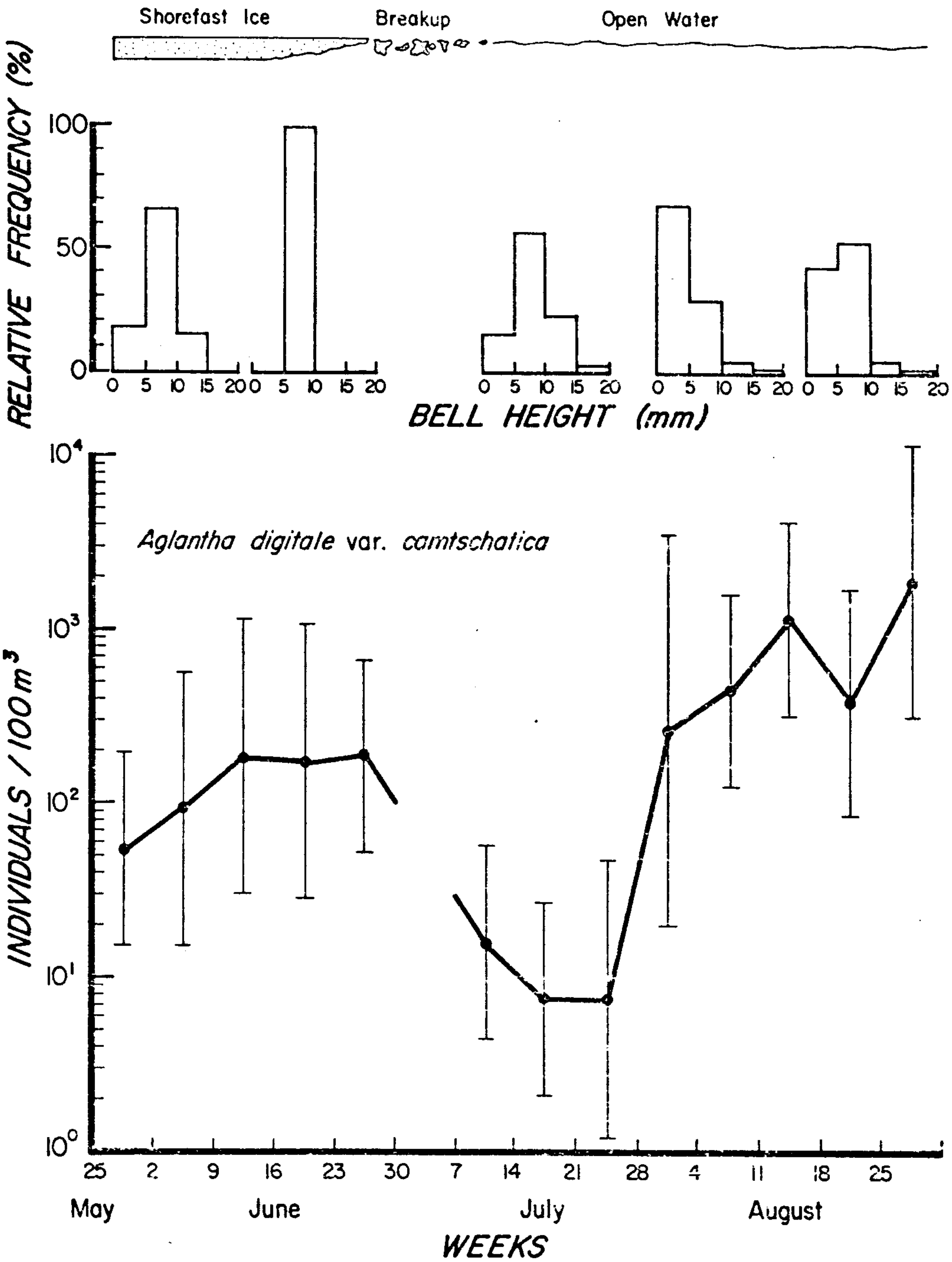
ORDER TRACHYMEDUSAE

Aglantha digitale (Muller) var. *camtschatica* (Brandt)

This species was the most common and abundant hydrozoan in the Barrow area. *Aglantha* was often present in concentrations exceeding 1000 individuals/100 m^3. The establishment of this geographical variety of the North Pacific and Arctic Oceans distinct from the Atlantic populations of *A. digitale*, is based on the shorter peduncle length and smaller size of the individuals found in the Pacific and Arctic material (Hand and Kan, 1961).

The population showed no significant variability during May and June, but dramatic changes occurred during open water conditions (Fig. 4). The lowest summer concentrations were recorded the week of July 21 to 27. A rapid significant increase occurred through mid-August, to levels of 1148 individuals/100 m^3, and stabilized for the rest of the month.

Figure 4. Quantitative distribution of *Aglantha digitale* from May 25 to August 28, 1972, with associated bell height-frequency histograms. Vertical bars indicate the 95% confidence limits of the weekly means


Shorefast Ice
Breakup
Open Water
RELATIVE FREQUENCY (%)
100
50
0
0 5 10 15 20 0 5 10 15 20
0 5 10 15 20
0 5 10 15 20 0 5 10 15 20
BELL HEIGHT (mm)
Aglantha digitale var. camtschatica
INDIVIDUALS / 100 m3
10⁴
10³
10²
10¹
10⁰
25 2 9 16 23 30 7 14 21 28 4 11 18 25
May
June
July
August
WEEKS

A shift in size-frequency groupings throughout the summer sampling period is evident. Both large and small individuals (rarely exceeding concentrations of 100 ind/100 m^3) were major constituents of the population through mid-July. Beginning the week of July 21, a large number of 3 mm, saucer-shaped specimens were recruited to the population, a phenomenon continuing to the end of August. Large increases in overall abundance accompanied these periods of recruitment.

Aglantha digitale is reported in the literature to be primarily carnivorous (Hardy, 1965). An examination of gut contents of several 10 to 14 mm specimens on August 28 indicated an omnivorous, rather than strictly carnivorous, feeding habit for this northern variety at Barrow. Animal matter in the gut included: tintinnids and copepod appendages; *Nitzschia closterium, Coscinodiscus* sp., and *Navicula* spp. were recognizable algae present in the gut contents. Detrital material was also present in modest abundance.

Immature, 10 mm high individuals of *A. digitale* were recorded from the February samples. No other hydrozoan was found at that time.

ORDER ANTHOMEDUSAE

Bougainvillea superciliaris (L. Agassiz)

A total of 66 specimens of *Bougainvillea superciliaris* were taken during the sampling period, the great majority in July. Mature and juvenile individuals were collected consistently in small numbers from a first reported occurrence on June 7, through August 3. After this time only 3 specimens were found in the samples. Population density was always small (less than 10 organisms/100 m^3), the greatest concentration existing on July 27 just prior to breakup. Bell height for the species measured from 2 to 10 mm. Sexually mature specimens were present on July 17 (1) and July 23 (3), and August 3 (1). The majority of individuals exceeded 5 mm in bell height.

Euphysa flammea (Linko)

Euphysa flammea was taken consistently in small numbers from May 27 to June 12. Thirty-two specimens were collected in total, all immature. This species occurred only very rarely from June 12 to July 10, its last reported presence in the plankton. Bell height ranged from 3 to 10 mm, with the greatest portion of individuals between 4 and 5 mm. Maximum bell height for *E. flammea* is reported to be 17 mm (Naumov, 1969).

Leuckartiara sp.

Leuckartiara was found commonly in the plankton under the ice during early summer, but rather infrequently once open water conditions prevailed. Hand and Kan (1961) report two species of this genus in the Chukchi Sea, *L. brevicornis* and *L. nobilis*. Their description of *L. nobilis* more closely resembles the present material. All specimens of the genus were immature and showed no advanced gonadal development. The maximum population density observed for the species was 159 organisms/100 m^3 in late June. The final record of *Leuckartiara* cf. *L. nobilis* in the Barrow area was August 4.

Rathkea octopunctata (M. Sars)

This small hydromedusa was first observed in the plankton on June 27, immediately prior to breakup in the nearshore area. Concentrations during this final week of the ice phase were about 5 individuals/100 m^3. The population increased significantly to a high of 1148/100 m^3 from July 21 to July 27, but disappeared by mid-August. The bell height of most specimens varied from 1 to 2 mm. Larger individuals were sexually mature and were observed to be "budding" smaller medusae from the manubrium.

ORDER LEPTOMEDUSAE

Obelia longissema (Pallas)

Species of this cosmopolitan meroplanktonic genus were differentiated on the basis of the extent of the peripheral location of the gonads on the radial canals (Naumov, 1969). *Obelia longissema* was not taken under the ice, its first occurrence coming on July 22. Rather large concentrations of individuals (up to 1000/100 m^3), measuring from 1 to 2 mm in diameter, were collected sporadically through August. Specimens in various stages of maturity ranging from fully mature to juvenile were represented.

Any significant trends in population abundance for the species were masked by the extremely high replication and within-week variability (Table 2).

Unidentified Medusae

Several unidentified medusae, none of which were abundant in numbers, were among the constituents of the plankton. Specimens of each species have been sorted and stored as part of the overall zooplankton reference collection at the University of Alaska Museum, Marine Division. It is hoped that future identification of these species will be assisted by this reference collection.

3.2.2.2 *Scyphozoa*

Aurelia aurita (L.)

Aurelia aurita was found only rarely in the nearshore environment, exclusively from August 8 to the end of August. A total of 14 organisms were identified and measured. A wide range in size was evident, with the following relative frequencies observed: 10 to 20 mm in diameter, 6 specimens; 20 to 30 mm, 3; 30 to 40 mm, 2; and 50 to 60 mm, 3. The largest individuals were taken on August 14 and August 28.

Cyanea capillata (L.)

Cyanea capillata was the most common scyphozoan taken from the inshore waters off Barrow. A total of 288 individuals were identified, of which 239 were collected during August. The first reported specimens on June 28 measured 4 mm in diameter, and probably represented the ephyra stage of the species. Size generally increased up to 25 mm diameter during July, with many larger individuals beginning to appear in early August. One 90 mm and two 85 mm specimens were sampled on

August 9; the largest individuals (100 mm) appeared on August 14 and also on August 19, when collections were made at Barrow Village and Point Barrow in addition to the usual sampling site.

Cyanea was observed on calm days to congregate in patches, scattered irregularly throughout the surface waters of the nearshore area. On these same days, an association was directly observed between the polar cod, *Boreogadus saida*, and *C. capillata*. The cod could be seen swimming amongst the tentacles of the scyphozoan, apparently unaffected by the nematocyst discharge.

3.2.2.3 *Ctenophora*

Four species of ctenophores were present in the summer collections or visually observed in the field. The following species were identified: *Mertensia ovum*, *Bolinopsis infundibulum*, *Beröe cucumis*, and *Pleurobrachia pileus*. Attempts were made to identify the specimens before preservation because of the extreme difficulty involved in adequately preserving these fragile organisms. The contribution of the group as a whole to community biomass was slight.

Beröe cucumis Fabricius

Beröe cucumis was absent from the nearshore area until July 8. However, collections taken on June 12 at the edge of the shorefast ice, seaward of the pressure ridge, proved the species was present at that time.

A total of 27 organisms were taken in open water, most ranging in height from 4 to 8 mm; two 10 mm individuals were collected on July 22, the last reported occurrence of *B. cucumis* at Barrow.

Bolinopsis infundibulum Fabricius

This species was rarely seen in the field, and the only specimen collected was taken directly with a bucket on the evening of July 26. Exact measurement of the organism was not possible because of extensive damage during collection. The approximate length was 200 to 250 mm.

Mertensia ovum (Fabricius)

A total of 73 specimens of *Mertensia ovum* were collected, 64 during the ice covered phase of the summer. This species was the most common ctenophore in numbers and duration in the plankton. Most individuals were 30 to 40 mm in height, with a few specimens 10 mm high. Large numbers were directly observed under the ice at times by SCUBA divers. *Mertensia* was also found in the February material collected at Barrow.

Mertensia ovum was found to possess bioluminescent capability as evidenced by agitation of specimens in laboratory darkness and resultant flashing of its comb plates. Such a phenomenon was not directly observed in the field because of the continuous light conditions during much of the summer.

Pleurobrachia pileus (Vanhoffen)

The presence of this common arctic species, often times called the "sea gooseberry", was first noted on June 26 and a total of 59 organisms were encountered up to its disappearance on August 9. The majority of the material was 5 to 8 mm in length. Two 17 mm specimens were taken on June 28.

3.2.2.4 *Pteropoda*

These pelagic molluscs, commonly called "sea butterflies," were represented by two species, both of which were discontinuously distributed in space and time.

Clione limacina (Phipps)

Sixty-three specimens of *Clione limacina* were recorded from the collections. No significant temporal population variability existed for the species over the summer sampling period (Table 3).

The size-frequency distribution for all combined organisms was as follows: 3 to 8 mm length range, 27 specimens; 10 to 18 mm, 26; and 20 to 25 mm, 10. The largest individuals of *C. limacina* were taken in open water, on July 16 and August 3 and 14; 3 to 8 mm specimens were the dominant size class throughout the sampling period.

Limacina helicina (Phipps)

Limacina helicina was present in 11 of 13 sampling weeks, with a maximum concentration of 80 individuals/100 m^3 the week of July 7 to July 13. Specimens captured during the under-ice sampling period were almost exclusively of 1 mm size. As open water conditions prevailed, more mature organisms in the range of 2 to 4 mm in diameter became present. The 1 mm and less than 1 mm organisms represented the quantitatively dominant size for the species averaged over the entire summer. The largest specimens collected from the nearshore waters were ttwo 6 mm individuals taken on August 4. Very few *L. helicina* were found in the plankton during August.

Comparative surface tows taken 4 to 6 km offshore on July 22, August 3, 4, and 5 indicated a more mature population of *L. helicina* existing in these waters, with sizes commonly in the 5 to 6 mm diameter range.

Limacina helicina was often visually observed to exhibit extreme spatial patchiness; this distribution is reflected in the high field replication and within-week sampling error determined for the species (Table 2). Swarms of this pteropod were seen in the shallow shoreline waters from July 30 to August 3; such concentrations were not present at a distance of 1 km from shore.

3.2.2.5 *Polychaeta*

Trochophore larvae, intermediate and late larval stages, and fully developed adults were well represented in the Barrow collections throughout the summer. All larval stages were combined as one and enumerated.

Trochophore larvae became very prevalent on June 17 and continued to persist in high concentrations through August along with a mixture of post-trochophore stages. Individuals of the families Phyllodocidae, Syllidae, and Polynoidae, contributed a large fraction of this total.

The polychaete larvae reached maximum concentrations June 16 to June 22, 48,887 individuals/100 m^3, after increasing rapidly from early June. The population cycle after early July showed no discernable trend until mid-August, when numbers significantly decreased to about 100 larvae/100 m^3.

Gravid females of the species *Autolytus fallax* (Syllidae) were observed regularly throughout the summer. Bright orange egg cases ere clearly visible on these specimens. The extended reproductive riod of *A. fallax* was further exemplified by the presence of igerous females in the late winter samples.

2.2.6 *Amphipoda*

The amphipods were very difficult to identify and in most cases ly genera could be determined with certainty. Time did not permit nding the organisms to specialists for accurate specific identifi- ation. Specimens were grouped into the families Gammaridae and yperidae and examined on this taxonomic level (Table 4).

Gammaridae

Specimens of the genus *Pseudalibrotus* were the dominant gammarid phipods in collections from May through mid-August in an admixture sizes ranging from 3 to 14 mm in length. A characteristic feature this genus was its yellow-brown coloration and bright red eyes. reserves were also seen in many organisms, adding to the overall llow color. No gravid females containing brood pouches with young were observed for *Pseudalibrotus*. Large numbers of the genus were often directly observed at the shoreline scavenging on the bottom and in one instance on August 2 one individual was seen exhibiting a cannabalistic feeding habit.

Examination of February collections showed *Pseudalibrotus* to also exist at that time of year.

Several additional unidentified gammarids were present in the plankton. A description of possible diagnostic morphological characteristics is given here as a guide to future identification.

A form looking very much like *Pseudalibrotus*, but with black rather than red eyes, was often sampled during the summer. This form perhaps represents a different species of the genus. Another gammarid species with long, brown speckled pereiopods (legs) and a brown pigmentation of the thorax was collected on June 27, July 17, and August 5. Measured lengths were 30, 8, and 15 mm, respectively. One reddish-colored species with a long hooked rostrum was taken in small numbers from June 28 to July 17, ranging in length from 5 to 10 mm.

A 5 mm long, translucent gammarid, with bright red pereiopods and first antennae, was observed in the July 17 material. One red-eyed individual, possessing one tooth on the dorsal midline of each thoracic and abdominal segment, was collected on August 3. The specimen measured 22 mm in length.

The Gammaridae as a group were most plentiful during the ice phase of the summer season. Population density experienced a significant decline in the transition to open water conditions. A maximal concentration of 68 individuals/100 m^3 was realized the week of June 9 to 15.

Hyperidae

Hyperid amphipods were both quantitatively and qualitatively less prevalent than the gammarids. The taxon *Hyperia* cf. *H. galba* (Montagu) appeared to be the dominant member of the family based on the structure of the processes on the fifth article of the first gnathopod (Tencati, 1970). The majority of specimens were juveniles of 3 to 8 mm rostrum to uropod length. One 18 mm long hyperid was reported on June 1; a 23 mm long specimen of *Hyperia* was taken on June 23.

Large numbers of hyperid amphipods were observed on several occasions on the gravel beach above the water line. A probable component of these assemblages is the genus *Themisto*, which although not positively identified from the present material, was similarly observed in small pools above the water line by MacGinitie (1955).

The temporal cycle of abundance of the Hyperidae showed a trend similar to the Gammaridae, i.e., maximal concentrations under the ice. Specimens were rarely found in the material after late July.

3.2.2.7 Cirripedia

Balanus spp.

Exceedingly large numbers of barnacle larvae of the genus *Balanus* were observed at times in the Barrow collections, often exceeding abundances of 250,000 individuals/100 m^3. The species of *Balanus* responsible for the high recruitment of larval stages to the plankton was not determined; MacGinitie (1955) reported *Balanus crenatus* to comprise the greatest portion of the sessile community near NARL, with *B. balanus* comparatively subordinate in numbers.

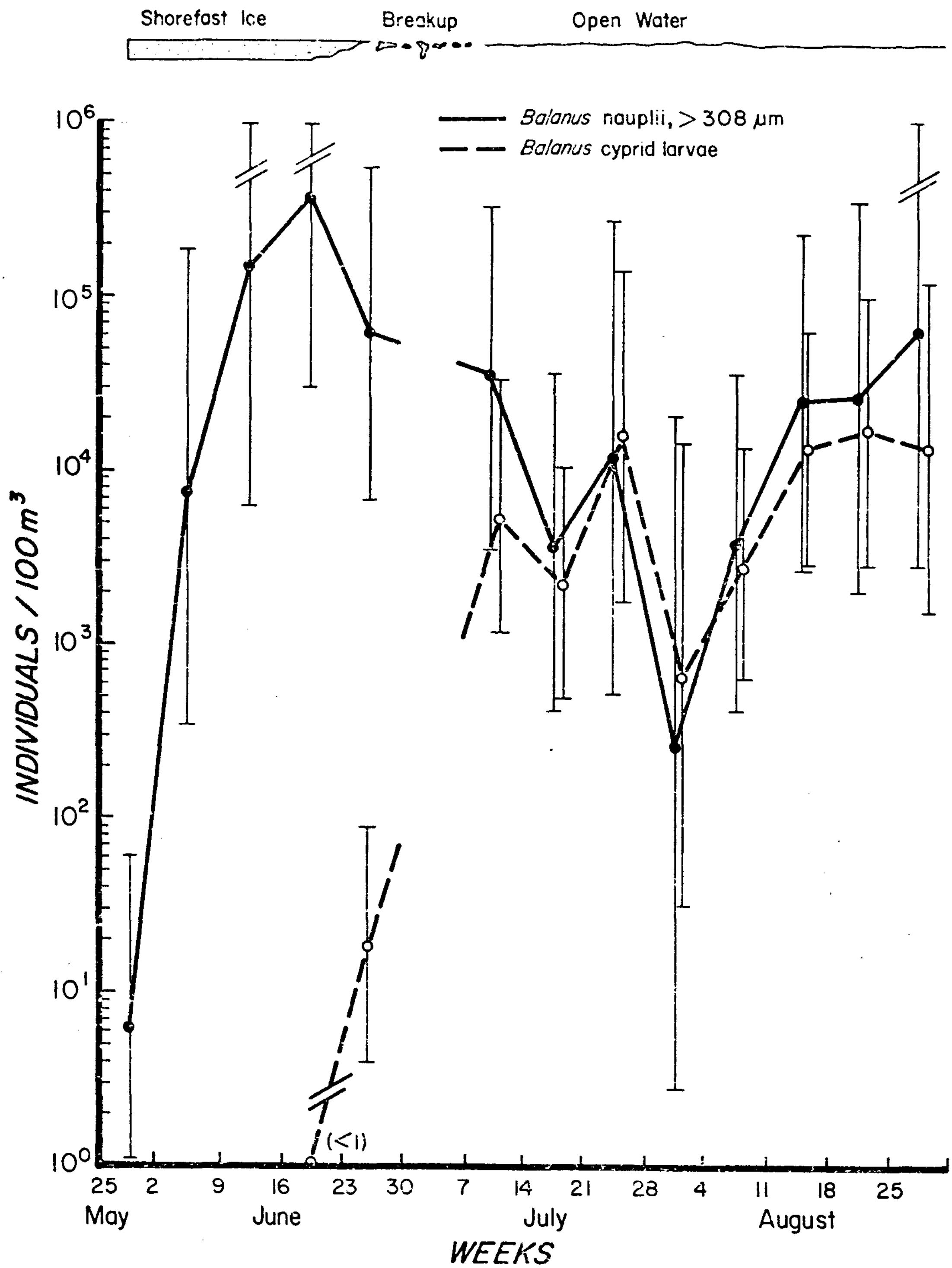
The quantitative cycles of both the cypris and nauplius stages are depicted in Figure 5. The initial appearance of the nauplius developmental stage was May 27. Recruitment was extremely rapid from this period through mid-June. The nauplii concentration reached its summer peak of about 400,000 individuals/100 m^3 at this time. A population low was experienced the week of July 28 to August 3, with a compensating increase in numbers through the remainder of August.

Cyprid larvae first appeared on June 27, indicating a 31 day developmental period from the nauplius to the cypris stage in the Barrow area. A rapid increase in cyprid recruitment was apparent by early July. The population cycle for this stage was closely correlated to the dynamics of the barnacle nauplii from late July through the remainder of summer (Fig. 5).

3.2.2.8 Copepoda

The copepods were easily the most diverse group of zooplankton in the inshore community (14 species), and along with barnacle larvae, were the major constituents of the community during the summer. Four species persisted in the plankton continuously during the entire sampling period, withstanding a highly variable temperature and salinity regime. Two of these four species in particular were most notable for their prevelance during the season, *Pseudocalanus minutus* (Krøyer),

Figure 5. Quantitative distribution of nauplii and cyprid larvae of the genus *Balanus* from May 25 to August 28, 1972. Vertical bars as in Figure 4



Shorefast Ice
Breakup
Open Water
Balanus nauplii, > 308 µm
Balanus cyprid larvae
10^6
10^5
10^4
10^3
10^2
10^1
10^0
(<1)
INDIVIDUALS / 100 m^3
25 2 9 16 23 30 7 14 21 28 4 11 18 25
May
June
July
August
WEEKS

and *Calanus glacialis* Jaschnov. The remaining, larger group of copepods, occurred only at distinct times in relation to specific hydrographic changes. Included in this group were species advected into the Barrow area from the Bering Sea.

The duration of the reproductive period and the time of maximum recruitment for individual species were highly variable for the group as a whole. Three major divisions existed based on the above criteria: (1) species whose breeding period was closely related with the blooming of the phytoplankton; (2) species with an extended breeding period during the summer, and (3) species showing indications of breeding before the flowering of the phytoplankton.

The single most dynamic event witnessed concerning the copepods was the gradual decline in the population abundance of the late May dominant, *P. minutus*, through the entire summer sampling period, with a compensating exponential population increase to early July by *C. glacialis*. The latter species attained its greatest concentration and biomass the first week in July, after which it similarly declined in numbers. No single copepod species was numerically dominant beyond late July.

Acartia spp.

Two species of this genus were collected at Barrow, *Acartia longiremis* (Lilljeborg) and *Acartia clausi* Giesbrecht. From late May through July, the former was clearly identifiable as the dominant species of the genus. However, after this period, it became exceedingly more difficult to distinguish both species based on easily determined diagnostic characteristics and the two species were thereafter combined.

Acartia spp. was one of four copepods persisting continuously from May through August. The population cycle showed no sustained trends, but a series of statistically significant fluctuations. A decline in numbers from week 1 through June 22 was observed, with a slight increase in abundance occurring just before breakup. Lowest numbers, 93 individuals/100 m^3, were recorded during the early open water period the second week of July. No significant changes in abundance were noted thereafter until early August. From early August to the end of the month, the population increased an order of magnitude over late July stocks, reaching a maximum of 1600 organisms/100 m^3 in late August. This represented the highest concentration attained by any one copepod species since late July.

Almost all the specimens collected were in the late stages of development, usually adults and stage V copepodids. Scattered individuals of stages III and IV were captured periodically during the entire sampling season.

Acartia longiremis was one of the few copepods present in both the summer and late winter (February) collections.

Calanus cristatus Krøyer

This very large copepod was sampled only qualitatively, appearing in the nearshore waters on only two days, July 16 and July 26. The individuals taken ranged from 8.5 to 9.2 mm in length, indicating the organisms were adults or stage V copepodids. No ovigerous females were present in the samples.

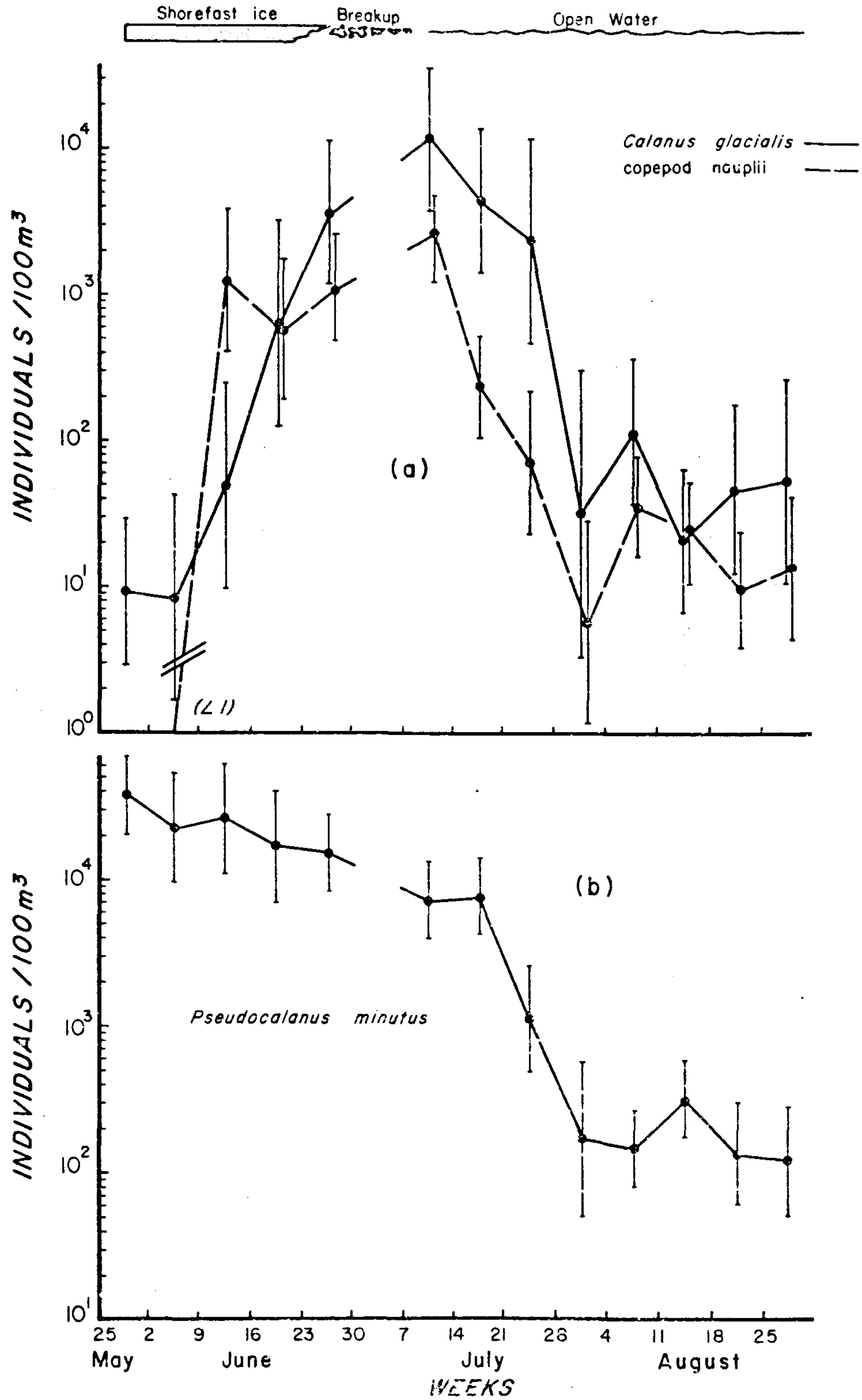
Calanus cristatus occurs commonly in high abundance in the Bering Sea during the spring and summer months (Heinrich, 1961).

Calanus glacialis Jaschnov

This copepod was historically thought to be a larger cold water form of the species *Calanus finmarchicus* (Gunnerus). Morphological variation in the number of denticles (teeth) on the proximal basipodite segment of the fifth pair of swimming legs and their relative curvature has established this northern variate as a separate species (Jaschnov, 1955). The ratio of the lengths of the proximal exopodal segment to the second endopodal segment of the male left fifth swimming leg has also been used to support Jaschnov's taxonomic revision (Frost, 1971).

Calanus glacialis shared the distinction with *Pseudocalanus minutus* of being the most numerically important copepod at Barrow. Figure 6 depicts the temporal variability in population abundance for the species in comparison with *P. minutus* and copepod nauplii. Very few specimens of *C. glacialis* were taken up to June 8; most were adult or stage IV or V copepodids although stage III individuals were also present in slight abundance. Several ovigerous females were noted on May 25, May 27, and June 5 with eggs in ripe condition and a larger number of gravid females began appearing from June 20 to 28. No gravid individuals were found after breakup. A peak in the copepod

Figure 6. Quantitative distribution of (a) *Calanus glacialis* and copepod nauplii, and (b) *Pseudocalanus minutus*, from May 25 to August 28, 1972. Vertical bars as above


Shorefast ice
Breakup
Open Water
Calanus glacialis
copepod nauplii
INDIVIDUALS /100m3
(a)
(b)
Pseudocalanus minutus
(<1)
25 2 9 16 23 30 7 14 21 28 4 11 18 25
May June July August
WEEKS

nauplii production was experienced approximately two weeks following the high incidence of ovigerous females (Fig. 6). Stage I specimens were first reported on June 15 in small numbers and by June 28 and well into July, immature copepodids I and II, and to some extent stage III were exceedingly plentiful, with abundances of 3,000 to 15,000 individuals/100 m^3.

The peak population density of 12,220/100 m^3 was reached the week of July 7 to July 13 at the onset of the open water period. The population declined rapidily thereafter and experienced a summer low of 23 organisms/100 m^3 between August 11 and August 17. The preponderance of early developmental stages continued through July 16, after which time stages III, IV, and V appeared in relatively equal concentrations. Developmental stages I and II became very rare during this period and disappeared from the plankton on August 8, with the exception of a few stage II individuals present through August 26. Copepodid III became the dominant form by the end of August, with large numbers of stage IV and V evident. Adult specimens were present throughout the summer, usually in small numbers.

Calanus hyperboreus Krøyer

Very few specimens of this large arctic-subarctic species were collected, appearing only through the first week of June, with the greatest number being taken during late May. Seventy-six individuals were classified according to developmental stage. The following relative numerical frequency of copepodid stages was observed:

adults, 22 specimens; stage V, 37; stage IV, 13; and stage III, 4. No ripe females were encountered in the collections. *Calanus hyperboreus* was also found in the February samples, apparently overwintering as stages IV and V.

Calanus plumchrus Marukawa

This species was present from the first open water sample on July 8, to a final occurrence on August 3. With the possible exception of one 3.8-mm animal, all of the 267 individuals collected were stage V or adults. Large lipid reserves were evident in the majority of these organisms. Peak concentrations of 9 individuals/100 m^3 were attained the week of July 7, most specifically on July 8. The population stabilized through the next two weeks and then decreased to 1 individual/100 m^3 before disappearing from the samples.

Calanus plumchrus represents one of the major constituents of the summer zooplankton community in the surface layers of the Bering Sea.

Centropages abdominalis Sato

Centropages abdominalis was first recognized on July 22 and gradually increased in numbers to 205 individuals/100 m^3 the week of August 11, declining significantly to 60 and 47 organisms/100 m^3 the last two weeks of August. Fully mature or stage V individuals dominated the population. No ovigerous females were observed.

Eucalanus bungii bungii Johnson

This large copepod was poorly represented in the collections. The first reported occurrence of *Eucalanus bungii bungii* was on July 8, coinciding with the initial appearance of *Calanus plumchrus* in the Barrow area. A total of 13 specimens were encountered in the samples prior to July 23, the time of dramatic change in the hydrographic regime (Fig. 2). A maximum weekly mean population density of 1 individual/100 m^3 was attained the week of July 14 to 20.

Euchaeta sp.

The population dynamics of this rarely captured genus closely followed those of *Calanus hyperboreus* and a third species, *Metridia longa; Euchaeta* sp. occurred in the plankton only through the first week of June. Forty individuals were collected, mostly stage III copepodids. The maximum population density was reached the first week of summer, at 82 ind/100 m^3. No specimens of *Euchaeta* were present in the February samples.

This zooplankter is probably *Euchaeta norvegica* Boeck, a species described from the area by Johnson (1956).

Eurytemora herdmanni Thompson and Scott

The presence of this calanoid was first reported on August 5 and continued to the end of the summer. The majority of specimens were fully developed or existed as stage V. Population size showed a significant increase from early August concentrations to a high of

73 organisms/100 m^3 for the week beginning August 18. No significant population variability existed during the final three weeks of August.

Gravid females were very plentiful from August 19 to 28 and relatively large numbers of adult males were also present.

Eurytemora herdmanni appeared in the Barrow area only when the surface water temperature exceeded 7°C.

Metridia longa (Lubbock)

Metridia longa appeared for only a short time at the beginning of the summer season. A breakdown of developmental stages included 7 adults, 13 stage V individuals, and 3 specimens of copepodid stage III or IV. Immature organisms (stage III and IV) were also reported from the February material. The largest numbers recorded for the species were 14 specimens/100 m^3 the week of May 25.

Oithona similis Claus

Oithona similis was the only cyclopoid copepod found in the summer collections. It was at times a very important constituent of the community in terms of abundance. The species persisted throughout the summer and was also collected in immature stages in February. The population cycle of *O. similis* was one of a series of significant increases and decreases. Population density ranged from a high mean of 1225 individuals/100 m^3 the week of June 9 to a low of 76/100 m^3 from July 21 to July 27. In general, no consistant pattern was observed for the remainder of the summer season.

Gravid females were observed sporadically throughout the summer on the following dates: June 1, 12, and 27; July 8 and 19; and August 3, 4, 19, 26, and 28. The maximum reproductive period for the species, based on the relative number of ovigerous females, was the last two weeks of August; rather large numbers were also recorded the first week of August.

Pseudocalanus minutus (Krøyer)

The quantitative summer cycle of population variability for the micro-calanoid copepod *Pseudocalanus minutus* is shown in Figure 6. A gradual decline in the population was evident during May and June. Through the first month of the season, copepodids IV, V, and gravid females dominated the population in quantity and biomass. Few stage III individuals were found during this period while copepodid II was very rare. No stage I individuals were taken although they should theoretically have been caught if present. Egg-carrying females were very abundant through June, with isolated occurrences up to July 12.

During the period of July 14 to July 27, *P. minutus* experienced an abrupt exponential decline in numbers, after which time the population stabilized at approximately 300 individuals/100 m^3 through August. Developmental stages IV and V predominated in July and August.

Mature *P. minutus* were collected in February.

Tortanus discaudatus (Thompson and Scott)

Tortanus discaudatus was found in the Barrow collections only during the final two weeks of August, when surface water temperatures were 7° to 9°C. Mean weekly concentrations attained a modest high of 5 individuals/100 m^3. The majority of specimens identified were non-gravid adult females, with males in slight abundance. One stage I copepodid was taken on August 19 and a number of stage III specimens on August 17.

Copepod nauplii

Variations in the copepod nauplii population with time were similar to those noted for *Calanus glacialis* (see Fig. 6). A maximum density, 2770 individuals/100 m^3, was observed the first week of July, with numbers declining to a low of 6/100 m^3 in late July. The initial occurrence of nauplii was on June 3.

3.2.2.9 Decapoda

The Decapoda were represented by crab zoea larvae and juvenile shrimp. The zoeal stages were differentiated into the Anomura or "hermit crab," and Brachyura or "true crab" varieties. The anomuran group included larvae of the king crab, *Paralithodes camtschatica* (Family Lithodidae). The zoea of the snow crab. *Chionoecetes opelio* (Family Inachidae) comprised the majority of the brachyuran larvae. The shrimp juveniles were not successfully classified to family.

The temporal trend of population abundance for the two groups of crab zoea was sufficiently similar to allow enumeration under one heading. Crab larvae were a very important meroplanktonic group, second in abundance only to the barnacles. The decapod zoea experienced an early increase in numbers from late May (763/100 m^3) to a peak concentration to 3865 individuals/100 m^3 in late June. The majority of specimens were immature zoea of stages I and II; the presence of megalop larvae was not indicated in the samples. A significant decrease in population density was observed during the open water period, with small numbers of zoea present to August. Extremely low quantities of larvae were found in the plankton during August.

Juvenile shrimp measuring up to 11 mm in length were plentiful in the plankton during the months of May and June, but experienced a significant decline in abundance with the transition to open water. Shrimp were initially found in the nearshore waters on June 5. This stock increased gradually to a peak concentration of 480 organisms/100 m^3 in late June. A relative paucity of organisms became evident beginning in early July and continued through August.

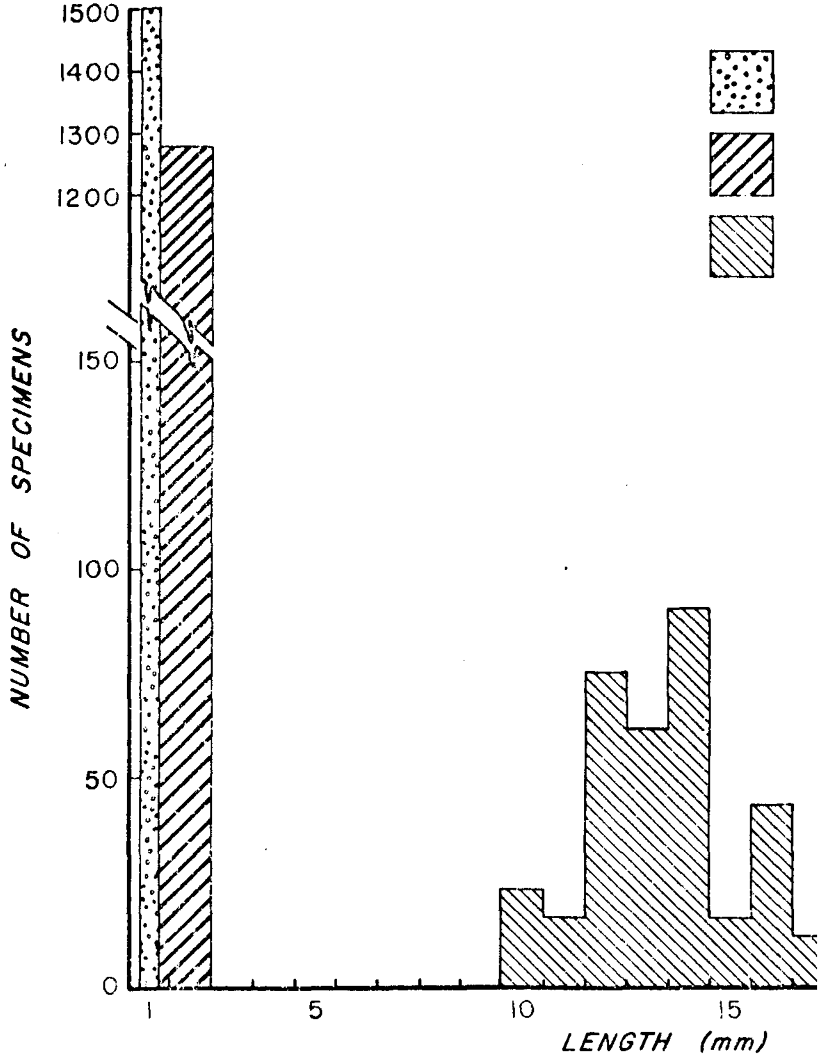
3.2.2.10 Euphausiacea

Thysanoëssa raschii (M. Sars)

A total of 364 individuals of *Thysanoëssa raschii* greater than 10 mm in length were sampled and measured. Ninety-four percent of these animals were in the size range of 10 to 16 mm. A size-frequency histogram of juvenile euphausiids, nauplii, and calyptopid larvae clearly indicates a bimodal size distribution (Fig. 7). No adult specimens were taken with the possible exception of three 24 mm individuals gathered on June 23.

The temporal distribution of the species was discontinuous during the summer. Juvenile euphausiids were found in greatest numbers.

Figure 7. Length-frequency relationships for the composite summer population of *Thysanoëssa raschii*, indicating nauplii, calyptopid, and juvenile stages


1500
1400
1300
1200
150
100
50
0
NUMBER OF SPECIMENS
1
5
10
15
LENGTH (mm)


euphausiid nauplii larvae
stage I calyptopid larvae
juvenile *Thysanoëssa raschii*
20
25

93 specimens/100 m^3, during the ice period on June 22. This population density represented a significant increase over the early summer stock. High concentrations were occasionally found in open water, as on July 10 and 17, specimens being in the 13 to 17 mm and 14 to 16 mm length ranges, respectively.

Thysanoëssa raschii became increasingly less abundant as the summer progressed and only one 10 mm specimen was taken from July 22 to the end of August. Euphausiid nauplii were present as early as June 12 and persisted continuously to the end of June, reappearing again from late July to August 4. Peak abundances of nauplii were reached during weeks 3 and 4 (June 15 to 21), declining to lower concentrations thereafter. High concentrations of the nauplii were closely correlated to high periods of phytoplankton biomass (see Figure 9).

Young calyptopids 1.0 to 2.0 mm long were first noted on June 12 and persisted from June 28 to the end of July. Calyptopid larvae were taken only rarely after July 23, as was the case for all euphausiid stages.

2.2.11 *Mysidacea*

Mysids were rarely seen in the collections. Two species were identified: *Mysis oculata* (Fabricius), and *Neomysis rayi* (Murdoch).

Mysis oculata was observed on May 27, July 10 and 12, and August 8. Rostrum to uropod length ranged from 5 to 9 mm for all specimens. No gravid females were present.

Only one 14 mm specimen of *Neomysis rayi* was taken during the summer, on August 19. The organism was in a gravid state, with a large brood pouch containing many young.

3.2.2.12 Ostracoda

Three species of ostracods were encountered at Barrow. Each existed only under specific ranges of temperature and salinity. The ostracods occurred exclusively at the beginning and end of summer.

Conchoecia borealis (Brady)

This species was taken only through early June, occurring at its highest concentration of 25 individuals/100 m^3 the last week of May. The length of most of the specimens was 2.5 to 3.5 mm.

Evadne nordmanni Loven

The quantitative pattern of abundance for *Evadne nordmanni* was closely correlated to that of its ostracod counterpart, *Podon leukarti* (Table 8). Both species prevailed only when the temperature of the nearshore waters in the Barrow area was at a summer maximum during August.

Many specimens of *E. nordmanni* possessed brood pouches containing large numbers of ripe, yolky eggs. Reproduction and egg development for this species is reported to occur parthenogenetically in the summer (Wimpenny, 1966). Immature individuals were also prevalent in the samples.

Podon leukarti Sars

This species was encountered only during the final three weeks of August. The population increased exponentially in numbers over this time period, from a low of 9 individuals/100 m^3 in mid-August to a maximum of 1325/100 m^3 the last week of the month. Fully mature and immature specimens were found in comparatively equal abundance.

3.2.2.13 *Echinodermata*

Larvae of this phylum were poorly represented in the material. Ophioplutei larvae (of brittle stars) and some echinoplutei were first reported in sparse numbers of about 30 individuals/100 m^3 on August 17. An abrupt population increase occurred from 100 larvae/100 m^3 on August 26 to over 50,000/100 m^3 on August 28, the last day of sampling.

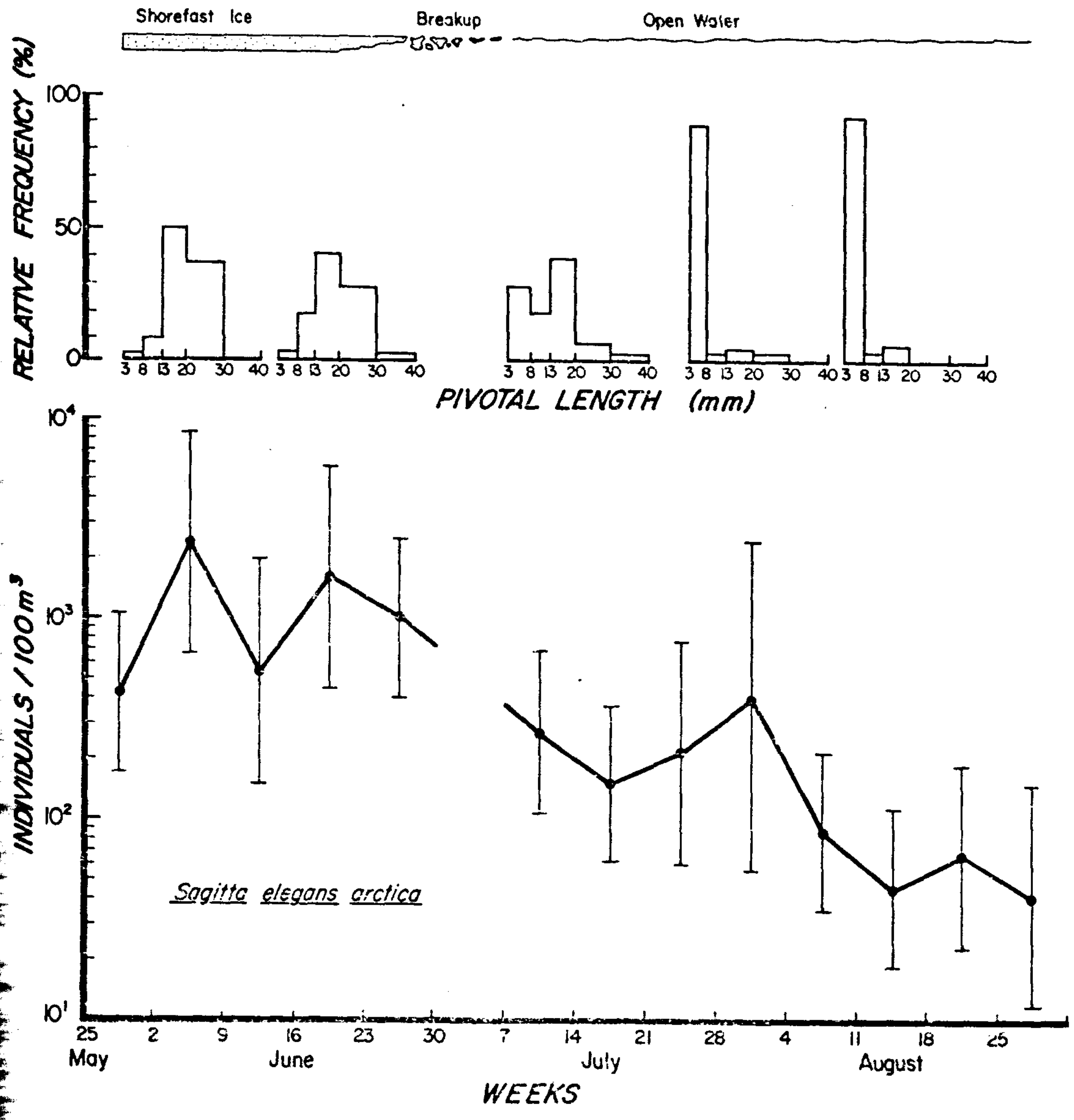
3.2.2.14 *Chaetognatha*

Sagitta elegans arctica Aurivillius

Sagitta elegans arctica was the only species of Chaetognatha present in the collections. The establishment of this northern, cold water variety distinct from the southern species is based on the comparatively larger size of the former. The species occurred in the plankton on all sampling dates during the summer.

The cycle of temporal variability in abundance and the concomitant change in length-frequency relationships for the species are depicted in Figure 8. The overall pattern observed in the population was a significant decline in numbers per unit volume from the beginning to

Figure 8. Quantitative distribution of *Sagitta elegans arctica* from May 25 to August 28, 1972, with concomitant changes in length-frequency relationships. Vertical bars as above



Shorefast Ice
Breakup
Open Water
RELATIVE FREQUENCY (%)
100
50
0
3 8 13 20 30 40
PIVOTAL LENGTH (mm)
INDIVIDUALS / 100 m³
10⁴
10³
10²
10¹
Sagitta elegans arctica
25 2 9 16 23 30 7 14 21 28 4 11 18 25
May June July August
WEEKS

the end of the sampling season; exceptions to this general pattern were found during weeks 3 and 10. A high incidence of larger specimens in the 13 to 20 and 20 to 30 mm size ranges resulted in an initial population maximum of 2400 individuals/100 m^3 for the species the first week of June. A smaller, secondary maximum occurred in late July, consisting predominantly of juvenile individuals of 3 to 8 mm pivotal length.

Gravid specimens in the 25 to 35 mm range were seen with distended oviducts on June 1, 5, and 21. Large numbers of 3 to 5 mm individuals first began appearing in the material by July 10. A trimodal size distribution is indicated by the July 8 - July 16 histogram; a composite plot of the entire summer catch reinforces this distribution. After July 16, a shift in size-frequency was evident, with 95 percent or more of the population of *S. elegans arctica* existing as immature stages.

The contribution of this chaetognath to community biomass was most significant during the early summer months of May and June.

Whole or semi-digested remains of the copepod *Pseudocalanus minutus* were often seen in the guts of *Sagitta*, to the exclusion of other prey items. *Sagitta* was present in the February plankton, as was *P. minutus*.

3.2.15 *Appendicularia*

Fritillaria borealis Lohmann

Fritillaria borealis was the numerically dominant appendicularian in the samples, although it was absent from the plankton until July 14.

Head lengths ranged from 0.3 mm to a maximum of 0.8 mm, suggestive of a juvenile stock. The population peaked on August 3 at 27,319 specimens/100 m^3, shortly after an eastern intrusion of warmer water into the Barrow area in late July. Population density declined significantly during August.

Oikopleura sp.

This is probably *Oikopleura vanhoeffeni* Lohmann, as the maximum eported head length in the present collections exceeds that of another rctic species, *O. labradoriensis* Lohmann.

June specimens were generally immature (1.0 to 1.5 mm ead length) with somewhat larger individuals appearing as summer ogressed. The presence of the species in the plankton was very rratic in general, with the largest concentrations found under e shorefast ice. *Oikopleura* was also encountered in the February llections.

2.2.16 *Pisces*

Three or more species of fishes, represented by both larval and venile stages, persisted through the summer. Larval fishes of undeter-ed identity ranging in length from 5 to 10 mm, were caught through e. Catches increased from May to a summer maximum of 93 individuals/100 the last week of June. Numbers declined significantly through the pletion of the summer.

Beginning in early July, an upward shift occurred in the major th mode to 10 to 13 mm; smaller individuals were still present in modest abundance. A few 21 mm larvae were collected on July 22. The final presence of larval fishes in the plankton was on August 4 and four days later juvenile fishes identifiable as *Boreogadus saida* (polar cod) were taken. By early August, juvenile polar cod were 25 to 30 mm long and increased in average size to a maximum length of 40 mm toward the end of the month. Eighteen *B. saida* were collected during the summer.

Two juvenile sculpins, *Myxocephalus scorpiodes* (Fabricius), the false sea scorpion, and *Icelus bicornis* Reinhardt, the two-horned sculpin, were introduced to the plankton beginning August 23. Average lengths were 30 to 35 mm for 18 juveniles of the two combined species.

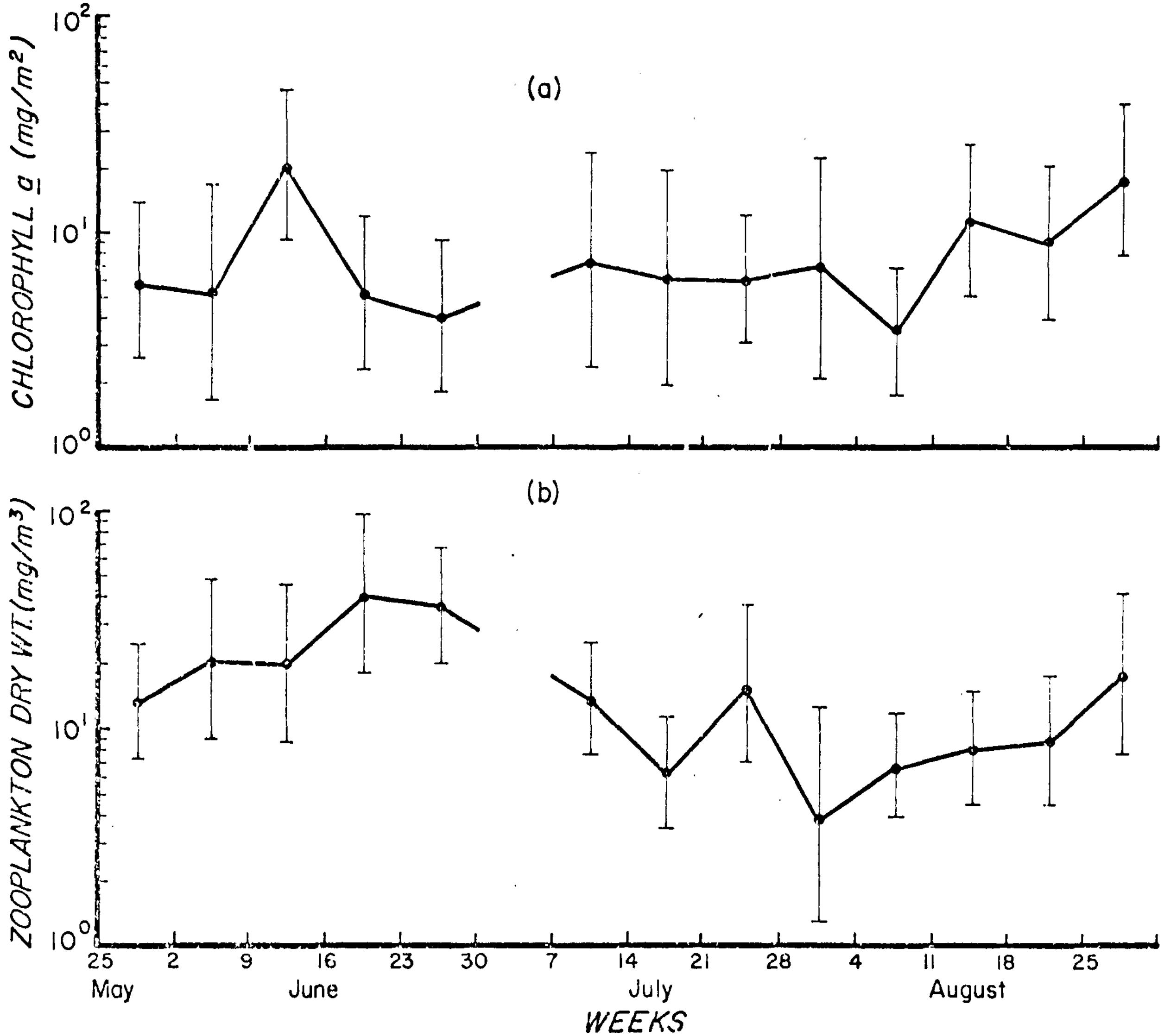
Fish eggs were present in the plankton regularly throughout the entire summer. A maximum density of 8900 eggs/100 m^3 was recorded on June 12. Concentrations during the early summer were generally on the order of 1000 eggs/100 m^3. After ice recession, the relative paucity of eggs was evident with few exceptions. No eggs were collected after August 19.

The polar cod, *Boreogadus saida*, was previously cited in the text for its association with the scyphozoan medusa, *Cyanea capillata*. No other species of fish found in my collections exhibited a similar behavior.

3.2.3 *Standing Stock*

The weekly quantitative trend of zooplankton community formalin dry weight is depicted with a similar accompanying curve of integrated chlorophyll *a* in Figure 9. The results of a one-way analysis of gure 9. Weekly distribution of (a) integrated chlorophyll *a*, and (b) zooplankton community formalin dry weight from May 25 to August 28, 1972. Vertical bars as above

(chlorophyll data after Horner)


(a)
CHLOROPHYLL a (mg/m²)
10²
10¹
10⁰
(b)
ZOOPLANKTON DRY WT. (mg/m³)
10²
10¹
10⁰
25 2 9 16 23 30 7 14 21 28 4 11 18 25
May
June
July
August
WEEKS

variance of zooplankton biomass with time indicated significant variability ($\underline{P} < 0.05$) between weekly means for the summer (see Table 3).

A maximum dry weight of 41 mg/m^3 was attained the week of June 16, approximately 2 weeks after the early June chlorophyll *a* maximum. Zooplankton biomass decreased through July and then rose to a secondary summer peak of 16 mg/m^3 later that same month. A decline was observed into early August, followed by a gradual increase. This August trend was also observed in the phytoplankton standing stock, measured as chlorophyll *a*.

The results of the determinations of average individual dry weight for various life history stages of the major planktonic groups at Barrow are listed in Table 9.

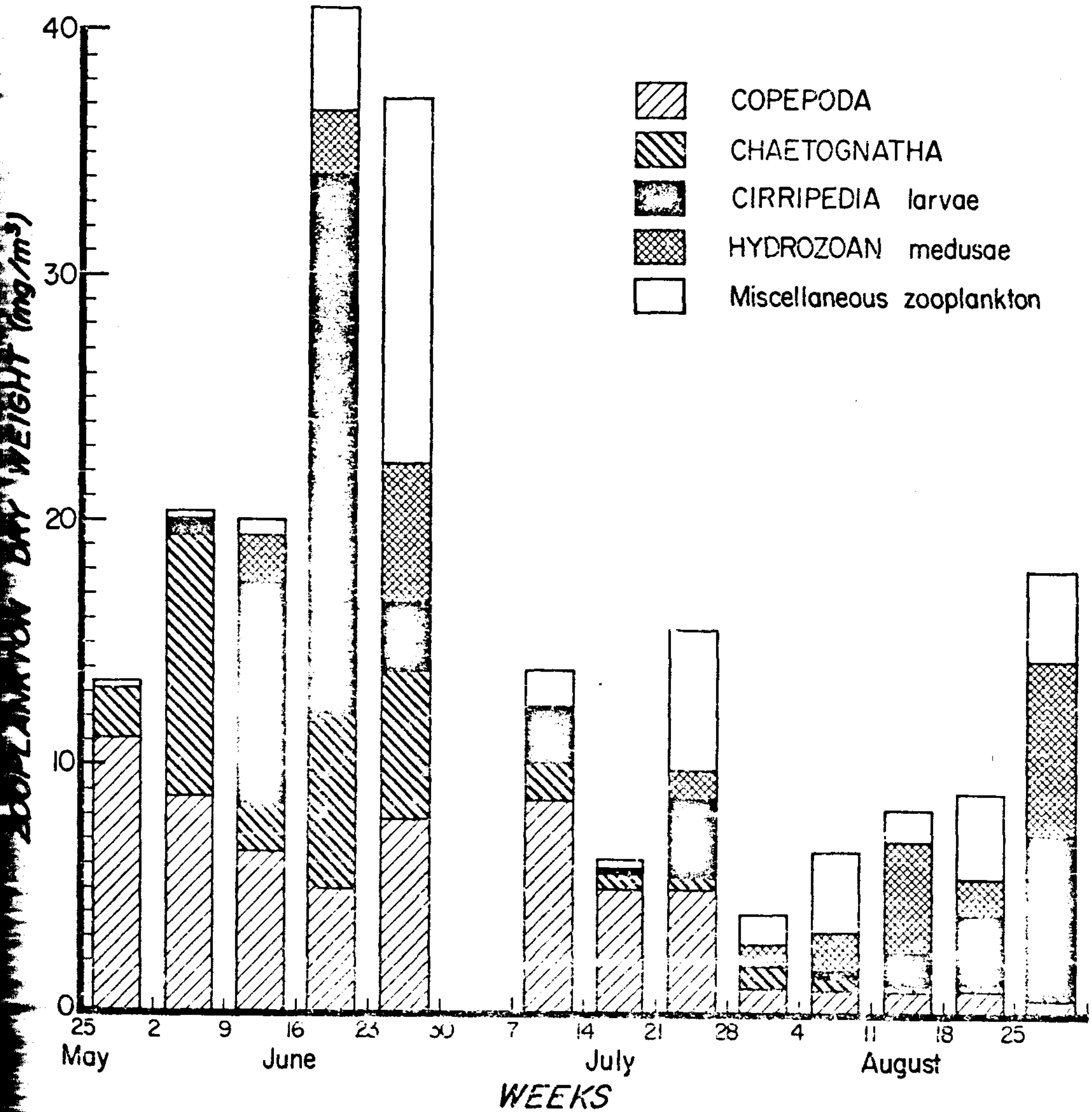
By multiplying the weekly population density for each of the selected categories of zooplankton (individuals/m^3) by the individual dry weight for the specific organism (mg/individual), a fractionation of total dry weight (mg/m^3) contributed by major members is possible at weekly increments. Total biomass for the zooplankton community was partitioned in this manner into four major constituent groups of the Barrow plankton with an additional group to incorporate all miscellaneous organisms (Fig. 10).

The copepods comprised the greatest proportion of total community dry weight averaged over the entire summer, constituting over 70 percent of weekly biomass at times (weeks 1, 7, and 8) and approximately 40 percent of total biomass during May and June. *Pseudocalanus minutus* was the major contributor to copepod biomass during this time. Following

Table 9. Average individual dry weights for selected developmental stages of major zooplankton categories

Category	Developmental Stage	Length (mm)	Individual Dry Weight (mg/ind)
Hydrozoa			
Aglantha digitale		12-16	3.65
		6-10	1.84
		3-6	0.37
Pteropoda			
Limacina helicina	juveniles	3	1.69
		2	0.80
		1	0.27
Cirripedia			
Balanus sp.	nauplius, cypris		26/8000 indiv
Copepoda			
Acartia spp.	adult	0.8-1.1	0.026
Calanus glacialis	adult	4.2-4.5	0.480
	IV-V	3.1-3.5	0.221
	III	2.6	0.062
	II	1.6	0.035
	I	1.1	0.023
Pseudocalanus minutus	adult	1.4-1.9	0.050
	V	0.8-1.4	0.032
	III-IV	0.5-0.8	0.024
Chaetognatha			
Sagitta elegans arctica		30-40	3.75
		20-30	0.84
		13-20	0.46

Figure 10. Qualitative and quantitative fractionation of average zooplankton community dry weight for 13 weekly periods from May 25 to August 28, 1972


ZOOPLANKTON DRY WEIGHT (mg/m³)
40
30
20
10
0
COPEPODA
CHAETOGNATHA
CIRRIPEDIA larvae
HYDROZOAN medusae
Miscellaneous zooplankton
25
2
9
16
23
30
7
14
21
28
4
11
18
25
May
June
July
August
WEEKS

breakup in late June, the copepods, predominantly *Calanus glacialis* and nauplii larvae and to a lesser extent *Acartia*, contributed a somewhat smaller relative percentage of total biomass, roughly 25 percent.

Cirriped larvae of the genus *Balanus* were the second most important group of the Barrow plankton with regard to community standing stock. Barnacle larvae constituted over 25 percent of community biomass during mid-June and late August, both periods of maximum recruitment.

Hydrozoan medusae and the chaetognaths were subordinate to the copepods and barnacles in their relative contributions to the summer community standing stock. However, these categories were very important at times during the summer season.

Sagitta elegans arctica was most notable early in the summer season, particularly from June 2 to 9, when it represented 50 percent of the weekly biomass. The species commonly accounted for about 10 to 20 percent of the weekly community dry weight through early August.

The greater portion of the hydrozoan medusae biomass was attributed to *Aglantha digitale*. The relative contribution of the hydrozoans to the community dry weight averaged over the entire summer was approximately 10 percent; the majority of this stock occurred during the month of August.

The miscellaneous zooplankton category included many sporadically important plankton groups. Polychaete larvae were of some importance to the mid-June community biomass. Crab zoea, juvenile shrimp, euphausiids, and larval fishes were major contributors from June 23 to June 30. A pelagic tunicate, *Fritillaria borealis*, was found in large concentrations in early August. The scyphozoans, mostly *Cyanea capillata*, figured significantly in community biomass during the later three weeks of August.

3.2.4 Trophic Relationships

Five feeding experiments were completed in the laboratory, examining energy interrelationships between the phytoplankton and zooplankton on both the species and community levels of organization (Table 10).

Four experiments treated the zooplankton on the individual or species level of energy budgeting. The results of one experiment were rejected because cellular activity in the zooplankton feeding jars after the experiment was higher at times than that for the phytoplankton control jar, suggesting no active feeding took place. However, bodily activity of the organisms indicated active filtration.

Assimilation efficiency was calculated by both the summation and difference methods using the equations listed in Appendix II. Efficiencies obtained by summing respiratory, excretory, and growth components, with the exception of a low value of 9.5 percent, ranged from 34.2 to 95.5 percent. A mean assimilation efficiency of 70.0 percent was determined for all zooplankton groups.

Assimilation efficiencies calculated by subtracting faecal activity from ingested activity were consistently very high, 95 to 100 percent for all individual zooplankton. Zooplankters actively defaecated in many cases as evidenced from the number of pellets removed from the feeding jars (see Appendix II). The pellets measured about 100 to 200

Table 10. Laboratory estimates of filtration and ingestion rates, respiration and excretion, assimilation and gross growth efficiency for zooplankton fed radioactive labelled phytoplankton.

Experiment 1: 4 hours; initial cell conc. (C_o) = 4 x 10^6 cells/liter; *Chaetoceros* sp. as food organism; *Calanus plumchrus* V as herbivore, feeding in dark @ 10°C; July 17

	Filtration rate (ml/anim/day)	Ingestion rate (cells/anim/day)	Resp+Excret (%)	Assim eff (%) (1)	Assim eff (%) (2)	Gross Growth eff (%)
Group 1	12.5	50,000	26.5	79.5	95	52.9
" 2	18.0	72,000	19.7*	34.2	97	14.5
" 3	4.8	19,200	5.8*	9.5	99	3.7

Experiment 2: 24 hours; C_o = 1 x 10^6 cells/liter; *Chaetoceros* sp.; *Calanus hyperboreus* V (1), *Pseudocalanus minutus* adults (2,3), *Calanus glacialis* V (4,5) fed in light conditions @ 1°C; July 29

	Filtration rate (ml/anim/day)	Ingestion rate (cells/anim/day)	Resp+Excret (%)	Assim eff (%) (1)	Assim eff (%) (2)	Gross Growth eff (%)
Group 1	8.0	8,000	82.3	84.4	100	2.1
" 2	5.1	5,100	33.5	48.7	97	15.2
" 3	6.0	6,000	63.0	77.8	98	14.9
" 4	5.1	5,100	32.5	70.3	96	37.8
" 5	5.7	5,700	94.8	95.5	100	0.7

Experiment 4: 24 hours; low concentrations of mixed, natural phytoplankton, consisting of green biflagellates, *Navicula* sp., *Nitzschia* spp.; *Acartia* spp. adults (1,2,3), *Pseudocalanus minutus* (4,5), *Balanus* spp. nauplii larvae (6,7) fed in 20/4 hour light/dark cycle @ 9°C; August 28

	Filtration rate (ml/anim/day)	Ingestion rate (cells/anim/day)	Resp+Excret (%)	Assim eff (%)	Gross Growth eff (%)
Group 1	2.6				7.5
" 2	14.5				2.1
" 3	14.7				4.1
" 4	12.5	NOT MEASURED	NOT MEASURED	NOT MEASURED	13.6
" 5	10.4				18.2
" 6	3.6				9.6
" 7	3.4				9.7

Experiment 5: 24 hours; endemic algal populations at natural concentrations used, including those species mentioned in experiment 4; random samples of zooplankton community, including *Balanus* nauplii and cyprid larvae, *Acartia* and *Oithona*, echinoderm larvae, and assorted minor categories were chosen and tested @ 10°C in light; August 30

	Filtration / Ingestion / Resp+Excret / Assim eff	Gross Growth eff (%)
Group 1		60.0
" 2	NOT MEASURED	25.7
" 3		32.8

* respiration and excretion measured by phenethylamine process.

[1] Assimilation efficiency measured by sum of resp+excret % and gross growth efficiency %;

[2] Assimilation efficiency as measured by difference of faecal pellet activity from ingestion activity

μm in length and were yellowish in color with tapering "tails" at the pellet end.

Active feeding by the Bering Sea expatriate copepod, *Calanus plumchrus* V, was indicated by the calculated filtration rates and faecal matter collected. Assimilation efficiency of ingested carbon was highly variable and a mean gross growth efficiency of 23.7 percent was determined. The relative amount of energy lost from metabolic processes was roughly balanced by energy diverted into growth. No consistent correlation of ingestion rate to gross growth efficiency appeared to exist for *C. plumchrus* V.

The mean assimilation efficiencies of *Calanus glacialis* V and *Pseudocalanus minutus* females in experiment 2 feeding on a unialgal *Chaetoceros* sp. culture of concentration 1 x 10^6 cells/liter were comparatively equal, ranging from 63 to 82 percent. For both species, over 75 percent of assimilated energy was lost through metabolic processes. *Calanus hyperboreus* demonstrated active feeding behavior, but only slight diversion of ingested energy into growth. Percentage respiratory and excretory losses for all zooplankton groups in experiment 2 (24 hours duration) were greater than for those groups in experiment 1 (4 hours).

The data available in Table 9 on the average individual dry weights of zooplankton organisms, coupled with certain assumptions on phytoplankton cell density, allowed the determination of the daily ingested ration for *P. minutus* and *C. glacialis*. The solitary *Chaetoceros* cells used in experiments 1 and 2 were examined under the microscope and measured in two dimensions, each about 10 μm long. A similar length was applied to the third dimension and a cell volume of $10^3 \mu m^3$ obtained. The density of seawater, about 1.02 g/cm^3 ($10^{-6} \mu g/\mu m^3$), was used for cell density. Cell wet weight was then calculated by multiplying cell volume by cell density. A conservative wet to dry weight conversion factor of 1/2 was used in determining cellular dry weight (0.5×10^{-3} μg). The average dry wet of an adult *P. minutus* was earlier determined as 0.05 mg or 50 μg. *Pseudocalanus* (groups 2 and 3) in experiment 2 daily ingested 5100 and 6000 cells, respectively. This figures to 2.6 μg and 3 μg dry weight of *Chaetoceros* cells ingested per day. The weight to weight ratios indicate *P. minutus* adults ingested 5 to 6 percent of their body weight daily grazing on *Chaetoceros* cultures. A similar calculation for *Calanus glacialis* V resulted in a predicted daily ration of 1.0 to 1.3 percent of dry body weight.

Experiment 4 used mixed, endemic algal populations diluted to concentrations of about 5000 cells/liter. Gross growth efficiency determined for *Acartia* spp. was relatively constant, ranging from 2.1 to 7.4 percent. Grazing rates for *Acartia* were comparable to those of *P. minutus*. Filtration rates for *P. minutus* were over twofold higher than those measured under conditions of highly concentrated *Chaetoceros* culture in experiment 2. Growth efficiency for *P. minutus* showed little variation under the differing experimental conditions of experiments 2 and 4.

Balanus nauplii demonstrated both consistent grazing rates and growth efficiency. The individual nauplius larva filtered smaller volumes than the copepods, but was more efficient than *Acartia* in diverting energy into growth.

The random assemblages of zooplankters used in the community experiment included: *Balanus* nauplii (approximately 64% by number) and cyprid larvae (32%); ophioplutei larvae (2.7%); the remaining portion was divided between copepods, *Aglantha digitale*, ostracods, polychaete larvae, *Oikopleura*, and *Sagitta elegans* juveniles.

The above community was more efficient in diverting ingested energy into growth than were individual species in the majority of cases. An average gross growth efficiency of 39.5 percent was obtained for the three community aliquots.

CHAPTER 4. DISCUSSION AND CONCLUSIONS

The zooplankton of the Arctic Ocean and peripheral seas have been broadly categorized into several groups based on horizontal and vertical distributions and association with the major arctic water masses: (1) the Arctic surface layer; (2) the Atlantic layer; and (3) the Arctic bottom water. Grainger (1965) described three major groups of associated zooplankton from the Arctic Ocean, southeast Beaufort Sea coastal waters, and Amundson Gulf from reported horizontal and vertical distribution patterns and through relationships with physical parameters. The first group comprises species of wide horizontal occurrence in the upper 100 m of both the inshore areas of the continental shelf and the offshore, oceanic regions. Species of this group include the holoplanktonic medusae, *Aglantha digitale* and *Aeginopsis laurentii*, the pteropods *Limacina helicina* and *Clione limacina*, the chaetognath *Sagitta elegans*, and the appendicularians *Oikopleura vanhoeffeni* and *Fritillaria borealis*. Eight species of copepods are also included as members of this group, represented by *Calanus glacialis*, *Calanus hyperboreus*, *Pseudocalanus minutus*, *Microcalanus pygmaeus*, *Pareuchaeta glacialis*, *Metridia longa*, *Oithona similis* and *Oncaea borealis*. All species of group 1 are able to tolerate a rather wide range of temperature and salinity.

Members categorized into group 2 include species restricted to offshore waters, at considerable depth in the cold, high salinity Atlantic water mass. The ostracod, *Conchoecia maxima*, and the copepods *Spinocalanus magnus* and *Gaidius brevispinus* are included here. Group three of Grainger's classification of the arctic zooplankton consists of the primarily neritic, shallow water species, thriving in freshened waters of high temperature. Reported members of this group are the meroplanktonic medusae *Obelia* sp. and *Euphysa flammea*, and the copepod *Eurytemora herdmanni*.

Brodskii (1956) reported that the largest density of zooplankton occupies the Arctic surface layer in the central Arctic Ocean, whereas the greatest diversity of forms is found in the intermediate, or Atlantic water mass. With specific reference to the Copepoda of the polar basin, the composite results of Brodskii and Nikitin (1955), Brodskii (1957), and Johnson (1963), indicate 30 species to exist in the upper 300 m and 50 species between 300 and 1000 m.

Johnson (1956) cited the distribution of an additional group of zooplankton, these being certain copepod species expatriated northward from the Bering Sea up to the edge of the ice pack and along the arctic coast of Alaska east of Barrow. Two species, *Calanus cristatus* and *Eucalanus bungii bungii*, were found as far east as the Alaska-Yukon boundary in 1951 and their presence was interpreted as indicating the penetration of Pacific water far to the east of Point Barrow.

The observed distributions of several neritic copepods and hydromedusae along the northern coast of North America are more difficult to interpret. The populations of some species common to both the eastern and western arctic of North America are discontinuously distributed along the northern coast. Included here are *Euphysa flammea, Acartia longiremis, Eurytemora herdmanni* and *Tortanus discaudatus*. Whether the original connection was made by transport via the Beaufort gyral or directly across the northern coast of America is not known, but the present tenuous connection between populations of these species could conceivably result in speciation.

4.1 The Ecology of the Inshore Zooplankton

Emphasis in the present study was towards the description of temporal distributions in abundance of members of an Alaskan neritic zooplankton community, and the establishment of life history patterns and associations of the primary constituents. The sequence of changes in the community were observed from a fixed location. Statistical analyses indicated significant differences in distributions of abundance of most zooplankton categories with time. Many of these observed differences can probably be attributed to hydrographic changes and the life histories of the zooplankton constituents.

A comparison of distributional and life history patterns of the constituents of the Point Barrow community with those reported in arctic oceanic areas indicates a distinctly different community exists in the neritic environment.

4.1.1 Distributional Patterns

The observed presence and temporal distributions of several species of the Copepoda, as well as certain hydrozoan medusae, indicated a northward penetration of Bering Sea water and its characteristic fauna into the study area during the summer of 1972.

Biological indications of this phenomenon were further substantiated by hydrographic observations.

The intrusion of North Pacific and Bering Sea water masses into the Chukchi Sea is well documented (Barnes and Thompson, 1938; Coachman and Barnes, 1961). American data suggest a summer northward transport of 1.4 million cubic meters of water per second through the Bering Strait, with a winter flow one-fourth this magnitude. This influx of warmer, more saline North Pacific water results in a subsurface temperature maximum in the central arctic below the cold, dilute Arctic surface layer. A description of the mechanics of mixing on the continental shelf is somewhat more difficult, particularly where distinct water properties are rather ill defined (Coachman, personal communication).

The inshore zooplankton community near Point Barrow, Alaska, can be differentiated into two groups, based on my summer collections: (1) fauna characteristic of the Bering Sea; and (2) fauna common to the Chukchi and Beaufort Seas.

Species included in the first group are the oceanic expatriate copepods *Calanus cristatus*, *C. plumchrus*, and *Eucalanus bungii bungii*, all previously cited by Johnson (1956) as indicative of the intrusion of Pacific water into the higher latitudes. These three species were present in small numbers for only a short time during July either as adults or stage V copepodids. A plausible explanation of their distribution can be found in the reported life history data for these copepods in the Bering Sea (Heinrich, 1961). All three species breed at considerable depth in early spring and by mid-summer have developed to stage V in the warm surface waters; the majority of stage V individuals have migrated to depth by mid-July. Since the shallow depth of the Bering Strait (75 m) would preclude transport of deeper forms into the Barrow area, specimens would not be expected to occur in late summer collections. That no specimens were taken before July 8 can possibly be attributed to any of the following: the lag time in water mass transport from the Bering Sea to the study area; the smaller volumes of water filtered; or the presence of the offshore pressure ridge imposing a physical barrier to transport into inshore waters during June.

Johnson cited an additional group of copepods, apparently advected northward along the western Alaskan coast and eastward around Point Barrow. Primary examples are *Tortanus discaudatus*, *Centropages abdominalis*, *Eurytemora herdmanni*, and *Acartia clausi*. All of these members abound in the warm neritic environment along the western coast of Alaska during summer (Johnson, 1934, 1953). All four species in my collections were present at Barrow only during the period of maximum surface water temperature in August, indicating the strong neritic character of the area with respect to these copepods. Their distributional patterns can be closely tied to reported reproductive periods along the western Alaskan coast. I concur with Johnson that the majority of specimens are transported into the nearshore environment of Barrow from the south.

The cladocerans *Evadne nordmanni* and *Podon leukarti* also appear to be advected into the Barrow area from more southerly latitudes. Both were found exclusively during the final three weeks of August, coinciding well with the presence of the above-mentioned neritic copepods. Johnson (1953, 1956) reported *E. nordmanni* and *P. leukarti* to occur commonly only in the shelf waters of the Chukchi Sea and in the vicinity of the Nome-Norton Sound area of western Alaska during August.

Further evidence supporting the contention that all of the seven previously mentioned copepod species and the two ostracods are indeed advectively introduced subarctic species is presented in that none of the above, with the exception of *Eurytemora herdmanni*, are included among Grainger's three categories of arctic zooplankton.

The second major group of zooplankton described for the inshore community at Barrow comprises the largest number of categories and the most significant members in terms of contribution to total numbers of individuals and biomass of the community. Both meroplanktonic and holoplanktonic constituents are well represented. Included among this group are all but two of the fifteen ubiquitous arctic species described by Grainger (1965) as the primary constituents of both the inshore and offshore zooplankton communities existing in the arctic surface layer. *Microcalanus pygmaeus* and *Oncaea borealis* were not found. Johnson (1956, 1958) similarly reported *M. pygmaeus* and *O. borealis* to be absent from coastal stations near Barrow and cited their major distribution beyond the 100 m contour.

The observed distributional patterns of three characteristically arctic copepods, *Calanus hyperboreus*, *Euchaeta norvegica* and *Metridia longa*, indicate that the main populations of these species are held back in the Chukchi Sea by the intruding flow of Bering Sea water into the study area. All of the above became absent from the plankton as the southern influence on the nearshore hydrography became very pronounced in June. Johnson found the southern limit of continuous distribution for *C. hyperboreus* and *M. longa* to exist at the 100 m depth contour and failed to observe specimens within this limit in July and August. The *Burton Island* collections also indicated larger numbers of *E. norvegica* to exist at the more offshore stations. The inshore, neritic environment near Barrow appears to be unsuitable for these arctic species under the influence of the warm southern water mass during the summer.

The remaining holoplanktonic members of group 2 (characteristic of the Chukchi and Beaufort Seas) are represented in the majority by the copepods *Calanus glacialis*, *Pseudocalanus minutus*, and *Oithona similis*, the chaetognath *Sagitta elegans arctica*, and an assemblage of pteropods, amphipods, euphausiids, appendicularians, and fishes. The population dynamics of the majority of these taxa are probably less the result of advective processes and more closely allied to biological phenomena, such as predation, natural death and sinking, and periods of spawning. A discussion of outstanding members is included in the following section on life history patterns.

The temporal distributions of abundance for the barnacle larvae and certain hydrozoan medusae appear, on the other hand, to be the result of both advective and biological processes.

Hand and Kan (1961) reported on all the hydrozoan species represented in the present collections and concluded that the distribution of these medusae correlated well with the general hydrographic circulation near Barrow. From known locality records, they surmised that a continuous breeding population exists for most species from the North Pacific to the Chukchi Sea, with relatively little local replenishment as far north as Barrow. The introduction through advection of certain members of the hydromedusae into the nearshore waters of the Chukchi Sea near Barrow is probable, based on the simultaneous presence of a large number of intermediate and mature stages collected for several species with an apparent absence of juveniles.

The distribution of cirriped larvae also suggests a hydrographic influence. Suitable substratum sites for the attachment of mature cyprid larvae are scarce in the inshore waters adjacent to Barrow as reported from direct observation by SCUBA divers and bottom dredges (MacGinitie, 1955). The majority of beds were found by MacGinitie to exist several miles offshore, in depths of 60 m or more. Johnson (1956) found the highest concentrations of barnacle larvae some distance northwest of Pt. Barrow during the summers of 1950 and 1951. These data suggest that a sizable portion of the present catch is possibly attributed to advection into the area of investigation and the observed temporal distribution is an admixture of this effect with local spawning.

4.1.2 *Life Histories and Reproductive Success*

Sufficient data were provided from the summer collections to establish the life histories of several major Chukchi-Beaufort Sea zooplankters as well as to allow comment on the reproductive success of advectively introduced species.

Specimens of the oceanic Bering Sea expatriate copepods, *Calanus cristatus*, *C. plumchrus* and *Eucalanus bungii bungii* were present in the Barrow collections exclusively as stage V copepodids or adults. The absence of early developmental stages for all of these species in the summer collections suggests no local reproduction occurs in the Barrow area.

The reproductive success of the more southern neritic copepods, *Tortanus discardatus*, *Eurytemora herdmanni*, *Acartia clausi*, and *Centropages abdominalis* in the inshore waters adjacent to NARL is uncertain. The present collections included a stage I copepodid of *Tortanus discaudatus* with adult females and males in relatively low abundance; Johnson (1958) found nauplii and egg cases of *T. discaudatus* in tows near NARL during the summer of 1957. It appears that a continuous breeding population exists from the western coast of Alaska to some distance east of Barrow. Gravid females of *Eurytemora herdmanni* were prevalent in the summer collections, similarly suggesting a continuous breeding population. No ovigerous females of either

Acartia clausi or *Centropages abdominalis* were noted, and until more samples are collected simultaneously in the vicinity of Barrow and along the western Alaskan coast, the geographical range of reproductive success of these latter two species cannot be established with certainty.

Podon leukarti and *Evadne nordmanni* were collected in both adult and juvenile stages, indicating some degree of reproductive success as far north as Barrow for these introduced cladocerans.

A combination of local replenishment and advection are probably responsible for the population fluctuations observed during the summer for several hydromedusan species. *Aglantha digitale* is the outstanding example, where large increases in population abundance were seen to accompany recruitment of smaller individuals in early August (see Figure 4); additionally, a wide range of developmental stages existed at any given time. *Bougainvillea superciliaris*, *Rathkea octopunctata*, and *Obelia longissema* were also present in an admixture of developmental stages, implying an advective influence. *Aeginopsis laurentii*, *Euphysa flammea*, and *Leuckartiara* sp. existed only as immature medusae and this is interpreted as indicating the major stock of these species is produced locally, with comparatively little outside introduction. Breeding appears to occur under the ice during May and June for these three hydrozoans.

The life history of the barnacles can be fairly well established from available data collected over the summer.

The period of maximum liberation of barnacle larvae presumably occurs from mid to late June, with the initial release of nauplii in late May. Spawning appears to continue at least through August, with a secondary peak occurring in mid-August. Population highs were well correlated to a rich phytoplankton standing crop. A period of 31 days is indicated as necessary for the development of the nauplius larva to the cypris stage.

The initial breeding periods of other meroplanktonic members of the community appear to be well timed to available phytoplankton. Decapod larvae occurred in greatest abundance during June; echinoderm larvae were most prevalent in late August, both periods of high plant stocks.

The most prevalent copepods in my collections were common Chukchi and Beaufort Sea species, existing in a variety of reproductive states and developmental stages. Several positive comments can be made on the breeding periodicity and life history patterns for many of these species.

Heinrich (1961) established several categories of northern latitude copepods on the relationship between breeding periods and development to the occurrence of high phytoplankton stocks. Heinrich places *Pseudocalanus minutus* and *Calanus glacialis* into a category including species breeding simultaneously with high phytoplankton abundance. Category 2, those species which may reproduce in the absence of high phytoplankton stocks, includes *Metridia longa* and *Calanus hyperboreus*. A third category includes species reproducing over extended periods, with maximum broods produced during times when the phytoplankton crop is rich. *Oithona similis* was the type species described for this group.

Observations on the reproductive state of the above mentioned copepods in relation to the summer phytoplankton standing crop at Barrow are in excellent agreement with Heinrich's classifications.

The majority of gravid females of *Calanus glacialis* and *Pseudocalanus minutus* were present during the early summer phytoplankton bloom, an optimal period for high egg production. *Metridia longa* and *Calanus hyperboreus* were found only at the beginning of summer, mostly as stages III and IV, apparently breeding at some period before the summer season. Too few specimens of *C. hyperboreus* and *M. longa* were collected to discern whether these copepods are annual breeders in the waters near Barrow. Conover (1962) reported mid-winter breeding of *C. hyperboreus* in the Arctic Ocean and described a two-year life cycle for the species. In subarctic and marginally arctic environments, the species is reported to reproduce annually (Digby, 1954; Grainger, 1959).

Oithona similis appears to fit Heinrich's third category of copepods, as it was found to be ovigerous throughout most of the summer at Barrow. Grainger (1965) also classified *O. similis* into a similar category.

The primarily carnivorous *Euchaeta norvegica* was found mostly as stage III at Barrow during the early summer, implying slight if any dependence of its breeding period on the phytoplankton.

The life cycle of *Calanus glacialis* in the vicinity of Barrow appears to be completed in one year. The large number of copepod nauplii found beginning in late June are probably the spawn of the gravid females of *C. glacialis* reported up through late June. Stage I copepodids became abundant during early July and most individuals of the species had reached stage III or IV by the end of August. All individuals found in late May and early June samples were mature stages, indicating development through stage V during the summer season.

Dunbar (1940) pointed out the phenomenon of polyphasic, or alternating, breeding cycles for major members of the zooplankton in the high arctic. The simultaneous presence of three distinct year classes or broods in the plankton for these species is taken to indicate a two-year life cycle. This prolongation of the life cycle is interpreted as being an adaptive response to the very short biological season in the high arctic. Type species included in this group are *Sagitta elegans arctica* and *Thysanoëssa raschii*, both present in the Barrow collections. Examination of the size-frequency histograms of both of these species (Figs. 7, 8) suggests an extended life cycle of the arctic variety.

Concerning *S. elegans arctica*, two modes are obvious in most cases and a third appears to exist in mid-July. Egg bearing individuals were reported in the 30 to 40 mm size range in mid-July and it was shortly afterwards that a large number of 3 to 8 mm individuals were recruited to the population. These data indicate a prolonged life cycle, if not two years, somewhat longer than one.

Thysanoëssa raschii existed in two very distinct population size classes. The absence of a third mode consisting of larger, mature individuals is interpreted as the inability to sample adults at depth in the more offshore waters. Johnson (1958) similarly reported only juvenile *T. raschii* in his collections at Barrow taken up to 4 miles offshore. The obvious size gap between the young calyptopid larvae and the 10 mm juveniles is too distinct to discount. It appears that *T. raschii* has a prolonged life cycle of two years in the Barrow area; however, the collection of adults simultaneously with the younger stages is required before this can be established with certainty.

Substantial evidence exists in support of active summer breeding in the coastal waters near Barrow for several other holoplanktonic taxa. Epyral stages of the Scyphozoa were collected in August. Female *Autolytus fallax* were observed with egg sacs during the entire summer and larval polychaetes were prevalent at times. Amphipods and appendicularians were present in juvenile stages for much of the summer. Eggs and larval stages of fishes occurred in maximum concentrations during June, indicating active reproduction at this time.

The plankton community in the neritic waters of Barrow seems to exist in an unbalanced state; the time lag between the phytoplankton and zooplankton peaks in Figure 9 bears this out. Seasonal fluctuations of this nature are commonplace in neritic environments throughout the world in contrast to the stable, balanced communities usually found in tropical oceanic environments. The lag time existing between zooplankton breeding periods (and effective grazing pressure) and the *initial* period of high primary productivity is probably partially responsible for this phase difference. Cyclic phenomena in arctic and high latitude areas are also perpetuated by the relative paucity of zooplankton species, allowing a few organisms to dominate through reduced competition. Dunbar (1968) hypothesizes a directional evolution toward a more stable, diverse community in arctic and subarctic areas.

4.1.3 Significance of the Meroplankton

Dunbar (1954, 1968) described the northern Alaskan coastal environment as marine subarctic based on existing biological and hydrographic differences in comparison to high arctic regions. The major criterion used in establishing this division is the mixing of arctic and non-arctic water masses. Additional characteristics distinguishing subarctic areas from arctic zones include: (1) lower percentage annual ice cover, (2) greater species diversity, (3) higher production rates, and (4) lesser seasonal oscillation in the biological community.

The application of the term subarctic to a marine environment based on the above criteria obviously encompasses a wide range of areas, some more "subarctic" than others. The intrusion of warm Pacific water into the Point Barrow vicinity imposes a marginally subarctic condition, in the biological as well as physical sense, especially for species with meroplanktonic life histories.

The meroplanktonic component of the Barrow inshore zooplankton community was significant during the summer of 1972. In particular, barnacle larvae were extremely prevalent, with hydrozoan medusae, crab zoea, and echinoderm larvae contributing a sizable fraction. Their abundance suggests that under the influence of the flow of warmer water from the Bering Sea, the conditions at Barrow are more typically subarctic than arctic with respect to the production of meroplanktonic larvae. A comparison of the 31 day nauplius to cyprid developmental period observed for the genus *Balanus* at Barrow with other reported developmental rates for the genus in arctic and subarctic areas (Barnes and Barnes, 1960) substantiates this conclusion.

It is the significant contribution of the meroplanktonic component at Barrow, with a commensurate increase in zooplankton standing stock and species diversity, that biologically differentiates this nearshore area from the central arctic. Reported zooplankton biomass, as measured by dry weight, indicates the standing stock of zooplankton in the nearshore waters off Barrow is an order of magnitude higher than that present in the central arctic under T-3 (Minoda, 1967; Hopkins, 1969). This differential is in part due to the paucity of benthic invertebrates in the central arctic that liberate planktonic larvae. Thorson (1936) concluded that only 5 percent of the benthic invertebrates in the high arctic of East Greenland have meroplanktonic life histories.

Johnson (1956) found that the continental shelf of the Beaufort Sea was less productive than the shelf areas of the Chukchi Sea. He surmised that this was the result of the composite effects of a narrower shelf width and a less favorable temperature regime in the Beaufort Sea in comparison to the Chukchi region, with a correspondingly smaller meroplanktonic contribution to the community.

4.1.4 Energetics and Secondary Production

Interest in the production rates and physiological processes of primary consumer organisms has been generated with the intent of determining the efficiency of energy transfer through the plankton and estimating the production available for higher trophic levels. Much research in recent years has been directed toward answering the fundamental question of whether or not grazing organisms can derive nutrition equivalent to or in excess of their respiratory demands by filtering particulate matter in concentrations naturally found in the sea. Research efforts have been divided between two approaches: (1) determining respiratory and filtration rates in the laboratory and with a knowledge of total particulate organic matter found in seawater, calculating the resultant uptake and comparing this with the food requirements necessary to balance metabolic losses; and (2) establishing filtration rates and the total energy budget in the laboratory and then determining the ingested daily ration necessary to balance this observed budget. This second approach was employed in my study to investigate carbon utilization and secondary production of selected members of the Barrow zooplankton community.

Assimilation efficiencies determined for the several species examined in this study generally ranged from 70 to 85 percent, indicating an efficient grazing community in terms of utilization of native algal species at varied concentrations. Although most assimilated energy was lost through metabolic processes, some fraction of assimilated carbon in excess of these losses was found to be channeled into growth for most organisms, suggesting some production was being realized. That some surplus of energy existed above respiratory requirements even at low cell concentrations appears to indicate that the grazing organisms are indeed able to meet and exceed their minimal metabolic demands by feeding on algal concentrations comparable to those found in the inshore waters off Barrow.

By integrating field observations and laboratory results, a quantitative estimation of secondary productivity attributed to two major copepods, *Pseudocalanus minutus* and *Calanus glacialis*, can be obtained for late July.

Daily ingested rations were earlier calculated for both species as 5 and 1.3 percent of dry body weight, respectively. Using additional data on integrated standing stocks (mg dry weight/m^2) during late July for each species and applying a dry weight to carbon conversion factor of 0.4 (Mullin, 1969) allows for determination of mgC/m^2/day ingested. Laboratory measurements indicated an average of about 15 percent of ingested energy was diverted into growth (production) for both *P. minutus* and *C. glacialis* V; this calculates to daily production rates of 0.0075 mgC/m^2 and 0.023 mgC/m^2, respectively. Integrated net primary productivity determined for July 24 was 0.37 mgC/m^2/hr or 8.9 mgC/m^2/day (Horner, unpublished data). The composite production of *P. minutus* and *C. glacialis* therefore appears to be less than 1 percent of daily primary production in the nearshore waters at this time. Additionally, the standing stock of these two species integrated over the photic zone amounts to only about 4 percent of the phytoplankton standing crop, if a chlorophyll *a* to carbon conversion factor of 50 is used (McAllister, 1969).

Since available data indicate that primary production in late July was relatively low in comparison to other periods during the summer and the concentrations of the two dominant copepods were, in contrast, relatively high, it would appear unlikely that grazing pressure by these copepods could be a major factor responsible for the fluctuations noted in the summer phytoplankton stock.

Barnacle larvae were the numerically dominant grazing zooplankton throughout most of the summer and, as such, warrant consideration with respect to their production and the potential grazing pressure they exert on the phytoplankton community.

An alternate method can be used for the calculation of secondary production of the barnacle larvae, which although perhaps less precise than the previous method, can nevertheless be a useful tool in arriving at rough estimates. The two potential drawbacks to the method are in assuming a filtration rate independent of phytoplankton standing crop and applying a chlorophyll *a* to carbon conversion factor.

The laboratory calculated filtration rate for an individual *Balanus* larva was 3.5 ml/day. By multiplying this grazing rate by the standing crop of phytoplankton converted to mgC/ml, and the concentration of larvae/m^2, an estimate of daily ingestion by the population is obtained in units of mgC/m^2. Growth was determined in the laboratory to be approximately 10 percent of ingestion. Production of barnacle larvae can therefore be calculated for any given period.

The week of June 16, *Balanus* larvae approached concentrations of 50,000 individuals/m^2. Using a factor of 50 to convert chlorophyll *a* to carbon, an individual larva would ingest 1.75 x 10^{-4} mgC/day or 8.75 mgC/m^2/day ingested by the entire population. The rate of production would calculate to 0.88 mgC/m^2/day, or roughly 2 percent of the average primary productivity determined for the week of June 16.

No values were obtained in the laboratory on the percentage of dry body weight ingested daily by *Balanus* larave. However, the late naupliar stages of copepods of the genus *Calanus* have been reported to often ingest over 300 percent of their body weight daily feeding on naturally existing phytoplankton concentrations (Paffenhöfer, 1971). If the previously calculated ingestion rates are underestimates and a daily ingestion ration of 100 percent of body weight is applicable, grazing pressure assumes a very significant role. An average standing crop of barnacle larvae of 65 mgC/m^2 for the week of June 16 can be calculated from earlier determinations of dry weight (carbon)/individual and average weekly abundance. The average phytoplankton biomass for the same weekly period would convert to 250 mgC/m^2. The ingestion by *Balanus* larvae could therefore represent 26 percent of the plant standing crop and very conceivably act to effectively reduce this stock through grazing pressure, especially during periods of low turnover rates in the phytoplankton stock.

It therefore appears that the Cirripedia, in contrast to the Copepoda, could potentially exert significant grazing pressure at specific times during the summer and possibly act to regulate fluctuations in the phytoplankton standing stock to some degree.

As yet, the biomass and feeding biology of the microzooplankton have not been examined; these organisms may perhaps be found to have a pronounced influence in the dynamics of the plankton community.

The zooplankton community adjacent to Barrow appears to be rather efficient at utilizing particulate organic matter that they ingest, of definite ecological importance due to the short biological summers existing in the area. However, the grazing community seemingly ingests only a small fraction of the total carbon produced by the phytoplankton during the summer, the majority of this production being lost from the pelagic system by sinking to the bottom. It would appear that the plankton community in this very shallow photic zone is very inefficient in this regard.

4.2 Sources of Error

The sampling design used in this study was chosen to provide a description of the temporal variability in abundances of zooplankton organisms on a time scale on one week, and to allow tests of hypotheses concerning observed distributions. Both the effectiveness of the sampling procedure and the appropriateness of methods of analysis are factors that must be considered in the interpretation of results.

4.2.1 Field Sampling and Data Analysis

An unknown component of the variability determined for all samples collected in the field was introduced by differences in the volumes of water filtered on successive tows. For the replication process, however, it was unlikely that the magnitude of these differences was very large, even though the means of estimating the speed of the skiff were rather crude. The net most certainly filtered water at less than 100 percent efficiency, but no correction was possible since a flowmeter was not available for the study. However, because low towing speeds were employed and nets were carefully rinsed following each tow, the average filtration efficiency was probably in excess of 80 percent. Slight underestimates of the abundance of organisms probably resulted, since numbers/100 m^3 were determined on the assumption of 100 percent filtration efficiency.

No attempt was made to assess the numbers of animals small enough to pass through the 0.308-mm mesh netting. Barnacle nauplii smaller than 0.308 mm total length were commonly retained in hauls, and their numbers were routinely estimated. This subjective appraisal is certainly subject to unknown error.

The statistical evaluation of variability associated with the subsampling procedure, with replicated tows on sampling days, and with collection on different days of the week, does suggest that a more efficient allocation of sampling effort can be applied to similar future studies. For all zooplankton categories, subsampling error was considerably less than either the replication or within-week variance. This result was gratifying yet hardly surprising since the technique employed is standard for most plankton surveys. However, more information (smaller confidence limits) can be obtained for weekly estimates of abundance by sampling more days of the week and eliminating the within-day replication, except perhaps during that time of the year when day-night changes in light are pronounced. For most organisms, samples taken at 1500 hrs. were not different ($\underline{P} < 0.05$) from collections made at other times of the day. Wind mixing in the shallow water and the absence of a marked diurnal cycle in incoming radiation operate to increase the homogeneity of organisms in the water column and supress variations in day-night distribution patterns often characteristic of lower latitudes.

Although the question of how representative samples taken adjacent to the NARL facility were of the general nearshore coastal area was only superficially examined, the evidence on hand indicates that for most organisms no differences in abundance can be detected between this location and others that were visited. Rather, the few samples obtained from further offshore suggest that most major gradients in numbers and community composition probably run perpendicular to the coast.

With regard to data analysis, it should be noted that a logarithmic transformation of counts does result in geometric averages which are negatively biased compared with arithmetic means of the same data. However, aside from preparing counts of animals in a format acceptable for analysis of variance, most workers feel that geometric averages are probably more representative than arithmetic information simply because the former are less affected by the occasional very high or low values that are characteristic in all plankton count data.

4.2.2 Laboratory Studies

Several potential sources of error are associated with the behavior of radioactive labels used in biological research. Investigations of the consumer organism must consider such problems on both the phytoplankton and zooplankton levels.

A major problem to be considered in using radioactive tracers in the study of the feeding biology of grazing zooplankton is the possibility of non-uniform labelling of the algal culture, resulting in inaccurate estimates of ingestion rates. This possibility was early recognized in this study and necessary precautions were taken by incubating the algal cultures for long periods of time in a concentration of label they could not possibly deplete. The calculation of filtration rates by zooplankters assumed a homogeneous distribution of cells in the feeding jar during the experimental period. Deviations from this distribution, such as would occur through sinking, would certainly have the effect of introducing errors in estimation. However, the possibility was thought to be at least partially obviated by periodically shaking the feeding jars during experiments.

The assumption of a strictly unialgal culture in estimating cell density could have led to underestimation of ingestion rates. Settings on the Coulter Counter were adjusted to count only a restricted size range based on this contention. This assumption indeed appeared to be valid, however, as the projected size-frequency distribution observed on the counter oscilloscope showed only slight deviations from the mean cell size.

The specific activity retained on filter paper from the filtration of radioactive phytoplankton has been reported to be inversely proportional to the volume filtered (Arthur and Rigler, 1967). This would result in increasing the filtrate activity and decreasing the calculated ingested activity, which was determined by differences in the filter paper activity measured at the beginning and completion of the experiments. No procedures were taken to allow for this possibility. The very "hot" cultures used in this study were perhaps less sensitive to such errors than would be weakly labelled cultures, if indeed errors did exist.

Incomplete removal of defecated material would have the effect of giving very high assimilation efficiencies. Significant errors in this regard would probably only be associated with diffusely egested material, as intact faecal pellets were clearly visible.

The measurement of the activity of the individual organism was used as an index of growth. Self-absorption problems were probably slight since organisms were thoroughly solubilized and were counted using efficient liquid scintillation techniques.

4.3 Future Plankton Research

Annual observations on the phytoplankton community have been conducted in the nearshore environment off Barrow for several years. Year round investigations on the zooplankton community should be undertaken concurrent with research on the phytoplankton to establish yearly distributions of the fauna and to define interactions in the plankton community as a whole. Only seasonal information exists to date on the dynamics of the zooplankton community, with very little research conducted during the winter months. Hydrographic measurements, including temperature, salinity, and nutrient concentrations, should continue to be taken along with investigations of the biota. Field sampling should be expanded to include the more offshore areas, with coincident investigations of the zooplankton elements for comparisons of community structure and dynamics. Sampling effort in the field should be most intensive during the dynamic summer period, when the short term temporal variability is expected to be most pronounced.

A more extensive study of life histories and spawning periods is necessary so that abrupt changes in abundance of particular species can be assessed with more certainty. Future research should include effort toward describing the presently little known microconstituents of the zooplankton and estimates made of their relative contribution to the total animal plankton biomass and community productivity. Biomass as determined from direct water samples should accompany estimates based on the net-caught community "biomass."

Continued research is proposed in the field of quantitative trophic dynamics, to include estimates of the efficiency of energy transfer through the pelagial and the definition of major pathways of energy flow in the nearshore system.

Efforts should be made toward estimating secondary productivity at specific times, applying the results of integrated research in both the laboratory and the field with the intent of establishing possible relationships between laboratory measured requirements and energetics and community dynamics observed in the field. An important component required in field estimates of secondary production is a knowledge of mortality rates at several levels of development for a particular species, a project necessarily involving a sampling program designed to include all such stages.

More intensive examination of the possible ecological repercussions of selective feeding and interspecific competition for available food sources are also needed. The relative importance of detritus as an energy source for the inshore zooplankton community at Barrow should receive considerable attention. Johnson postulates that in addition to the local organic production in arctic areas of the northern Chukchi Sea and central basin, a considerable amount of particulate food matter must be advected into the higher latitudes through the Bering Strait by the northward flowing current. Parsons and Strickland (1962) found large quantities of detritus in the northeast Pacific Ocean in the form of faecal pellets, fibers and animal chitin, and consider it a potential source of food for marine consumers. The role of animal material in the diet of zooplankton commonly thought to be "classic grazers" should also receive attention.

CHAPTER 5. SUMMARY

The composition and quantitative variability of the inshore marine zooplankton community near Point Barrow, Alaska, were investigated from May 25 to August 28, 1972. In addition, laboratory trophic studies were conducted as a supplement to field investigations. The objectives of this research were (1) to describe the pattern of temporal variability in species abundance and the composition and standing stock of the summer inshore zooplankton community; (2) to examine the relationship of this variability to the local hydrography and phytoplankton community; (3) to study life histories, associations, and periods of recruitment for dominant members; and (4) to investigate the bioenergetics and feeding biology of grazing zooplankton in the laboratory.

Zooplankton were collected from horizontal hauls both under the ice and in open water conditions. Replicate tows were taken on most sampling dates; 107 samples were examined. Animals were subsampled for estimates of numbers, identified, sized, and enumerated within distinct taxonomic categories.

Numbers of organisms per 100 m^3 were transformed logarithmically, with sums of squares for analysis of variance and comparison of geometric means generated by an IBM 360 computer. Data were grouped into calendar weeks for the analysis of variance. Upper percentage confidence limits were determined about three levels of sampling for comparison of variability associated with these levels. Subsampling, replication, and within-week error were compared and, in all cases, the error associated with subsampling was less than that for the other two levels; replication error was usually smaller than within-week error. Differences in weekly mean abundances for 30 categories of zooplankton were tested using the F-statistic, with 29 of 30 categories showing significant temporal variability over the summer ($\underline{P} < 0.05$). Tests of both diel and spatial effects on the abundance of organisms showed no significant differences in numbers in the majority of cases ($\underline{P} < 0.05$).

Forty-six categories of zooplankton on several taxonomic levels were analyzed. The copepods were the major community constituents in terms of both biomass and species diversity. Hydromedusae were the second most diverse assemblage of organisms. Chaetognaths and barnacle larvae were additional major summer constituents in terms of numbers and biomass. The meroplankton were a very significant component of the inshore zooplankton community. The Barrow community can be differentiated into fauna characteristic of the Bering Sea, and fauna commonly found in the Chukchi and Beaufort Seas.

The intrusion of Bering Sea water into the Point Barrow area, as evidenced by the presence of several expatriate copepods and hydromedusae, as well as the warmer water temperatures, imposes a marginally subarctic condition on the zooplankton community with respect to diversity and productivity. The presence of large numbers of meroplankton especially reflects this condition and is further suggested by the short developmental period observed for the barnacle larvae. The temporal patterns of distribution recorded for many organisms were highly influenced by this dynamic hydrographic regime. Biological processes probably play a more significant role than do advective processes in influencing the distributions of fauna characteristic to the Chukchi and Beaufort Seas.

Continuous breeding populations from Barrow to the Bering Sea appear to exist for several neritic copepods and hydromedusae taken in the collections. Some holoplankton, such as the copepod *Calanus glacialis*, seem to exhibit one-year life cycles characteristic of subarctic areas. *Sagitta elegans* and *Thysanoëssa raschii*, however, appear to be characterized by polyphasic, or two-year life cycles. Active breeding during the summer was also noted for the holoplanktonic scyphozoans, polychaetes, amphipods, appendicularians, and fishes. Recruitment of meroplanktonic larvae was extensive and was well correlated to peaks in the available food supply.

The zooplankton community biomass was an order of magnitude higher than that reported for a similar period in the central arctic; the relatively significant contribution of the meroplankton is proposed as an explanation. The summer plankton community at Barrow exists in an unbalanced state, such that the periods of high zooplankton standing stock lag one to two weeks behind the phytoplankton peaks.

Laboratory trophic studies involved investigations of the feeding biology of grazing zooplankton fed ^{14}C-labelled algae and the examination of the relative apportionment of ingested energy into several parameters. Parameters estimated included assimilation and gross growth efficiency, filtration and ingestion rates, and metabolic losses. It was desirable to attempt to access the impact of grazing zooplankton on the natural phytoplankton community based on laboratory measurements of these critical indices.

Experiments ran either 4 or 24 hours, under varied conditions of algal composition and concentration. Assimilation efficiency was usually high for most species, generally 70 to 85 percent. Metabolic losses accounted for the majority of assimilated energy, but a considerable amount of carbon was at times diverted into the growth of the organism. The results obtained for the Bering Sea expatriate species, *Calanus plumchrus* V, indicated active feeding in the Barrow area. The daily ration determined for *Calanus glacialis* V was 1.0 to 1.3 percent of dry body weight. *Pseudocalanus minutus* females appeared to necessitate 5 to 6 percent of dry body weight daily. Secondary production for these species was very low in comparison to the primary production and it appears unlikely that these copepods could effectively regulate fluctuations in the plant standing crop. The extremely high concentration of barnacle larvae found in mid-June, however, could conceivably impose such grazing pressure as to act in a regulatory capacity. The grazing community seemingly ingests only a small fraction of the total carbon fixed by the phytoplankton during the summer, most being lost to the pelagic system by sinking. It would appear that the plankton community in the shallow inshore environment adjacent to Barrow is very inefficient in this regard.

Future research is urged in both the areas of laboratory trophic investigations and field studies. Year round studies of the zooplankton community, including the microconstituents, are needed. Life histories should be more extensively examined to account for abrupt population fluctuations. Field sampling should be expanded to include an examination of the more offshore elements coincident with investigations of the inshore fauna for comparison of community structure. More extensive research in the field of quantitative trophic dynamics is urged, including estimates of the efficiency of energy transfer through the pelagial and the definition of major pathways of energy flow in the nearshore system. Efforts toward estimating secondary productivity should integrate research in both the laboratory and the field, directed with the intent of establishing possible relationships between laboratory measured energetics and population dynamics observed in the field.

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APPENDIX I

Abundance of zooplankton categories/m^3 as sampled near Point Barrow from May 25 to August 28, 1972. The values calculated for each of the replicate tows are included under each sample date and are separated by a hyphen.

COPEPODA	1.	*Acartia* spp.
	2.	*Calanus glacialis*
	3.	*Calanus cristatus*
	4.	*Calanus hyperboreus*
	5.	*Calanus plumchrus*
	6.	*Centropages abdominalis*
	7.	*Eucalanus bungii bungii*
	8.	*Euchaeta* sp.
	9.	*Eurytemora herdmanni*
	10.	*Metridia longa*
	11.	*Oithona similis*
	12.	*Pseudocalanus minutus*
	13.	*Tortanus discaudatus*
	14.	copepod nauplii
CHAETOGNATHA	15.	*Sagitta elegans arctica*
CIRRIPEDIA	16.	*Balanus* nauplii larvae > 0.308 µm
	17.	*Balanus* nauplii larvae < 0.308 µm
	18.	*Balanus* cyprid larvae
HYDROZOA	19.	*Aeginopsis laurentii*
	20.	*Aglantha digitale*
	21.	*Bougainvillea superciliaris*
	22.	*Euphysa flammea*
	23.	*Leuckartiara* sp.
	24.	*Obelia longissema*
	25.	*Rathkea octopunctata*
SCYPHOZOA	26.	*Aurelia aurita*
	27.	*Cyanea capillata*
AMPHIPODA	28.	Gammaridae
	29.	Hyperidae
DECAPODA	30.	Crab zoea larvae
	31.	Juvenile shrimp
MYSIDACEA	32.	*Mysis oculata*
POLYCHAETA	33.	Pelagic larvae
PTEROPODA	34.	*Clione limacina*
	35.	*Limacina helicina*
CTENOPHORA	36.	Combined species
OSTRACODA	37.	*Conchoecia* sp.
	38.	*Evadne nordmanni*
	39.	*Podon leukarti*
APPENDICULARIA	40.	*Oikopleura* sp.
	41.	*Fritillaria borealis*
ECHINODERMATA	42.	Pelagic larvae
EUPHAUSIACEA	43.	*Thysanoëssa raschii* juveniles
	44.	Nauplii and calyptopid larvae
PISCES	45.	Larval and juvenile fishes

DATE TIME	25 May 0900	27 May 0900	27 May 1600	129 May 1600
1.	3.41	71.25	5.26-8.90	13.64-15.42
2.	3.41	0.01	0.30-0.30	0.42-0.54
3.	.	.	.	.
4.	5.0	0.3	1.68-1.19	0.54-0.43
5.	.	.	.	.
6.	.	.	.	.
7.	.	.	.	.
8.	0.45	0.25	0.79-0.59	1.19-5.57
9.	.	.	.	.
10.	0.34	0.06	0.59-0.20	0.43-0.43
11.	3.41	2.48	1.30-2.23	10.9-5.14
12.	415	188	234-200	504-487
13.	.	.	.	.
14.	.	.	.	.
15.	1.82	0	3.70-2.37	7.25-8.20
16.	.	.	.	+
17.	.	.	.	.
18.	.	.	.	.
19.	0.1	0.07	0-0.1	0.4-0.2
20.	0.11	0.18	1.28-1.48	0.43-0.76
21.	.	.	.	.
22.	.	0.1	0.8-0.3	0-0.1
23.	0.11	0.06	1.28-4.45	0.76-0.34
24.	.	.	.	.
25.	.	.	.	.
26.	.	.	.	.
27.	.	.	.	.
28.	.	0.06	.	0.22-0
29.	0.11	.	0.20-0.10	0.43-0
30.	10.23	0.18	7.9-4.5	6.05-8.5
31.	.	.	.	.
32.	.	0.1	.	.
33.	6.82	5.56	0.50-1.73	0.65-0.43
34.	0.61	0.20	.	.
35.	0.61	.	0-0.2	0.23-0.18
36.	0	.	0.1-0	0.2-0.1
37.	10	0.2	4-1	1-0.2
38.	.	.	.	.
39.	.	.	.	.
40.	.	0-2	0.1-0.1	0.32-0.22
41.	.	.	.	.
42.	.	.	.	.
43.	.	.	.	0.11-0.33
44.	.	.	.	.
45.	.	0.06	0.10-0	.

DATE TIME	1 June 1600	5 June 1539	8 June 1100	12 June 1530
1.	13.34-7.11	2.34-2.21	10.85-447	7.34-2.05
2.	0.6-0.59	0.401-0.134	0.103-0.05	0.32-0.494
3.	.	.	.	.
4.	0.49-0.40	0.13-0.13	0-0.10	.
5.	.	.	.	.
6.	.	.	.	.
7.	.	.	.	.
8.	0.30-1.09	0.13-0.13	0-0	.
9.	.	.	.	.
10.	0.0	0.13-0.13	0.10-0	.
11.	2.3-7.11	2.34-13.4	1.19-1.11	4.52-13.03
12.	517-402	122-321	242-229	355-327
13.	.	.	.	.
14.	.	.	.	7.2-7.2
15.	6.62-8.90	39.4-115	7.33-7.75	6.1-8.4
16.	31-30	8.6-94	130-116	1298-1460
17.	94-93	17-187	195-175	1948-2192
18.	.	.	.	.
19.	0.9-0.7	0.93-1.2	0.1-0.4	0.1-0
20.	0.99-0.99	2.1-2.3	0.21-0.72	0.49-1.09
21.	.	.	.	.
22.	0.1-0	0.2-0.8	0.1-0	.
23.	0.10-0.10	0.40-0.27	0.1-0.21	0.10-0.10
24.	.	.	.	.
25.	.	.	.	.
26.	.	.	.	.
27.	.	.	.	.
28.	0.10-0.3	0.2-0.27	0.1-0.62	0.1-1.09
29.	0.40-0.20	0.13-0.4	0-0.1	.
30.	8.92-10.7	14.1-49	19.4-18	44.5-54
31.	.	0.40-0	0.21-0.62	0.49-0.10
32.	.	.	.	.
33.	13.35-3.66	2.34-26.7	10.8-13.4	118-196
34.	0.1-0.2	.	0.10-0.3	0.1-0.3
35.	0.1-0	0-0.27	0-0.1	0-0.1
36.	0.1-0.2	0.2-1.7	0.1-0.3	0.1-0.3
37.	0.1-0	0.1-0.1	.	.
38.	.	.	.	.
39.	.	.	.	.
40.	0.25-0.18	0-0.13	0.1-0.1	0.1-0
41.	.	.	.	.
42.	.	.	.	.
43.	.	0.67-0.5	.	.
44.	.	.	.	14.7-10.1
45.	.	0.13-0	0-0.10	0.10-0.4

DATE TIME	12 June 2130	15 June 1030	17 June 1600	20 June 1630
1.	1.0-1.0	2.0-2.0	5.30-4.0	3.50-2.09
2.	0.56-0.36	0.464-0.45	.	.
3.	.	.	.	.
4.	.	.	.	.
5.	.	.	.	.
6.	.	.	.	.
7.	.	.	.	.
8.	.	.	.	.
9.	.	.	.	.
10.	.	.	.	.
11.	2.10-1.56	17.27-19.55	22.3-4.90	2.09-4.17
12.	119-86	86-216	222-245	177-92
13.	.	.	.	.
14.	3.18-304	9-39	12.6-15	3.2-4.1
15.	5.73-5.82	3.20-4.09	4.55-5.45	40-73
16.	302-252	414-1641	7721-7948	1810-2250
17.	455-403	8636-3284	15442-15896	1811-2250
18.	.	.	.	.
19.	.	.	.	.
20.	7.45-7.45	5.00-4.54	0.91-2.27	0.72-6.10
21.	.	.	.	.
22.	0.1-0	.	.	0.2-0
23.	0.10-0.05	0.30-1.36	0.0	0.10-0.12
24.	.	.	.	.
25.	.	.	.	.
26.	.	.	.	.
27.	.	.	.	.
28.	0-0.1	0.91-1.36	0-0.45	0.12-0
29.	0-0.1	0-0.45	.	.
30.	12.7-18.5	2.7-3.2	29.4-21.3	31.3-52.3
31.	1.64-0.91	1.36-0	2.73-5.45	0.36-3.11
32.	.	.	.	.
33.	89-235	16-98	445-293	565-775
34.	0-0.09	.	0-0.91	.
35.	0-0.09	0-0.45	.	.
36.	4.4-1.8	0-0.2	.	0.4-0
37.	.	.	.	.
38.	.	.	.	.
39.	.	.	.	.
40.	.	.	0.45-0	.
41.	.	.	.	.
42.	.	.	.	.
43.	0.82-0.17	.	.	0-0.36
44.	3.2-30.4	8.6-39.1	8.1-10.3	1.7-2.3
45.	0.18-0.27	.	.	0.24-0.36

DATE TIME	23 June 1400	26 June 1000	26 June 1545	27 June 1400
1.	2.50-1.75	2.61-13.24	5.15-10.45	9.20-10.12
2.	21.90-5.54	27-45	58-65	45-23.4
3.	.	.	.	.
4.	.	.	.	.
5.	.	.	.	.
6.	.	.	.	.
7.	.	.	.	.
8.	.	.	.	.
9.	.	.	.	.
10.	.	.	.	.
11.	2.50-2.50	2.61-3.31	7.72-11.6	5.48-4.40
12.	227-136	62-235	190-163	143-141
13.	.	.	.	.
14.	16.4-1.7	10-5	10.4-8.2	13.2-15.3
15.	157-9.3	1.47-3.07	4.95-4.81	4.95-4.14
16.	2215-988	136-326	261-338	195-205
17.	2215-990	78-184	197-255	65-68
18.	.	.	.	1.4-1.35
19.	0.1-0.1	.	.	0.1-0
20.	1.41-2.72	0.27-0.53	1.07-1.60	1.34-1.60
21.	.	.	.	0.13-0.10
22.	0.1-0	.	.	0.1-0
23.	1.41-0	0-0.40	0.94-1.74	3.61-4.28
24.	.	.	.	.
25.	.	.	4.95-5.08	.
26.	.	.	.	.
27.	.	.	.	.
28.	0.43-0.32	0.3-0.1	0.67-0.40	0.67-0.67
29.	0.32-0.21	0.1-0	.	0.13-0.13
30.	44.5-57.7	15.64-33	36-14.5	60.1-44.5
31.	0.87-2.71	1.20-3.35	5.21-6.68	10.7-11.4
32.	.	.	.	.
33.	96-108	28-172	293-320	275-218
34.	.	.	.	.
35.	.	0-0.13	+	0.05-0.1
36.	0.9-0.4	0.2-0.1	0.2-0.1	0.4-0.3
37.	.	.	.	.
38.	.	.	.	.
39.	.	.	.	.
40.	.	.	.	.
41.	.	.	.	.
42.	.	.	.	.
43.	0.87-0.97	0.13-0.67	2.27-3.34	0.40-0.32
44.	8.2-0.7	6.2-7.1	5.4-3.7	2.1-3.0
45.	1.30-0.5	0-0.54	0.80-0.80	1.55-1.47

DATE TIME	28 June 1400	8 July 1530	10 July 0945	11 July 1130
1.	9.34-1.25	1.38-1.38	0.78-0.78	0.74-0.78
2.	96-82	75-63	398-495	20-126
3.	.	.	.	.
4.	.	.	.	.
5.	.	0.33-0.19	0.03-0.02	0.17-0.13
6.	.	.	.	.
7.	.	0.06-0.05	0.02-0.01	0.01-0.01
8.	.	.	.	.
9.	.	.	.	.
10.	.	.	.	.
11.	3.08-3.95	1.70-1.70	0.79-0.39	0.48-1.83
12.	140-135	54-56	122-170	25-86
13.	.	.	.	.
14.	24-11.7	37.5-79.2	23.6-19.3	9.8-15.7
15.	16.10-0.89	4.52-10.4	8.27-3.94	1.59-1.86
16.	1422-2005	1181-351	4090-3225	18-146
17.	222-313	234-48	+	0.26
18.	18.7-7.9	58-5.3	200-162	39-60
19.	0-0.2	.	0-0.01	.
20.	2.27-3.88	1.23-0.11	0.54-0.42	0.02-0.01
21.	0.13-0.10	0.03-0.01	0.05-0	0.01-0
22.	.	0-0.01	0.01-0	.
23.	10.23-11.50	0.11-0.05	0.32-0.10	0-0.02
24.	.	.	.	.
25.	.	0.06-0.01	0.04-0.77	1.23-1.31
26.	.	.	.	.
27.	0.25-0.12	.	0.05-0.01	.
28.	0.88-0.13	0.01-3	0.05-0	0.14-0.01
29.	0.38-0.13	0.03-0.01	0.03-0	0.30-0.01
30.	42-102	2.7-1.0	3.6-1.8	0.69-0.3
31.	6.44-4.28	0.03-0.01	0.65-0	0.01-0
32.	.	.	0.01-0	.
33.	355-395	58-71	118-135	12-58
34.	.	.	0.01-0	.
35.	.	0.23-0.23	16-11.6	2.8-0.3
36.	1.1-0.8	0.13-0.02	0.02-0	0.01-0.01
37.	.	.	.	.
38.	.	.	.	.
39.	.	.	.	.
40.	.	.	.	.
41.	.	.	.	.
42.	.	.	.	.
43.	0.25-3.88	0.02-0	0.63-0	.
44.	4-2.1	.	.	.
45.	0.88-0.8	0.11-0.06	0.58-0	0.23-0.03

DATE TIME	12 July 1600	12 July 1630	14 July 1430	16 July 1300
1.	1.06-0.82	0.18	2.81-1.62	1.48-2.36
2.	157-85	1.45	30-18.4	39-25
3.	.	.	.	+
4.	.	.	.	.
5.	0.08-0.03	0.08	0.06-0.05	0.08-0.19
6.	.	.	.	.
7.	.	.	.	.
8.	.	.	.	.
9.	.	.	.	.
10.	.	.	.	.
11.	1.33-0.82	0.18	1.73-1.62	0.43-0.36
12.	108-63	8	84-80	48-33
13.	.	.	.	.
14.	60.9-27.3	.	7.42-6.9	5.75-3.45
15.	0.67-1.04	0.04	2.09-1.59	0.81-0.52
16.	28-668	9.45	10.8-3.7	242-8
17.	+	3.27	0.5-0	26.7-0.7
18.	28-172	0	9.9-3.7	65-8.7
19.	.	.	.	.
20.	0.25-0.28	.	0.01-0.01	0.18-0.01
21.	0.02-0.02	.	0.02-0.01	0.02-0
22.	.	.	.	.
23.	0.03-0.08	.	0-0.01	0.02-0
24.	.	.	.	.
25.	0.80-0.01	0.05	0.22-0.20	0.03-0
26.	.	.	.	.
27.	.	.	.	0.01-0
28.	0.23-0	.	0.23-0.05	0-0.06
29.	.	0.01	0.01-0.01	0.02-0.05
30.	0.1-0.27	1.09	0.1-0.11	0.1-0.18
31.	.	0.01	.	0.01-0
32.	0.01-0	.	.	.
33.	30-60	15	26-19.7	40-7.4
34.	.	.	.	0-0.01
35.	0.11-0.14	.	0.1-0.28	0.05-0.14
36.	0.01-0.06		0.01-0	0.04-0
37.	.	.	.	.
38.	.	.	.	.
39.	.	.	.	.
40.	.	.	.	.
41.	.	.	25.5-16.2	0.2-0
42.	.	.	.	.
43.	0.03-0	.	.	0.02-0
44.	.	.	0.23-0	0.93-0.55
45.	0.02-0.2	.	0.04-0.04	0.04-0.07

DATE TIME	17 July 1030	19 July 1600	19 July 1630	22 July 1230
1.	1.43-0.97	1.94-2.05	5.98-	0.62-1.01
2.	107-106	64-65	126	33-20
3.	.	.	.	.
4.	.	.	.	.
5.	0.21-0.20	0.06-0.05	0.08	0.11-0.05
6.	.	.	.	.
7.	0.01-0	.	.	.
8.	.	.	.	.
9.	.	.	.	.
10.	.	.	.	.
11.	2.86-0.97	0.48-0.57	1.80	0.12-0.22
12.	125-120	144-65	85	12.3-10.1
13.	.	.	.	.
14.	1.82-0.5	1.45-1.14	1.80	4.83-0.81
15.	2.53-1.38	3.80-1.78	2.49	1.00-0.67
16.	5.10-1087	10-8.5	18	24.6-155
17.	51-71	0-0.73	.	3-20
18.	99-215	13.6-11	25	20.8-114
19.	.	.	.	.
20.	0.45-0.58	0.17-0.16	0.25	0.03-0.07
21.	0.08-0.05	0.02-0	0.01	0-0.02
22.	.	.	.	.
23.	0.08-0.11	0.01-0.04	0.04	0.01-0
24.	.	.	.	3.07-4.07
25.	0.95-0.80	0.50-1.48	4.43	9.85-7.82
26.	.	.	.	.
27.	0.01-0.02	0.03-0.01	0.04	0.16-0.05
28.	0.08-0.07	0.02-0.03	0.03	0.02-0.04
29.	0.05-0.07	0.03-0.02	0.02	0.02-0.03
30.	7.6-4.3	0.48-0.68	1.60	3.94-4.69
31.	1.67-1.45	0.02-0.01	0.01	0-0.17
32.	.	.	.	.
33.	11.5-12.1	11.8-3.07	4.8	94-94
34.	0-0.01	.	0.01	0.01-0.03
35.	0.24-0.20	0.39-1.53	1.27	3.36-3.16
36.	0.02-0.01	.	.	0.05-0.02
37.	.	.	.	.
38.	.	.	.	.
39.	.	.	.	.
40.	.	.	.	.
41.	.	.	+	+
42.	.	.	.	.
43.	0.36-0.46	.	0.01	0-0.05
44.	.	0.73-0.23	1.00	3.07-1.30
45.	0.07-0.07	0.47-0.10	0.04	0.19-0.35

DATE	23 July 1330	3 August 0930	3 August 1000	4 August 1400
1.	6.70-5.71	3.35-2.02	1.48	4.14-1.48
2.	21-27	0.52-0.2	2.55	7.88-1.6
3.	.	.	.	.
4.	.	.	.	.
5.	0.02-0	0.01	.	.
6.	.	1.03-0.21	0.85	0.98-0.57
7.	0.01-0	.	.	.
8.	.	.	.	.
9.	.	.	.	.
10.	.	.	.	.
11.	3.55-3.35	7.76-11.77	22.77	15.56-3.64
12.	12.6-11	2.6-1.2	1.70	7.09-1.14
13.	.	.	.	.
14.	0.15-1.1	0.1-0.1	0.84	0.23-0.33
15.	5.88-5.87	3.67-4.50	2.28	1.48-1.65
16.	215-262	2.9-2.6	2.23	.
17.	41.6-34.5	.	.	.
18.	553-455	12-3.7	0.64	5.91-0
19.	.	.	.	.
20.	0.22-0.06	1.50-2.67	2.86	18.32-9.59
21.	0.02-0.02	0-0	.	0.01-0
22.	.	.	.	.
23.	0.01-0	0.00-0.05	.	.
24.	3.07-4.07	0.41-1.38	.	.
25.	18.20-12.41	0.77-1.06	.	0-1.14
26.	.	.	.	.
27.	.	.	.	0-0.02
28.	0.02-0	0.01-0	.	.
29.	0.02-0.03	.	.	0.01-0
30.	0.20-0.39	.	.	0-0.11
31.	.	.	.	.
32.	.	.	.	.
33.	41-30	10-131	23	95-176
34.	0.02-0.01	.	0.04	0-0.02
35.	0.10-0.04	0-0.02	3.56	2.59-0.37
36.	0.01-0	0-0.02	0.01	0.03-0.02
37.	.	.	.	.
38.	.	.	.	.
39.	.	.	.	.
40.	0-0.4	0.01-0	0.02	.
41.	.	310-240	232	153-129
42.	.	.	.	.
43.	.	.	.	.
44.	1.30-4.1	0.15-0.7	.	.
45.	0.04-0.01	0.01-0.01	.	0-0.01

DATE TIME	4 August 1430	4 August 1500	5 August 0200	5 August 0230
1.	0.27	0.50	0.71-0.23	0.30
2.	2.77	6.10	0.55-0.59	+
3.	.	.	.	.
4.	.	.	.	.
5.	.	.	.	.
6.	0	0.27	0.15-0.12	.
7.	.	.	.	.
8.	.	.	.	.
9.	.	.	0.12-0.11	0
10.	.	.	.	.
11.	3.97	0.53	1.54-1.59	0.93
12.	5.30	0.80	1.15-1.23	+
13.	.	.	.	.
14.	26.50	0.26	0.70-0.76	.
15.	0.53	2.81	2.18-2.67	2.50
16.	26	88	239-113	503
17.	.	.	28-7.3	.
18.	46	93	134-62	233
19.	.	.	.	.
20.	4.38	32.88	0.31-1.00	0.92
21.	.	.	.	.
22.	.	.	.	.
23.	.	.	0.01-0	.
24.	5.30	.	0-0.23	.
25.	10.61	3.45	1.48-1.17	.
26.	.	.	.	.
27.	0.2	0.3	0.03-0.01	0.12
28.	.	.	0.02-0	0.17
29.	.	0.03	0.01-0	0.01
30.	5.3	2.12	0.83-1.8	0.31
31.	0.15	.	0.01-0.03	.
32.	.	.	.	.
33.	742-	472	42.3-76	149
34.	0.61	2.73	.	0.02
35.	0.05	0.05	0.12-0.02	1.24
36.	.	0.03	0.04-0.01	0.01
37.	.	.	.	.
38.	.	.	.	.
39.	.	.	.	.
40.	1.2	.	0.01-0.01	.
41.	212	.	.	.
42.	.	.	.	.
43.	.	.	.	.
44.	5.30	0.27	.	.
45.	.	0.04	.	.

DATE TIME	8 August 1500	9 August 2100	13 August 1300	14 August 1500
1.	1.19-2.25	9.45-11.88	8.48-6.73	16.50-6.01
2.	6.89-2.78	0.41-0.91	1.81-0.82	0.03-0.26
3.	.	.	.	.
4.	.	.	.	.
5.	.	.	.	.
6.	0.34-0.12	0.62-0.62	4.40-4.42	2.76-2.83
7.	.	.	.	.
8.	.	.	.	.
9.	0.33-0.12	0.31-0.31	1.12-1.15	0.27-0.53
10.	.	.	.	.
11.	0.89-0.48	0.40-0.93	7.16-5.38	6.97-4.77
12.	1.56-1.58	0.80-1.06	9.82-12.6	10.80-5.61
13.	.	.	+	.
14.	0.34-0.30	0.13-0.66	0.49-1.48	0.20-0.14
15.	0.45-0	0.40-0.80	0.31-1.13	0.32-0.30
16.	162-306	46-45	413-295	1803-561
17.	24.6-23	7.9-4.0	37-31	381-115
18.	23-68	82-68	152-187	355-124
19.	.	.	.	.
20.	4.06-5.79	13.96-8.85	1.45-1.93	21.30-8.30
21.	.	.	.	0.01-0
22.	.	.	.	.
23.	.	.	.	.
24.	.	0.27-0	0.20-0	0.91-0
25.	.	.	.	.
26.	0.02-0.01	0.02-0.03	0.01-0	0.01-0
27.	0.2-0.08	0.18-0.09	0.02-0.03	0.09-0.15
28.	0.01-0.01	0.023-0	.	0.02-0.02
29.	0-0.02	0.02-0	.	0-0.01
30.	0.34-0.24	.	0.40	0.15-0
31.	.	.	.	.
32.	0-0.01	.	.	.
33.	98-69	212-189	23-25	57.6-35
34.	0.02-0	0.01-0	.	0.01-0
35.	0.03-0	.	.	.
36.	0.01-0.02	0.03-0.03	.	.
37.	.	.	.	.
38.	.	.	.	+
39.	.	.	.	+
40.	.	.	.	.
41.	.	3.1-5.7	1.30-0	.
42.	.	.	.	.
43.	.	.	.	.
44.	.	.	.	.
45.	0.02-0.01	0.01-0.02	.	0-0.02

DATE TIME	16 August 2230	17 August 1130	19 August 1415	19 August 1515
1.	16.50-6.01	8.64-8.75	1.76-4.52	8.76-7.00
2.	0.03-0.26	0.02-0.03	0.35-0.75	1.10-0.34
3.	.	.	.	.
4.	.	.	.	.
5.	.	.	.	.
6.	2.00-0.31	3.10-1.01	0.20-0.40	0.42-0.31
7.	.	.	.	.
8.	.	.	.	.
9.	0.79-0.21	0.64-0.32	0.72-1.20	0.73-0.42
10.	.	.	.	.
11.	7.87-4.97	2.59-1.86	0.35-1.02	2.48-0.58
12.	1.02-1.31	1.15-1.06	0.35-0.87	0.92-0.58
13.	.	.	.	.
14.	0.15-0.26	0.14-0.14	0.16-0.09	1.05-0.14
15.	0.51-0.26	0.58-0.8	0.01-0.01	0.78-0.31
16.	26-39	552-224	56-44	13.6-29
17.	5.2-29	109-61	35-89	16-34
18.	64-73	135-121	111-224	152-155
19.	.	.	.	.
20.	65.48-39.47	16.70-14.05	14.44-21.5	15.3-4.81
21.	.	.	0-0.01	.
22.	.	.	.	.
23.	.	.	.	.
24.	.	10.36-6.89	0.12-1.17	0.65-0
25.	0.51-0.78	0.50-0.53	.	.
26.	0-0	.	.	.
27.	0.02-0.08	0.04-0.06	0.03-0.07	0.07-0.09
28.	0.06-0.02	.	.	.
29.	.	.	0.02-0	0.01-0.01
30.	.	.	.	.
31.	.	0.08-0	.	.
32.	.	.	.	.
33.	7.7-2.6	2.30-1.06	0.47-0.44	2.35-1.68
34.	.	.	.	.
35.	0-0.26	.	.	+
36.	0-0.01	.	0-0.01	.
37.	.	.	.	.
38.	+	0.29-0.29	0-0.1	0-0.15
39.	+	0.29-0.29	0.23-0.29	0.13-0.44
40.	.	.	.	.
41.	50-67	12-42	0.5-2	0.1-0.44
42.	.	0-0.27	.	.
43.	0.01-0	.	.	.
44.	.	.	.	.
45.	0.01-0	.	0.01-0	0-0.01

DATE TIME	19 August 1630	21 August 0945	23 August 1500	23 August 1515
1.	1.13-1.05	35.64-45.09	42.0-45.08	25.45-
2.	0.43-0.27	0.43-0.47	0.50-0.53	0.24
3.	.	.	.	.
4.	.	.	.	.
5.	.	.	.	.
6.	0.08-0.07	1.20-2.40	0.08-0.56	0.04
7.	.	.	.	.
8.	.	.	.	.
9.	0.48-0.31	0.50-1.20	0.38-1.25	0.08
10.	.	.	.	.
11.	0.56-0.13	2.83-1.41	1.33-1.77	0.85
12.	0.56-0.23	1.27-2.79	1.67-3.54	0.61
13.	.	0.14-0.31	0.14-0.14	0.12
14.	0.22-0.10	0.08-0.10	0.15-0.11	.
15.	0.45-0.10	0.99-1.45	0.40-0.49	0.15
16.	3.1-1.6	516-525	561-902	250
17.	7.1-1.8	526-445	415-397	19.4
18.	68-50	383-412	102-49	84.5
19.	.	.	.	.
20.	11.8-8.63	2.60-4.52	0.37-2.09	1.65
21.	.	.	.	.
22.	.	.	.	.
23.	.	.	.	.
24.	.	0.85-0.63	.	.
25.	.	.	.	.
26.	.	0.01-0	0-0	.
27.	0.14-0.10	0.01-0.01	0.12-0.12	0.04
28.	0.11-0.10	.	.	.
29.	0.08-0.15	.	.	0.02
30.	.	.	0.15-0	.
31.	.	.	.	.
32.	.	.	.	.
33.	0.67-0.26	4.24-3.29	0.25-0.18	.
34.	.	.	.	.
35.	.	.	.	.
36.	0.02-0	.	.	.
37.	.	.	.	.
38.	0.11-0.09	0.21-0.47	0.50-0.71	0.36
39.	0.34-0.17	0.21-0.47	1.00-1.24	0.61
40.	.	.	.	.
41.	0.45-0.26	1.9-1.88	2.5-2.1	+
42.	.	0-0.25	.	.
43.	.	.	.	.
44.	.	.	.	.
45.	0-0.01	.	0.08-0	0.03

DATE TIME	26 August 2015	28 August 0930	28 August 1530	28 August 2330
1.	27.35-25.61	9.14-2.91	3.75-6.30	63.33-60.0
2.	1.33-1.11	0.25-0.25	0.25-0.24	0.22-0.27
3.	.	.	.	.
4.	.	.	.	.
5.	.	.	.	.
6.	0.36-0.57	0.60-0.82	0.50-0.10	4.00-5.50
7.	.	.	.	.
8.	.	.	.	.
9.	0.36-0.57	0.31-0.41	0.23-0.05	0.67-1.39
10.	.	.	.	.
11.	6.91-10.39	15.23-19.20	4.25-3.39	4.00-2.12
12.	2.59-1.86	2.28-0.49	0.25-1.94	3.3-1.59
13.	.	.	.	0-0.53
14.	0.43-0.93	.	0.17-0.10	.
15.	0.58-0.82	0.20-0.25	0.50-0.30	1.01-1.10
16.	209-227	2970-2672	2030-1928	1742-1145
17.	101-91	6151-4047	3249-2994	2230-2018
18.	92-133	451-530	144-197	146-128
19.	.	.	.	.
20.	17.56-12.62	72.59-67.76	29.50-19.39	24.67-44.02
21.	.	.	.	.
22.	.	.	.	.
23.	.	.	.	.
24.	.	0.25-0	.	0-0.33
25.	.	.	.	.
26.	.	0.01-0	0.03-0.01	0-0.01
27.	0-0.03	0.06-0.05	0-0.03	0-0.06
28.	.	.	.	0-0.01
29.	.	0.01-0.01	0.01-0	0.01-0
30.	.	.	.	.
31.	.	.	.	.
32.	.	.	.	.
33.	0.58-2.04	7.11-7.30	3.00-2.42	34.09-25
34.	.	.	.	.
35.	0-6.15	.	.	.
36.	.	.	.	.
37.	.	.	.	.
38.	1.44-2.23	56.7-43	76.1-48.5	88.6-98
39.	3.37-5.57	38.64-37.50	25.38-58.2	40.9-70.9
40.	.	.	.	.
41.	2.59-5.6	46-42	30-34	81-49
42.	0.86-1.13	123-100	213-964	487-272
43.	.	.	.	.
44.	.	.	.	.
45.	0.02-0.01	0.05-0.03	0.01-0.02	.

DATE	28 August
TIME	0630
1.	25.91-37.52
2.	0.33-0.23
3.	.
4.	.
5.	.
6.	1.75-1.25
7.	.
8.	.
9.	0.40-0.17
10.	.
11.	1.08-0.57
12.	1.08-0.85
13.	.
14.	.
15.	0.04-0.28
16.	1327-2304
17.	2267-4313
18.	35.5-79
19.	.
20.	6.89-5.62
21.	.
22.	.
23.	.
24.	0-0.57
25.	.
26.	.
27.	0.01-0.01
28.	.
29.	.
30.	.
31.	.
32.	.
33.	6.72-6.53
34.	.
35.	.
36.	.
37.	.
38.	68-74.9
39.	68.2-57.6
40.	.
41.	22-17
42.	6.8-5.2
43.	.
44.	.
45.	.

APPENDIX II

Phytoplankton cellular activity in control jar at beginning (t_o) and end (t_1) of the experimental period; phytoplankton cellular activity in the zooplankton feeding jar at time t_1; initial filtrate activity; filtrate activity in the phytoplankton control jar at time t_1; filtrate activity in the zooplankton feeding jar at time t_1; zooplankton body activity; and faecal pellet activity as measured during five trophic experiments employing radioactive tracers. All values listed are in disintegrations per minute (DPM).

Included are formulae used for the calculation of ingested activity, filtration rates, and assimilation and gross growth efficiency for zooplankton grazing on ^{14}C-labelled phytoplankton.

	Phyto cells, t_0	Phyto cells, t_1	Zoopl jar cells, t_1
Experiment 1			
Group 1			1,938,297
" 2	2,104,314	2,113,735	2,013,226
" 3			1,888,339
Experiment 2			
Group 1			31,088
" 2			73,940
" 3	94,640	85,890	71,451
" 4			73,747
" 5			72,231
Experiment 3			
Group 1			48,176
" 2			38,332
" 3			35,174
" 4	41,841	47,459; 50,994	39,910
" 5			41,427
" 6			29,227
" 7			23,068
" 8			34,218
Experiment 4			
Group 1			447,341
" 2			337,626
" 3			333,498
" 4	615,093	470,009	396,343
" 5			439,671
" 6			309,410
" 7			316,546
Experiment 5			
Group 1			16,461
" 2	21,874	18,925	14,156
" 3			9,542

Filtrate, t_o	Filtrate phytopl, t_1	Filtrate, zoopl, t_1	Zoopl Body	Faecal pellets
		175,400	92,842	4,921
185,008	128,950	134,823	3,677	7
		173,407	32,577	1,996
		12,900	702	0
		12,950	1,844	0
1,910	8,950	18,050	2,020	28
		12,900	4,589	126
		21,900	83	0
		180,500	--	0
		170,000	8,031	340
		178,750	9,326	502
217,861	189,700	187,400	7,266	424
		182,400	7,564	313
		187,850	14,310	403
		88,600	531	0
		--	2,897	0
			4,358	
			2,508	
NOT MEASURED	NOT MEASURED	NOT MEASURED	4,915	NOT MEASURED
			7,745	
			4,898	
			13,796	
			13,327	
NOT MEASURED	NOT MEASURED	NOT MEASURED	1,476	NOT MEASURED
			1,106	
			3,077	

List of Formulae

(1) ingested activity (I) = $DPM_{t\ phyto} - DPM_{t\ zoopl}$

(2) filtration rate (ml/amin/day) = $\frac{I}{n \cdot t \cdot DPM/ml\ phyto}$

(3) percent assimilation efficiency (AE) =

$$\frac{I-(R+E+G)}{I} \times 100$$

or

$$\frac{I-F}{I} \times 100$$

(4) gross growth efficiency (GGE) =

$$\frac{G}{I} \times 100$$

where:

$DPM_{t\ phyto}$ is the phytoplankton cellular activity in the control jar at time t

$DPM_{t\ zoopl}$ is the similar activity from the zooplankton experimental jar

n is the number of zooplankton in the experimental jar

t is the experimental time in days

DPM/ml phyto is the activity per ml of phytoplankton culture

R + E is zooplankton respiratory and excretory losses

G is zooplankton bodily activity, and

F is egested or faecal pellet activity

APPENDIX III

Simple correlation matrix between 28 categories of zooplankton, surface water temperature, average water column salinity, and chlorophyll *a* from May 25 to August 28, 1972. Data were entered as weekly means for each parameter.

<u>List of Variables in Correlation Matrix</u>

Pseudocalanus minutus	1
Calanus glacialis	2
Acartia spp.	3
Oithona similis	4
Podon leukarti	5
Evadne nordmanni	6
Clione limacina	7
Limacina helicina	8
Sagitta elegans arctica	9
Polychaete larvae	10
Chinocoetes zoea larvae	11
Fritillaria borealis	12
Balanus nauplii, >308 μm	13
Balanus cyprid larvae	14
Aglantha digitale	15
Thysanoëssa raschii	16
Zooplankton biomass	17
Fish larvae	18
Gammarid amphipods	19
Hyperid amphipods	20
Copepod nauplii	21
Centropages abdominalis	22
Eurytemora herdmanni	23
Shrimp juveniles	24
Paralithodes zoea larvae	25
Balanus nauplii, <308 μm	26
Leuckartiara sp.	27
Rathkea octopunctata	28
Temperature	29
Salinity	30
Chlorophyll *a*	31

CORRELATION MATRIX

VARIABLE NUMBER	1	2	3	4	5
1	1.000	0.202	-0.357	0.123	-0.595
2		1.000	-0.536	-0.513	-0.285
3			1.000	0.144	0.700
4				1.000	0.101
5					1.000
6					
7					
8					
9					
10					

6	7	8	9	10
-0.578	0.591	0.179	0.776	0.492
-0.279	-0.217	0.458	0.066	0.548
0.671	-0.286	-0.465	-0.365	-0.654
0.135	0.109	-0.433	0.293	-0.013
0.995	-0.432	-0.032	-0.551	-0.544
1.000	-0.420	0.006	-0.642	-0.516
	1.000	0.170	0.589	0.370
		1.000	-0.088	0.138
			1.000	0.469
				1.000

VARIABLE NUMBER	11	12	13	14
1	0.911	-0.836	-0.005	-0.800
2	0.246	-0.368	0.372	0.276
3	-0.394	0.357	-0.129	0.162
4	0.118	0.246	0.070	-0.529
5	-0.620	0.524	0.251	0.477
6	-0.604	0.519	0.249	0.463
7	0.677	-0.633	-0.006	-0.660
8	0.119	-0.316	0.056	0.238
9	0.832	-0.558	0.020	-0.841
10	0.693	-0.669	0.535	-0.349
11	1.000	-0.875	0.123	-0.808
12		1.000	-0.192	0.531
13			1.000	0.089
14				1.000
15				
16				
17				
18				
19				
20				

15	16	17	18	19	20
-0.528	0.521	0.597	0.525	0.764	0.770
-0.602	0.404	0.210	0.697	0.089	0.012
0.555	0.003	0.002	-0.340	-0.298	-0.104
0.597	0.014	0.240	-0.096	0.345	-0.010
0.622	-0.313	-0.029	-0.368	-0.475	-0.455
0.626	-0.305	-0.012	-0.350	-0.460	-0.444
-0.338	-0.058	0.443	0.056	0.497	0.493
-0.579	-0.064	0.022	0.287	0.068	0.297
-0.338	0.549	0.577	0.533	0.704	0.536
-0.253	0.418	0.594	0.615	0.557	0.200
-0.441	0.602	0.749	0.632	0.800	0.736
0.574	-0.462	-0.665	-0.535	-0.625	-0.638
0.214	0.133	0.535	0.377	0.274	-0.304
0.070	-0.362	-0.564	-0.229	-0.717	-0.601
1.000	-0.193	-0.008	-0.429	-0.198	-0.465
	1.000	0.559	0.861	0.609	0.561
		1.000	0.584	0.573	0.366
			1.000	0.651	0.476
				1.000	0.715
					1.000

VARIABLE NUMBER	21	22	23	24	25
1	0.275	-0.942	-0.751	0.671	0.902
2	0.790	-0.348	-0.372	0.298	0.085
3	-0.591	0.474	0.673	-0.271	-0.232
4	-0.059	-0.020	-0.059	0.334	0.236
5	-0.248	0.567	0.794	-0.387	-0.529
6	-0.237	0.585	0.766	-0.377	-0.519
7	-0.109	-0.460	-0.502	0.349	0.585
8	0.269	-0.279	-0.318	-0.163	-0.069
9	0.105	-0.757	-0.798	0.754	0.875
10	0.722	-0.498	-0.465	0.727	0.580
11	0.325	-0.868	-0.744	0.797	0.949
12	-0.375	0.769	0.540	-0.578	-0.784
13	0.654	-0.023	0.198	0.522	0.117
14	0.044	0.724	0.595	-0.672	-0.828
15	-0.262	0.575	0.705	-0.086	-0.263
16	0.271	-0.536	-0.411	0.707	0.654
17	0.353	-0.550	-0.290	0.784	0.757
18	0.535	-0.589	-0.570	0.743	0.564
19	0.341	-0.701	-0.564	0.827	0.800
20	-0.049	-0.707	-0.581	0.386	0.694
21	1.000	-0.361	-0.277	0.511	0.194
22		1.000	0.787	-0.662	-0.856
23			1.000	-0.499	-0.639
24				1.000	0.831
25					1.000
26					
27					
28					
29					
30					

	26	27	28	29	30
	0.145	0.811	-0.254	-0.949	0.423
	-0.051	0.109	0.491	-0.200	-0.462
	0.226	-0.125	-0.391	0.501	0.223
	0.265	0.194	-0.427	-0.062	0.418
	0.335	-0.453	-0.328	0.732	-0.117
	0.328	-0.441	-0.314	0.714	-0.124
	0.305	0.389	-0.098	-0.730	0.447
	-0.181	0.147	0.381	-0.240	-0.312
	0.140	0.655	-0.142	-0.826	0.622
	0.396	0.369	0.064	-0.511	0.023
	0.303	0.820	-0.198	-0.910	0.483
	-0.304	-0.694	0.125	0.812	-0.312
	0.803	-0.074	-0.166	0.107	-0.125
	-0.253	-0.681	0.515	0.783	-0.703
	0.373	-0.315	-0.528	0.648	0.193
	0.164	0.727	-0.064	-0.400	0.228
	0.715	0.568	-0.392	-0.503	0.533
	0.223	0.639	0.206	-0.474	-0.022
	0.413	0.830	-0.252	-0.698	0.290
	-0.035	0.920	-0.141	-0.738	0.357
	0.273	0.130	0.165	-0.213	-0.332
	-0.073	-0.753	0.248	0.894	-0.340
	0.256	-0.596	-0.279	0.837	-0.210
	0.588	0.625	-0.286	-0.590	0.320
	0.346	0.809	-0.415	-0.843	0.622
	1.000	0.126	-0.502	-0.025	0.201
		1.000	-0.231	-0.730	0.471
			1.000	0.046	-0.544
				1.000	-0.408
					1.000

VARIABLE NUMBER	31
1	-0.026
2	-0.407
3	0.213
4	0.520
5	0.510
6	0.528
7	0.143
8	0.187
9	-0.252
10	-0.242
11	-0.140
12	0.137
13	0.226
14	-0.070
15	0.382
16	-0.419
17	0.084
18	-0.305
19	0.147
20	0.014
21	0.015
22	0.109
23	0.276
24	-0.105
25	-0.146
26	0.367
27	0.029
28	-0.383
29	0.118
30	0.040
31	1.000