

SCATTERING LAYERS, OXYGEN DISTRIBUTION AND THE COPEPOD PLANKTON IN THE UPPER 300 METRES OF THE BEAUFORT SEA.

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I. GENERAL INTRODUCTION: THE ENVIRONMENT

The Arctic Ocean is a three-layered system, with a fourth water type, originating in the Pacific, apparent in the Canadian Basin, especially in the Beaufort Sea. The three layers, established at the turn of the century by Fridtjof Nansen are the Arctic layer, the Atlantic layer and the Arctic Deep Water.

The Arctic Layer

The Arctic Layer comprising the upper 200-300 m of the waters of the Canadian Basin, with which this study is concerned, can be divided into four distinct water masses. These have been studied by Coachman and Barnes (1961, 1963), and their description of them was confirmed by the data taken on T-3 by Hansen (Hansen and Dunbar, 1970).

The Arctic Surface Layer occupies the upper 50 m, and is isothermal and isohaline. This is the coldest (-1.65°C) and the least saline $(30.4 - 30.6^{\circ}/\text{oo})$ water in the depth range under consideration (0 - 300 m).

At 50 m there is a sharp increase in both salinity and temperature which creates a strong density interface. The 50 to 200 m layer is known as the Arctic Intermediate Layer and in the Beaufort Sea area is sophisticated by Pacific water flowing through Bering Strait. A temperature maximum at 75 m identifies the upper half of the layer (50 - 100 m) as Arctic water modified by water which entered the Arctic Ocean from the Bering Sea during the summer. Below this (100 - 200 m) the temperature decreases to a minimum at 150 m indicating that the denser winter water from the Pacific is influencing the lower part of the Arctic Intermediate Layer. The salinity increases throughout the whole Intermediate Layer to 33.2 0/oo.

From about 150 m, the temperature and salinity begin to increase more rapidly to maxima of 0°C and 34.6% oat 300 m (the deepest extent of this study). This is the area of mixing of the Arctic water above with the Atlantic water below. Dunbar and Harding (1968) have discussed the difficulty

of defining an exact boundary between the Arctic and Atlantic Water Layers. It should be noted that the Northern Chukchi and Beaufort Sea area is the furthest away in time and space from the point of entry of Atlantic water into the Arctic Basin between Spitsbergen and east Greenland. It has lost many of its identifying characteristics of temperature and salinity (Coachman and Barnes, 1963), although a temperature maximum of +0.5°C is observable at 500 m.

Beneath the Atlantic Layer, from 900 m to the bottom, lies the Deep Water, with which this study is not concerned.

Fig. 3 shows curves of temperature, salinity and sigma-t for a typical station from T-3 in 1967 and indicates the stratification of the upper 300 m of the waters of the Canadian Basin. In this figure the water from 200 m down has been labelled "Atlantic water".

In general, the water of the Arctic Layer (0 - 300 m) moves round the Canadian Basin in a clockwise, slow moving gyre. Pacific water entering the Arctic Intermediate Layer in the Chukchi Sea may flow west along the Siberian Continental Shelf with offshoots in the form of counterclockwise gyres. It may also flow from the Chukchi Sea across the central part of the Arctic Ocean via the North Pole. These two flows join and leave the Arctic Ocean as part of the East Greenland Current. A smaller outflow from the Canadian Basin gyre passes through the Canadian Archipelago.

More detailed discussions of the circulation of the surface waters of the Arctic Ocean may be found in Gordienko (1961), Dunbar (1951), and Collin and Dunbar (1964). The simplified account given above is illustrated in Fig. A.

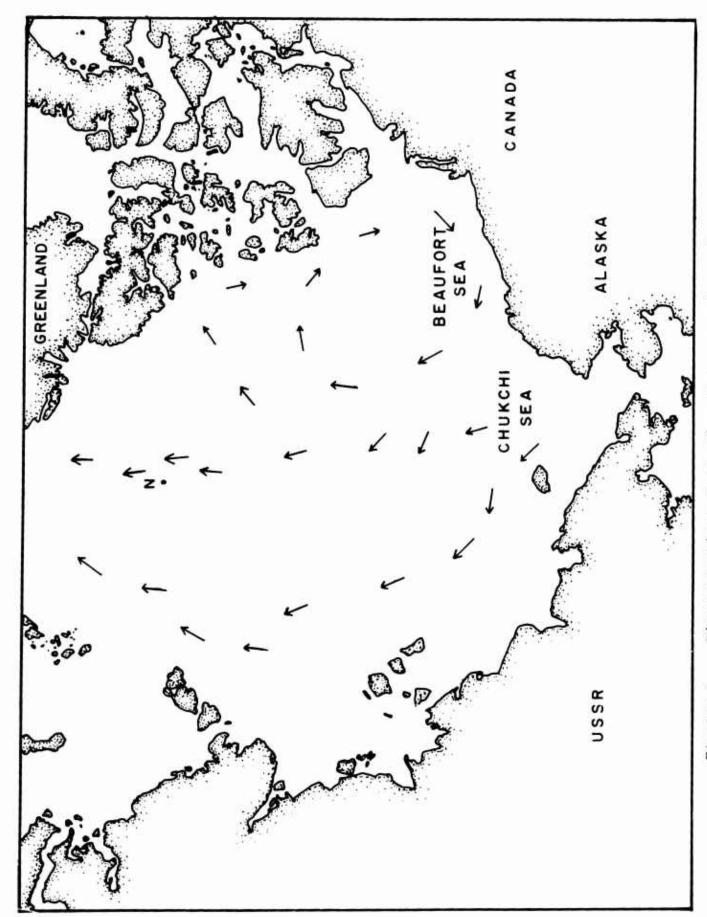


Figure A. Diagrammatic map showing the general surface circulation of the Arctic Ocean (after Harding, 1966).

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II. SOUND SCATTERING LAYERS

Introduction

The mid-water scattering of sound, as observed on recording fathometers, has been known for the past four decades. In the early 1930's, traces observed on the echosounder paper, termed "scattering groups", were correctly interpreted by Captain Ronald Balls (194c, 1951) as representing fish schools. His setting of fish nets according to sonar observations of the schools was a major advance in fishery technology. During the Second World War acoustical research connected with submarine warfare, and the development of deep-penetrating echo sounders, led to the detection of extensive mid-water reverberating layers in the ocean. These early investigations are reported by Duvall and Christensen (1946), Eyring et al. (1948), and Raitt (1948). Investigations during the late 1940's and 1950's, using increasingly refined echo-sounding equipment and recorders, led to more detailed descriptions of the layers, and the term Deep Scattering Layer (DSL) became a generic term for extensive mid-water scattering agents.

The biological nature of the phenomenon was early recognized on account of the vertical migratory behaviour of the layers, but the specific organisms concerned have proved somewhat elusive. Theoretical estimates of the population density of scatterers required to cause an effective layer in a given echo-sounder system were made by various In the field, Kanwisher and Volkmann (1955) showed workers. concentrations of approximately one scatterer per β ,500 cubic metres off New England; Johnson et al. (1956) found one scatterer per 650 cubic metres of water in a scattering layer off Puerto Rico. From these observations it is apparent that capture of the scatterers by mid-water trawling devices is likely to be very difficult, as the number of scatterers can be quite small and the volume of water very large; nevertheless various attempts at capture have met with some success. Interpretation of net haul results, however, in correlation with echo-sounder observations, must be handled cautiously. Most net hauls contain a variety of organisms, and to ascribe the scattering to any one species is not always easy, even though one is guided by the presence or absence of sound-scattering elements such as air bladders and solid skeletal parts.

Boden (1950) showed that plankton volume was greatest at the depth of maximum reverberation and that euphausids were the most important part of the plankton in his studies.

Barham (1957) made an extensive study of scattering layers off Monterey Bay and found that the major scatterers seemed to be two myctophid species, a euphausid and a prawn. Myctophids (lantern fishes) have long been recognized as important targets in the DSL (Marshal, 1951; Tucker, 1951; Barham, 1957; Capen, 1967). Euphausids are very frequently found associated with scattering layers, but their role as sound scatterers may be questionable (Hersey and Backus, 1962), especially at lower frequencies. Kristjonsson (1968) has shown that shrimp schools and even large individual shrimp may be detected at frequencies down to 50 kHz. Observations by Barham (1963, 1966) and Pickwell (1967) from submersible vehicles have demonstrated the great importance of physonect siphonophores as scatterers in the DSL. It is probable that numerous creatures other than abyssal fishes and physonects also contribute to the structure and occurrence of the scattering layer, for instance large crustaceans, cephalopods such as Spirula, Nautilus and squid, and many pelagic fish species (Hersey and Backus, 1962). The use of submersibles is perhaps the most satisfactory method of acquiring direct observations of scattering layers, and in most situations where submersibles or divers have been used in midwater scattering studies researchers have instantly acquired excellent data on causal agents, distribution and behaviour just by going down and taking a look. Unfortunately, such techniques have not yet been possible in the Arctic.

Apart from the vertically migrating scattering layers, non-migratory layers occur frequently (Cushing et al. 1956; Weston, 1958; Hersey and Backus). These layers are normally associated with some major discontinuity of the water column such as a pycnocline or thermcline. Hersey and Backus suggest that such occurrences may represent the "trapping" of organisms at some optimal level of physical or chemical parameters. The present study deals with an example of this phenomenon in the Arctic Ocean.

The results reported here are based on three years of observations from Ice Island T-3, a large tabular berg from the Ellesmere Ice Shelf circulating in the Beaufort Sea Gyral (Figure 1). The ice island carries a permanent manned research station administered by the U.S. Naval Arctic Research Laboratory, Point Barrow, Alaska.

A scattering layer at about 100 m depth was reported first from the Arctic Ocean by Kenneth Hunkins (1965) of the Lamont-Doherty Geological Observatory.

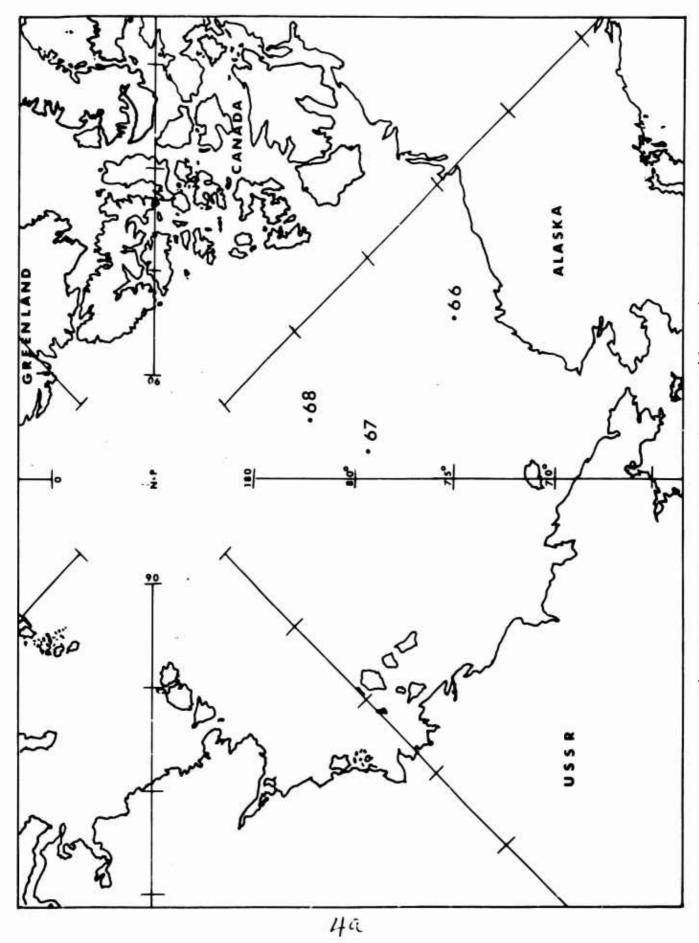


Figure 1. Areas of Sampling, 1966, 1967, 1968.

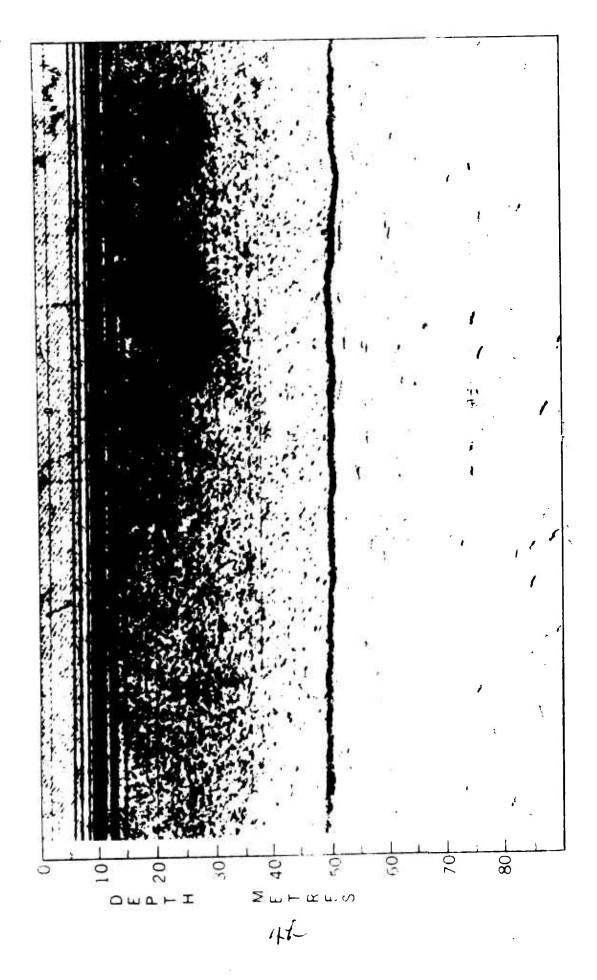
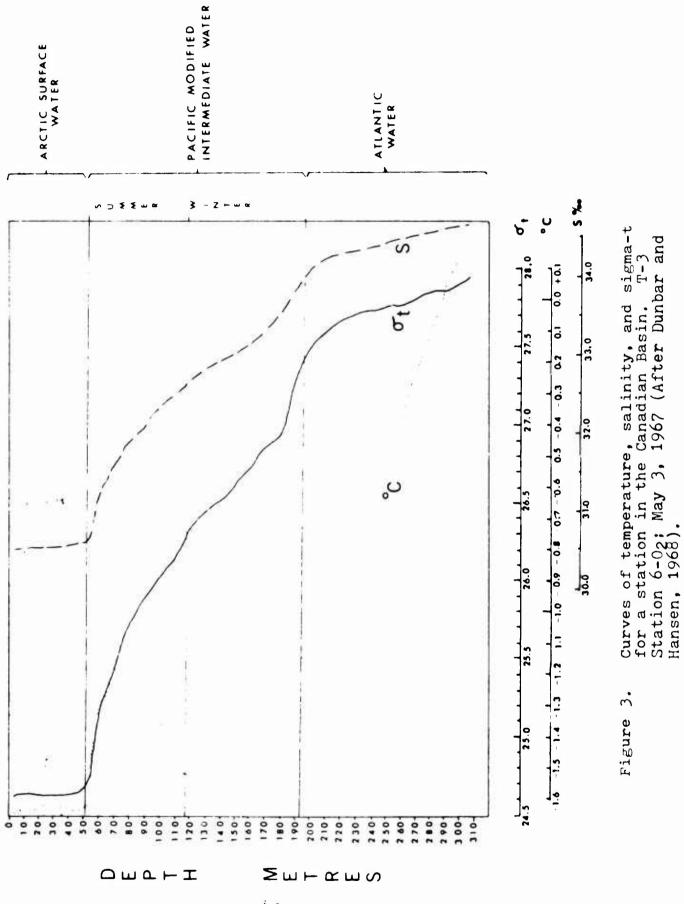


Figure 2. Common appearance of the PSL (19 Oct. 1967, 0700 hours Greenwich Mean Time)





igure 4. Typical appearance of the Arctic DSL on the

This observatory has been operating a 12 kHz Precision depth recorder almost continuously from T-3 for the past six years. An earlier study by Dietz and Shumway (1961) of echograms from nuclear submarine traverses of the Arctic showed no mid-water sonar targets. Hunkins suggested that perhaps the submarines were moving within or below the scattering layers. However, there is strong evidence that Arctic sound-scattering layers are both seasonally and geographically restricted; thus when the traverses took place they may have missed the season, the location, or both (K. Hunkins, personal communication).

In 1966 the Marine Sciences Centre of McGill University, in cooperation with the Lamont-Doherty Geological Observatory, undertook a study of the presumed biological causes of the Arctic deep scattering layer (DSL). During the first season of study, June to November 1966, no DSL was detected; the Ice Island was drifting westward about 400 miles north of the Alaskan coast at that time. In March 1967 a 100 kHz Ross Model 200A Fineline depth sounder was installed on T-3 by the Lamont-Doherty Geological Observatory. Immediately athin, shallow scattering layer was observed at approximately 50 m (Fig.2). This layer was not detected on the 12 kHz Precision depth recorder. It was found to conform with a water mass boundary separating the upper Arctic water from the Arctic intermediate water, the latter being marked by a distinct Pacific water layer in the Canadian Basin of the Arctic Ocean (Figure 3.)

At the interface the temperature increases suddenly with depth, from -1.65° to -1.31°C in 10 m. Salinity behaves similarly, increasing from 30.4°/oo to 31.3°/oo over the same distance. This is an increase of 0.55 sigmate. The scattering layer that occurred on this boundary was named the pycnocline scattering layer (PSL).

In late March 1968, a major DSL of the type and at the depths described by Hunkins (1965) appeared. It was detected between 20 and 180 m on both the Precision depth recorder (Figure 4) and the Ross recorder.

METHODS AND EQUIPMENT

Sonar

Two fathometers operated by the Lamont-Doherty Geological Observatory were used. These were: (1) a 12 kHz Precision depth recorder with a standard Edo transducer, Gifft sonar transceiver, and spark-type rotating drum recorder; the time base advanced 1 cm/hr, and the pulse length was 80 msec; and (2) a Ross model 200A Fineline depth sounder and recorder with a 365 m (200 fm) range and 100 kHz frequency. The beam angle is 10° x 5° . The chart paper speed is variable from 6 to 24 in/hr, and the pulse duration is 0.4 or 1.5 msec. The instrument operates by switching through 90 m increments; thus the whole thickness of the layer could not be viewed instantaneously. A reasonable facsimile of the full range of scatterer distribution could be obtained however, by switching every minute, thus obtaining a narrow cross-sectional view in a 4-minute period.

Hydrography

Routine hydrocasts were made during the study. Temperature was measured using a thermistor and Wheatstone bridge. Salinity samples were stored and then sent to the Bedford Institute, Dartmouth, Nova Scotia, for analysis.

Biological Sampling

Plankton: Mesh nets numbers 6 and 0 mounted on 0.5 and 1 m rings were used throughout the study. Both vertical and horizontal tows were made. Horizontal tows were made using the drift of the island during periods of high wind, when drift speeds up to 0.5 knot relative to the water beneath can occur. The actual relative drift rate and filtration-coefficient of the nets can be estimated only roughly, but the multiple-net horizontal tows gave excellent simultaneous collections from various depths. This method involves hanging the net rings on a heavily weighted cable, one above the other, so that the net will stream at the desired depth (Figure 5). Corrections of depth for wire angle were made in the field. It was found that with practice one could attach or remove the nets from a moving cable, so that they were set or hauled with a minimum of contamination from depths other than those under scrutiny.

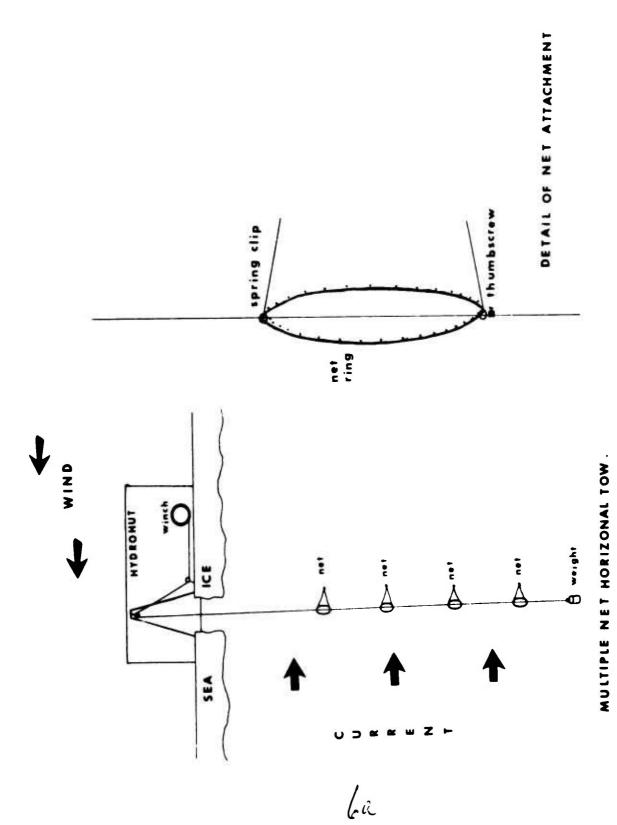


Figure 5. Technique used for the multiple-not horizontal tows. Nots may be removed from a moving cable by the spring clip.

Fishes: Attempts were made to capture fishes by hook and line, gill nets, and baited minnow traps; all were unsuccessful. Fishes were taken in the surface water of hydroholes in all years of the study by hand-held dip nets. It was observed that polar gadoids often follow any hanging object, such as cable, hose pipe, etc., that they encounter at depth up to the surface. Fishes almost invariably were taken in holes through which cables were hanging; one specimen was sucked into a pump hose at a depth of 12 m.

Pteropod Injector: To place potential sound scatterers in the water in a controlled manner beneath the Ross recorder transducer, a small device, the "pteropod injector", was constructed in the field from a sawn-off plastic hypodermic syringe. The device was assembled using a second piston in a reverse position so that a small toroidal space was left between the two pistons. A wire bridle passed through the plunger in such a way that a messenger would strike the plunger and eject the second piston with the contents of the toroidal space (Figure 6). Great care was necessary to remove the possibility of air bubbles being carried down into or on any part of the device. Normally the injector was held just beneath the surface of the hydrohole and agitated for a few minutes to shake free surface bubbles, though none actually were seen. Next, the outside was rubbed, under-water, with a cloth. The assembly, on a single strand of 12-gauge copper wire, was lowered by hand through a bunched cloth underwater. The messenger likewise was cleaned of air bubbles.

THE PYCNOCLINE SCATTERING LAYER

Observations and Results

The appearance of this layer (Figure 2) on the Ross recorder is a thin, usually continuous, line approximately 1 m thick (N.B.: one pulse length). The thickness is often greater (Figure 7), however, especially during periods of high wind when internal waves become visible in the records. Occasionally, especially in midsummer and early fall, the layer becomes very thin and patchy, even disappearing completely for many days.

Initially it was thought that this scattering layer perhaps could be interpreted physically as an acoustic reflection from the density discontinuity. At the

high frequencies (100 kHz) used, however, this is unlikely. Detailed examination of the records shows that diurnal splitting of the layer occurs; one fraction remains at the discontinuity and the other migrates either upward or downward from the discontinuity.

This is especially notable in the months bracketing the equinoxes, when greatest diurnal light variations occur. Figure 8 shows six sections of the chart record for 26 and 27 October 1967. At midday, a thick PSL is present with a few single targets visible. At 1500 hours, an ascending cloud of scatterers appears. At 2100 hours, two fractions of the layer are apparent, but the upper fraction tends to descend slowly. By midnight, however, a dense scattering layer has formed with fairly even distribution throughout the water column; a PSL is still visible. Then at about 0900 hours on the 27th, fairly rapid descent of the main scattering cloud occurs, leaving once more a PSL with a few single targets visible. The cycle repeated itself on subsequent days.

There is an interesting seasonal variation in the chart records. In winter, when continuous darkness prevails, the migrating fraction remains continuously above the PSL (Figure 9a) as might be expected and as was predicted by Bogorov (1946). Interestingly, however, the same distribution seems to prevail during the summer (Figure 9b) rather than occurring at greater depths.

Analysis of the plankton offers evidence of the cause of this layer. The cosmopolitan thecosomatous pteropod Spiratella helicina (Figure 10) occurs in enormous numbers at the interface of the two water masses. These are little calcareous shelled planktonic snails. In our samples, they were very small individuals, usually less than 1 mm in diameter, in contrast to the large specimens of 6 to 8 mm normally taken in subarctic waters. This small size in itself is extremely interesting and requires further study. They are not juveniles; strings of eggs were observed within the body and exuding from the gonopores of many of the living specimens.

McGowan (1963) examined the geographical variation in <u>Spiratella</u> in the North Pacific. He found two varieties with differences in shell texture and height/diameter ratios. Harding (1966) notes that his Arctic Ocean specimens fall into McGowan's category var. B texturally and proportionally, but that they are of small size.

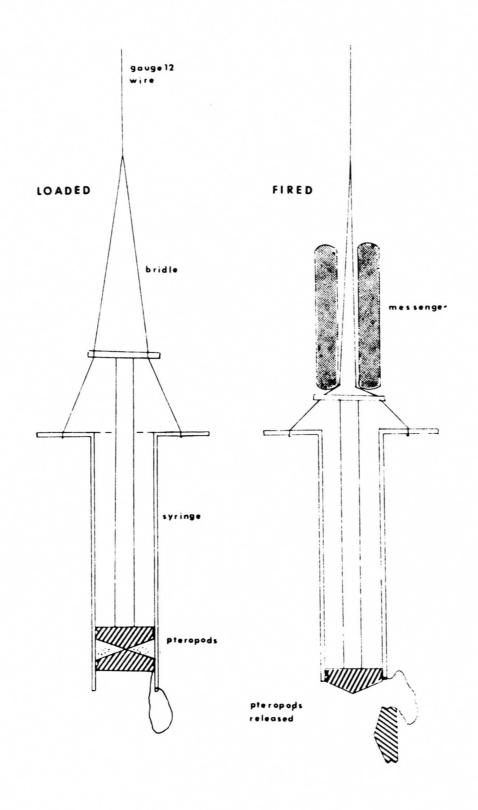


Figure 6. The pteropod injector. Specimens of <u>Spiratella</u> are placed in the space between the two pistons.



Figure 7. Very thick PSL. Turbulence possibly caused by the motion of Ice Island (23 Oct. 1967, 2300 hours Greenwich Mean Time).

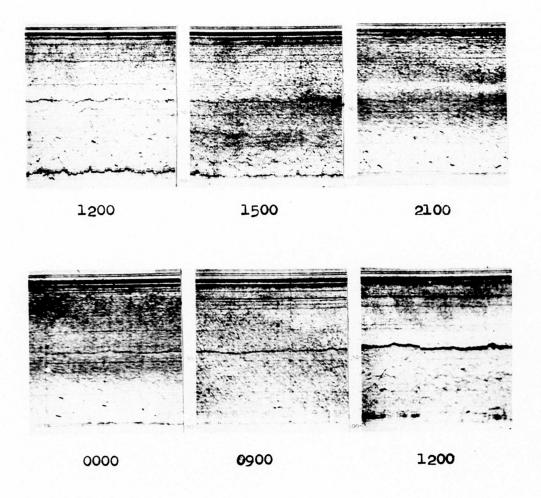
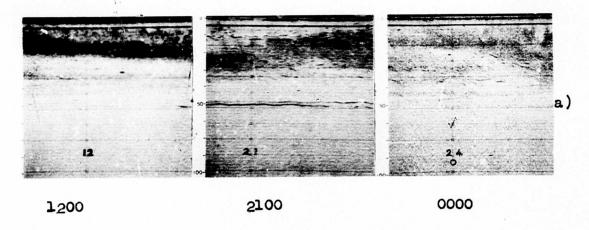


Figure 8. Six sections of the chart record for 26 and 27 October 1967.

15 Jan.1968



13 July 1967

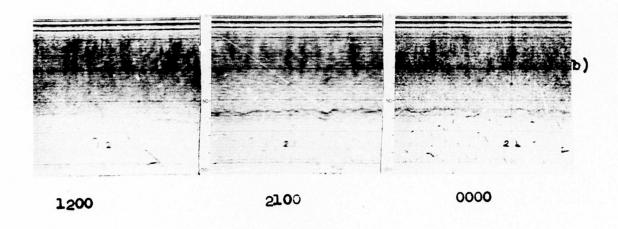


Figure 9. Sections of chart record in winter (a) and summer (b).

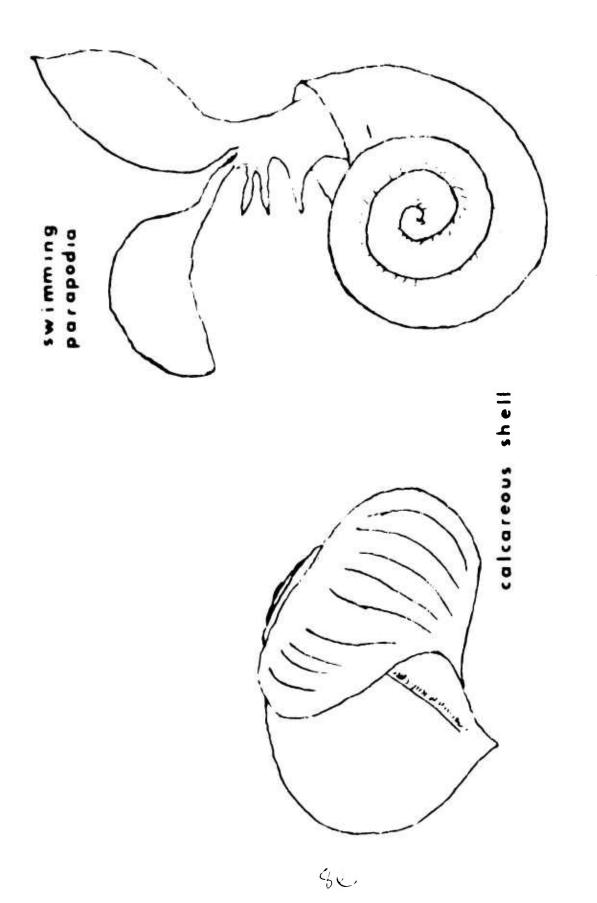


Figure 10. The thecosomatous pteropod Spiratella helicina. The specimens taken from the scattering layers are extremely small compared with those found further south.

EEL

Because of the thinness of the layer and the general difficulty of hauling nets horizontally from the ice, it was not possible to stream a net at the correct depth with any accuracy. By placing a thermistor on the net, however, the discontinuity could be detected and the net held as close as possible to the layer depth. At Station 5, 79°57.9'N, 174°24'W, on 3 May 1967, a multiple net horizmontal tow was made with 0.5 m nets at 40, 45, 50, and 55 m. Internal waves of 6 m amplitude and approximately 10-min period were visible in the chart record at 50 m. The layer at this time appeared to be about 8 m thick. The windspeed was a steady 20 to 25 knots, and the drift of the island an estimated 0.5 knot. Figure 11 is a histogram of pteropod distribution correlated with the depth-sounder record, demonstrating the correlation of pteropod numbers with the scattering layer. Other stations with horizontal net tows verify these distributions. A series of subtractive vertical tows was made using a 2 m increment for each tow. The net was triple washed and inspected visually to make sure no pteropods were missing. Counts were made immediately.

Station V.T.4, 30 May 1967, showed a typical vertical distribution found by this method. Figure 12 is a histogram of pteropod distribution and numbers on a 2 m subtractive tow series, showing maximum concentration between 50 and 48 m. It is correlated with the chart record of the day.

The data presented here are excellent correlative evidence that <u>Spiratella</u> is the cause of the PSL.

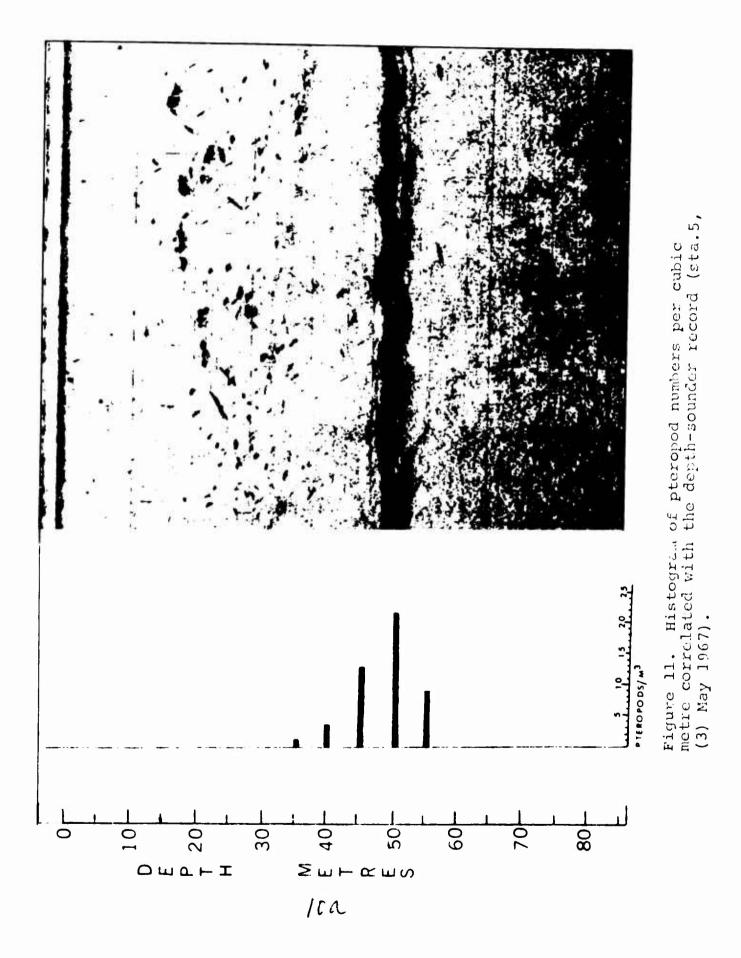
Field tests with the Ross echo sounder were made, using small BB shot as test targets. Individual pellets, approximately 1.4 mm in diameter, were detectable down to An experiment was performed with the pteropod injector containing 80 live specimens of Spiratella helicina. Careful precautions were taken to eliminate air bubbles. and the injector was lowered to a depth of 60 m and allowed to nang for 4 min. The injector was then fired by messenger and, at the moment of impact, the injector was raised 10 m. On the chart record (Figure 13), a residual line of echo remained, slowly dispersing over a period of 1 min. experiment was repeated three times with live specimens and once with a blank run (only water in the injector barrel). The results were identical on two out of three runs; on the third run, air bubbles, showing as rising streaks, occluded the record. The blank run showed no scattering. Spiratella has a hard calcareous shell, which probably can be classified acoustically as a solid body; thus, if large numbers of Spiratella were present in a thin layer at 50 m depth, they would be expected to form a detectable scattering layer.

The behaviour of the organism as observed on the echo sounder deserves analysis. The sinking rates of the creatures in water from above and below the discontinuity were measured in the laboratory. The average sinking rate of 20 nonswimming specimens in water from 45 m (sigma-t 24.65) was 1.782 cm/sec. In water from 55 m (sigma-t 25.10), it was 1.521 cm/sec. One can postulate that less energy is required for Spiratella to maintain a constant depth by remaining at or below the PSL; the significance of this is doubtful, however, especially in such an actively swimming organism.

Harder (1968), reviewing plankton behaviour at water-mass boundaries, suggested that density interfaces act as concentrating levels for organic detritus and that many species feed at the interface. Other species may respond to physiological stress induced by salinity changes, which alter the osmotic pressure differential across the cell membranes.

Hunkins, Thorndike, and Mathieu (1969) examined the nepholometry of the Canadian Basin. They found no light-scattering layer indicative of a detrital accumulation at the interface depth. Thus, a feeding response seems unlikely to explain the behaviour; but see Kinney et al., 1971, and Section III below).

There is a recurrent, though unresolved, suggestion in vertical migration studies (Lance, 1962; Loeb, 1893; Rose, 1952) that vertically migrating plankton organisms within a light field tend to some physiologically limited level of salinity (or temperature) as well as light intensity; once one constraint passes beyond a certain threshold, the sign of the migratory drive is changed. Thus, a stenohaline individual organism moving upward at sunset and passing into more brackish water will stop at the critical salinity level. As the light intensity drops lower, the triggering stimulus diminishes. In this condition, the physiological stress of the brackish water causes a reversal of sign in the migration, and the organism tends to sink slowly toward the more saline water during the night. At dawn the increasing light tends to reverse the sign once more, and a second upward migration occurs toward the optimal halophotic level. Once the light intensity and the osmotic stress become too strong, however, a downward migration occurs, taking the organism back to optimum daylight depths.



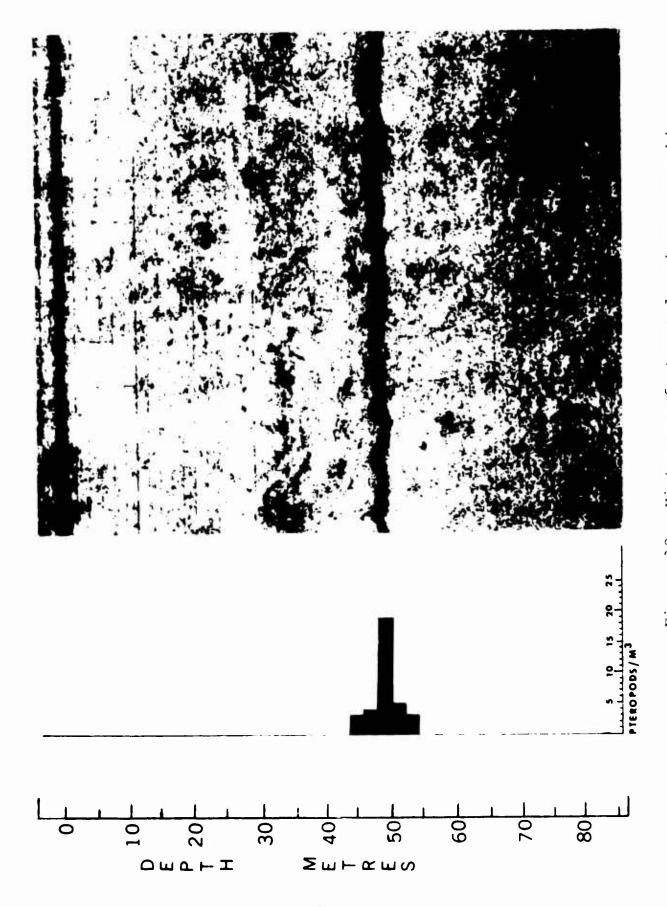


Figure 12. Histogram of pteropod numbers per cubic metre correlated with the depth-sounder recorder (from subtractive vertical tow, sta. V.T. 4, 30 May 1967).

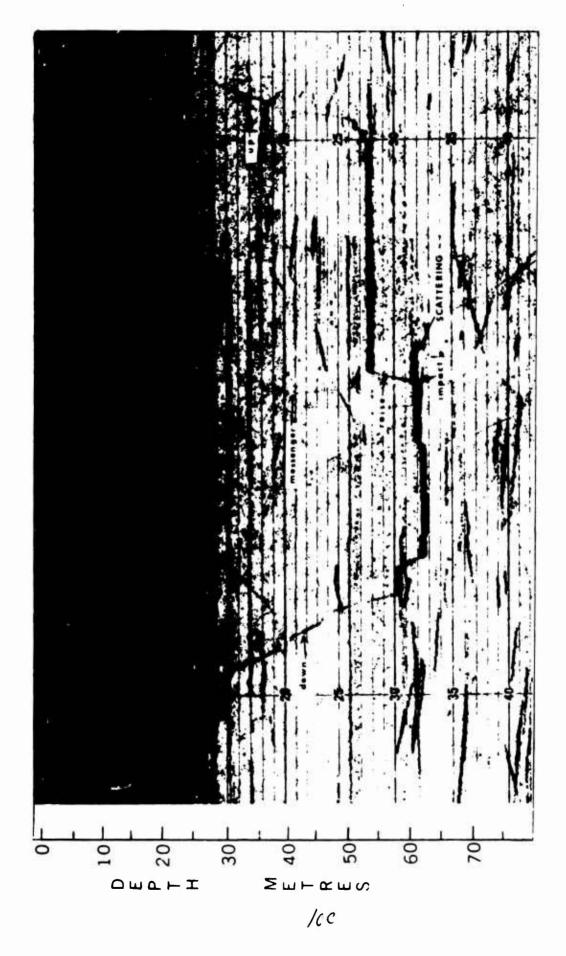


Figure 13. Experiment with pteropod injector (sta.P.I. 2, 24 April 1968).

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In an ocean with a marked salinity boundary layer, there tends to be a segregation of individuals. Those of low tolerance to high salinity tend to remain on the boundary layer during downward migration at dawn. Those of low tolerance to brackish water tend to remain on the boundary layer during upward migration at sunset. The hardier or more euryhaline members of the population go through the layer, albeit with some short delay to allow for the rapid change of osmotic balance.

This hypothesis would explain the general behaviour of the Arctic PSL as caused by pteropods whose salinity limits lie between 33.5°/oo and 30.5°/oo, approximately, in this population (Harding, 1966). It does not explain the reason for the high position and nonmigratory behaviour of the summer and winter layer. The reason for this might be that during these long, continuous light or dark periods, the primary trigger stimulus is absent; thus, the organism tends to remain at depths favourable in factors other than light, such as feeding.

THE DEEP SCATTERING LAYER

Observations and Results

Hunkins (1965) has described the Arctic DSL observed at 12kHz as a "diffuse reverberation", similar in general appearance to the DSL in other oceans. The Arctic layer tends to be shallower (20 to 200 m) in distribution than elsewhere in the world and also to have an annual rather than a diurnal migration pattern, no doubt a result of the special Arctic daylight pattern. The layer has been recorded only during the summer months and only in the northern and northwestern part of the Beaufort Sea Gyral. Soundings elsewhere and at other times of the year were negative. Hunkins has shown that diurnal vertical migrations are, in fact, observable in this layer, especially about the time of the autumnal equinox. The layer usually is not present at the time of the vernal equinox.

Figure 14 is a continuous record of the development of the DSL in 1968, transcribed from the original daily chart records. The layer first appeared as isolated scattering groups, which developed into a thin, slightly discontinuous layer that was not particularly migratory. It later became thicker, and through mid-April the layer showed definite diurnal migrations. As the summer progressed, the layer tended to split into two components and become a little patchy.

At the 100-kHz frequency, it was possible to observe only a 90 m layer of the water at any one time, but a good composite picture could be gained by switching through the depth ranges in sequence and placing the records in order one above the other. Figure 15 is such a composite of four chart records offering a complete section through the DSL as seen on the Ross recorder. The PSL is traversed freely by the DSL scatterers (Figure 16), and it does not appear in general to be a significant barrier.

Kanwisher and Volkmann (1955) found one scatterer per 8,500 m³ off New England, and Johnson, Backus, Hersey, and Owen (1956) found one scatterer per 650 m3 off Puerto Rico. In order to compare various features of the DSL with the findings of these workers, an index of scatterers per unit volume was calculated. The first step was to switch through the depth ranges of the 100-kHz instrument over a short period of time. The scatterer counts were then corrected by dividing the number of scatterers in each 10 m of the insonified cone by the volume of a 10 m deep segment and multiplying the result by 104 to place the decimal point in a convenient position. Figure 17 shows a histogram of the vertical distribution of the scatterers per 10,000 m3. This gives the highest concentration of scatterers as approximately 1/5,000 m3. Much higher concentrations can occur in the scattering groups, but because the echo traces tend to merge, no reliable count is possible.

Attempts to capture the organisms responsible for this layer were unsuccessful. In two different years only two larval polar gadoids were taken from horizontal plankton tows below the surface, at depths of 15 and 40 m respectively. One of them was taken when no scattering layer was present. Fishes (Arctogadus glacialis) frequently are captured, however, in the hydroholes cut through the sea ice.

The lack of positive evidence in the form of specimens taken at the layer depth is not surprising considering the impossibility of trawling from the surface of pack ice. It is obvious from the echograms that the scatterers are relatively large, scattering both 12- and 100-kHz sound. When the scatterers are viewed at 100-kHz as individual targets, they frequently are seen as fast-swimming hyperbolic traces, which are indicative of rapid relative motion between transducer and target. Furthermore, the organisms frequently move in dense shoals and are seen as scattering groups; they are therefore most

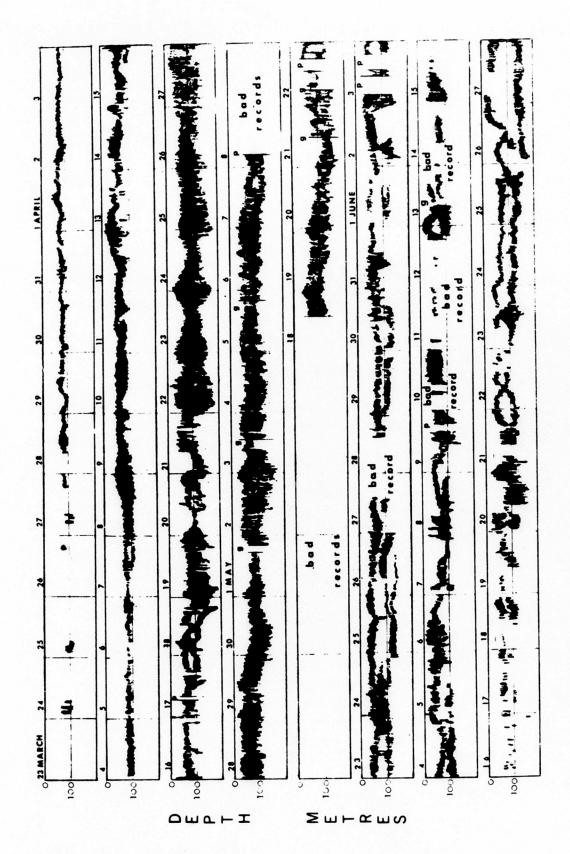


Figure 14. Continuous record of DSI, sketched from daily records. P represents power failure and g, gain adjustment.

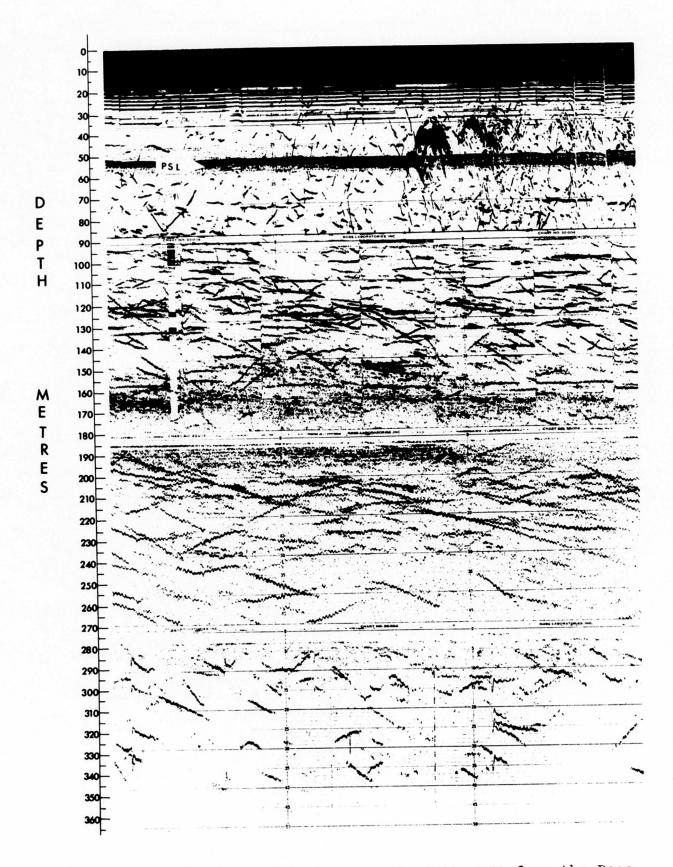


Figure 15. Composite record of the DSL from the Ross echo sounder.

12h



Figure 16. Scattering groups from the DSL traversing the pycnocline marked by the thin PSL (14 April 1968)

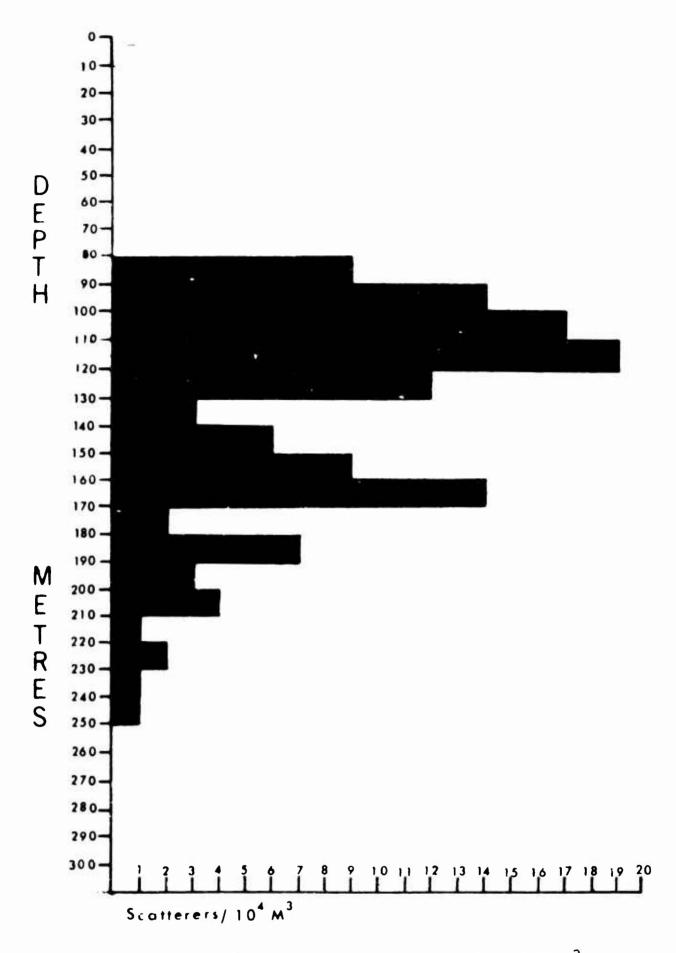


Figure 17. Histogram of scatterers per 10,000 m³ made by counting a random section down a Ross depth-sounder chart and correcting to a unit volume from the transducer geometry.

probably nektonic fish, and the most likely species is Arctogadus glacialis, the polar cod (Figure 18).

The biology of Arctogadus is not well known. It is certainly the most frequently found species in the central Polar Sea. Walters (1961) identified and described 35 specimens of this species taken from Station Charlie in the winter of 1959-60. During this period up to 500 specimens sometimes were taken from the hydroholes following seismic explosions at shallow depths below the ice. Andriashev (1957) took 11 specimens from the same general area as the Station Charlie material, i.e., over the Chukchi Rise. In 1966 we took two specimens in this area; in April and May 1967, three were taken much farther north; and in May 1968, four were taken farther west.

Walters (1961) suggests that this species undertakes winter feeding migrations over the Chukchi Rise, moving in the winter in a generally southwest direction. The DSL has been detected only in summer and well north of the Chukchi Rise in the present work, and it is therefore possible that these fishes migrate back into the central Polar Sea from the Chukchi Rise by a northeasterly route during the summer.

Two specimens of the Arctic cod <u>Boreogadus saida</u> also have been taken in the course of this work. This species also must be a sound scatterer in the Polar Sea, but its significance cannot be estimated at present.

SUMMARY

Two types of sonar-scattering layers are reported from the Beaufort Sea. In the present study, one is visible only at 100-kHz, the other at 12- and 100-kHz. The 100-kHz layer migrates vertically but only in part; part of it remains trapped on the interface between the Arctic surface water mass and the Arctic intermediate water mass, formed of Pacific water. It is concentrated at 50 m depth and is shown to correlate with an accumulation of the thecosomatous pteropod mollusc Spiratella helicina. The layer that was detected at both 12- and 100-kHz frequencies appears and behaves much like a classic deep scattering layer, except that the vertical migrations are modified to harmonize with the Arctic summer daylight pattern. It is found between 20 and 180 m and probably is caused by shoals of the polar cod Arctogadus glacialis.

III. THE OXYGEN DISTRIBUTION

Introduction

The Arctic Ocean is generally well oxygenated at all depths. Biological productivity is greatly restricted (English, 1961) and circulation and flushing of the upper and intermediate water masses are relatively rapid (Coachman and Barnes, 1961, 1962, 1963). Under these conditions marked extremes of oxyty would not be expected. The term "oxyty" means "concentration of dissolved oxygen". It was formally proposed by Montgomery (1969) although it had been used intramurally by Scripps Institute oceanographers before that date. As it has now been introduced to the literature (White, 1971), we have used the term in this report as analogous to salinity, etc.

The term "low oxyty layer" means "oxygen minimum layer". The objection to the new term on the grounds of priority is invalid in that "oxygen minimum layer" is not a proper name - or should not be allowed to become one. "Low Oxyty layer" is semantically neutral. The attitude implicit in the term "The Oxygen Minimum Layer Problem" is partially responsible for the conflict in theories and the convolutions of ideas about a basically simple phenomenon, i.e. water containing less dissolved oxygen than that above or below. It is becoming clear that numerous coincident processes such as dynamic circulation, minimal vertical exchange, biochemical cycling and possibly complex food webs based on assimilation and metabolism of some fraction of the dissolved organic carbon of deep water (see Fournier, 1966); Holm-Hansen, 1970, and Craig, 1971) occur more or less together in the water column at the depth of low oxyty It is probable that the divergence of extremes. scientific opinion is the result of differences between locally dominant causes. Thus the basic cause is always respiration (cf. Wyrtki, 1962) - or oxygen demand - but the immediate causes determining position and snape in the water column will vary in space and time in the continuum of the whole ocean circulation; sometimes the minimum oxyty will be in the water containing the maximum oxygen demand; at other points it will be older water which contains the extremum; and at others it will be a mixing process which conditions the vertical profile. The term low oxyty layer thus describes a condition in the water column - not a single type of water in the world ocean which "the oxygen minimum layer" has tended to imply.

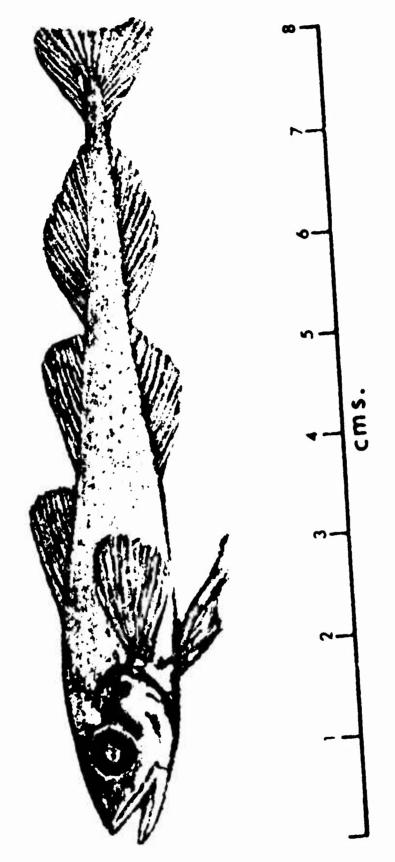


Figure 18. Arctogadus glacialis (drawn from a preserved specimen)

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The data of the Soviet drift station NP-2 of 1950-1951 revealed a distinct low oxyty layer in the northwestern region of the Beaufort Sea (Somov, 1955). Gudkovich (1955) tentatively interpreted its cause as the oxidation and decomposition of organic matter derived from the death of plankton entering the Beaufort Sea gyral from Bering Strait.

Harding (1966) observed a low oxyty layer at about 200 m in the Beaufort Sea, and considered that it was probably caused by the decomposition of organic detritus on a density interface (personal communication). Previous analyses of vertical oxyty distribution in the Arctic Ocean failed to show any very marked minimum layer, and in fact there is some indication that it is most strongly developed only in the northwestern region of the Beaufort Sea gyral and is not so obvious elsewhere, although all oxygen profiles do show some lower concentration extremum.

Kinney et al (1970) presenting extremely detailed hydrographic, oxygen and nutrient data from the Beaufort Sea, consider that the low oxyty water is partly due to advection of shelf water into the basin rather than to in situ oxidation alone. This view is supported and developed in this report.

Sverdrup (1938) examined the theories concerning the formation of low oxyty layers, describing the two different approaches to the subject which have evolved. The first, originally proposed by Jacobsen (1916) and extended by Wüst (1935) and Dietrich (1936) is based on a physical concept of dynamic circulation; the oxygen minima occur in almost stationary boundary layers between different water masses of the deep sea circulation. The second approach developed by Wattenberg (1938) considers that vertical oxygen distribution depends on sinking of organic matter, its concentration, isolation of water masses by discontinuity layers, and temperatures conducive to decomposition. Seiwell and Seiwell (1938) proposed that the oxygen minimum, conditioned mainly biochemically, occurs at depths at which the specific gravity of sea water and sinking detritus are equal, so that the detritus accumulates and oxidizes, thus lowering the oxygen concentration. This view has been revived by Miyake and Saruhoshi (1956) on the basis of density of detritus and the fact that low oxyty water is superficially associated with isopycnal surfaces around sigma-t 27.0.

Redfield (1942) and Redfield et al. (1963) introduced a useful new concept into the discussion. They consider that the oxygen minimum occurs in the layer of water which contained the largest amounts of organic material when it sank at high latitudes. They explored the chemical balance of nutrients and oxygen, and separated the nutrients into various fractions according to their origins, ie., preformed, organic, particulate, etc. Richards (1957) reviewing the field, produced an integrated model of circulatory and biochemical processes though he left certain aspects of the question rather open, such as the relationship between oxygen minima and nutrient maxima. This aspect has since been studied by Redfield and Richards together (Redfield et al. 1963). Wyrtki (1962) reexamined the circulation models, and in a paper somewhat critical of Richards' review, resolved many of the early discrepancies in both the physical and biochemical theories. He found that the difficulties of earlier theories were probably due to certain misunderstandings and unfortunate choices of examples of oxygen minima. His conclusions were "that the oxygen minimum layer is caused by the biochemical process of oxygen consumption, that its position and distribution are determined by circulation, and that the shape of the oxygen profile, especially the high position of its minimum is due to the exponential decrease of oxygen consumption." This view is not seriously contested at the present time, except in a "mixing model" proposed by Menzel and Ryther (1968) to explain the low oxyty layer in the Antarctic Intermediate Water of the South Atlantic. Menzel and Ryther do not subscribe to the theory of "deep respiration" or in situ oxygen consumption once a watermass sinks below a shallow depth. Craig (1971) reviewing the problem quotes them as stating: "The entire biochemical cycle of organic matter appears to occur at depths probably not in excess of 200-300 metres." (Menzel and Ryther 1971). In view of the work of Fournier (1966) who presents evidence for microbial populations in the deep Atlantic with up to 2 x 105 cells per litre; and Holm-Hansen (1970) who estimates from ATP assays that oxidation proceeds at between 5 to 50 μ l 0_2 /litre/year in deep waters in general, it seems unreasonable to suppose that the biochemical cycle is restricted to the surface layers only.

The problem is refractory, for the time scales required to bring about deep water low oxyty layers by purely circulatory and mixing processes or by in situ respiratory processes, are of the same magnitude. Bubnov (1966) proposed that the oxygen minimum in the Atlantic is formed in the regions of upwelling off the West African coast and that tongues of low oxyty extended west, south

and north from these zones; the depths of the extremes varying with the dynamic topography of the isotrophic lines. It is implied that no further in situ oxygen demand exists once the water has sunk from the region of eastern tropical upwelling.

In the Arctic context, Coachman and Barnes (1961) consider that the maximum and minimum temperature layers in the Upper Arctic Water of the Canadian Basin can be ascribed to the seasonal influx of Bering Sea water through Bering Strait, the temperature maximum representing summer inflow and the minimum representing winter inflow. The inflowing waters mix with large quantities of shelf water and are advected into the general circulation. An examination of the distribution of nutrients appears to confirm this view. The decrease in oxygen concentration with depth throughout the Pacific-conditioned layer corresponds to an increase in nutrients (PO4, P, and silica) which can, like temperature, be interpreted in terms of seasonal inflow (see Figure 19). This overlooks the possible importance of in situ processes in the Chukchi Sea.

Kinney et al. (1971) find comparable values of dissolved organic carbon (DOC) in samples from the northern Chukchi Sea and the "Bering Strait - Chukchi Sea" water at depth in the Beaufort Sea. These values are slightly lower than those found in Bering Strait.

The work described here confirms the existence of low oxyty layer associated with the division between "Atlantic" and "Pacific" waters in the northwestern Beaufort Sea. Data are presented which are in good agreement with those of other workers, although absolute values of PO4, O2, silica, etc, are often extremely difficult to obtain under the conditions of high Arctic field laboratories — this section is concerned not with the biochemical determinants of nutrient regeneration, but with oceanographic conditions which would give rise to the vertical profiles described.

METHODS AND EQUIPMENT

It has been the usual practice in hydrographic studies in the Arctic Ocean, as elsewhere, to sample at the "standard depths" as proposed by the International Association of Physical Oceanography in 1936. This practice is sound enough in any routine survey and, as it is universally practiced, it enables comparisons to be made throughout the world ocean; but in the process of standardization

of technique much fine detail of the structure may be missed. To coincide with the multiple net horizontal tow techniques used in the scattering layer studies, it was desirable that hydrographic samples should be taken at least at 10 m intervals, down to 300 m, in order to relate plankton observations to water mass structure. This close spacing of the samples shows the finer detail of the water masses.

A four-speed oceanographic winch equipped with a four-conductor electromechanical cable was used to make the hydrocasts. Nine 6-litre van Dorn bottles spaced at 10 metre intervals were placed on the cable, and a station to 300 m consisted of three consecutive casts of these nine bottles plus one cast of three bottles. Normally these stations took four hours to complete; there were two such stations in 1967 (Stations 6 and 7). Stations 2,3,4, and 5 were made on different days, each sampling deeper than the preceding one by 80 metres, producing a composite series of profiles. (See Fig. 20 for station positions.)

Samples for oxygen analysis were drawn first, followed by salinity and nutrient samples. As the cast was lowered, the cable was stopped every ten metres and the temperature measured using a thermistor and Wheatstone bridge circuit. See Appendix III for raw data.

Oxygen was measured by the standard Winkler procedure, the iodine titration being done within ten hours of the completion of the station. Salinity samples were shipped to the Bedford Institute of Oceanography. Inorganic phosphate was measured in the field by the method of Murphy and Riley as described by Strickland and Parsons (1965). Reactive silicate was determined by the method of Mullin and Riley as modified by Strickland and Parsons. A Beckman D.U. spectrophotometer was used to measure the extinctions.

RESULTS

Curves of the properties analyzed are shown in Fig. 19 drawn from the data of Station 6-02. The upper 50 m are supersaturated with oxygen and are homogenous for that property; between 50 and 200 metres the oxyty diminishes. Below 200 m it increases rapidly over about 20 m, and thereafter rather more gradually down to the core of the Atlantic layer. The nutrients on the other hand increase rapidly between 50 and 150 m and then decrease through the 200 m level; they then remain fairly steady down into the Atlantic water.

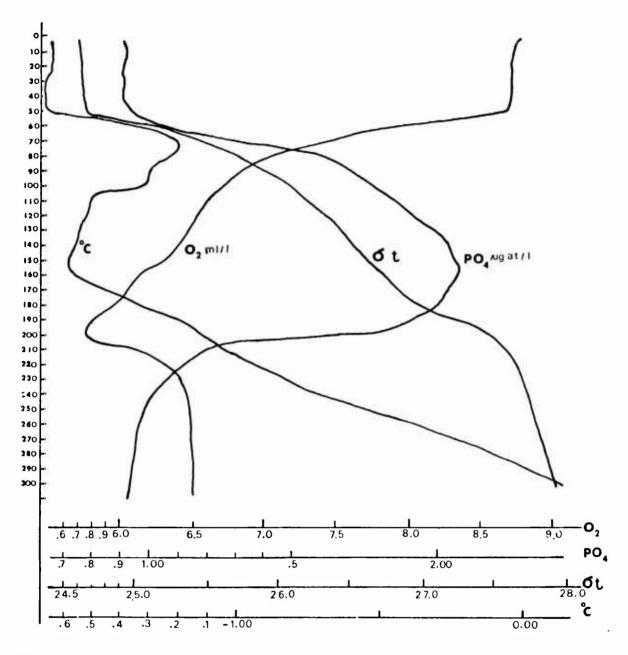


Fig. 19. Curves of oxyty, density, phosphate and temperature. Station 6-02, 3 May, 1967.

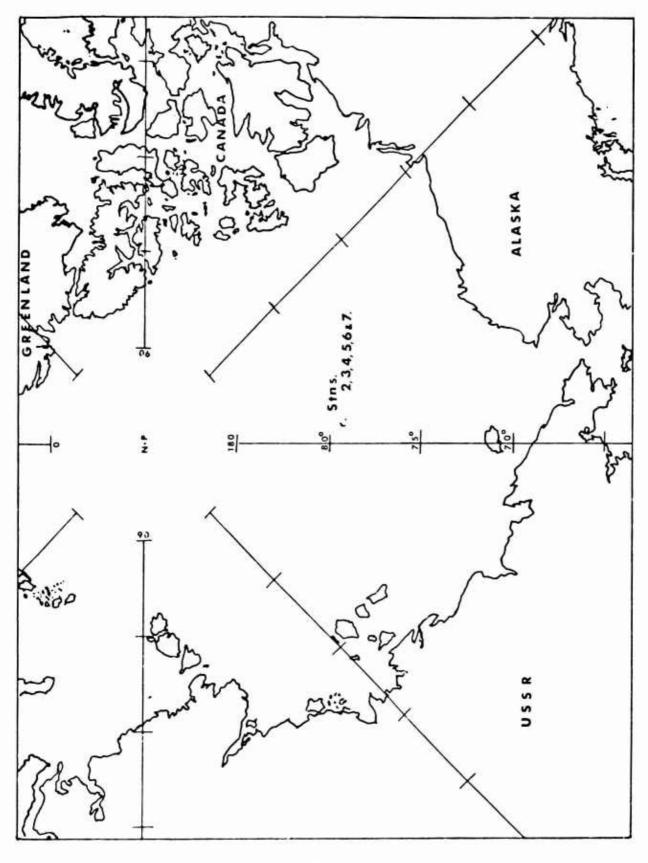


Fig. 20. Oxygen station positions, 1967.

The distinct temperature maximum is visible at 75 m and the minimum at 150 m; below that depth the temperature rises steadily into the Atlantic core. As the actual range of temperature throughout is very small (-1.76° to 0.1°C) it is clear that it is the salinity which controls the density; there are marked pycnoclines at the 50 and 200 m levels.

DISCUSSION

From a study of the curves it is apparent that the low oxyty layer lies within a very steep gradient in sigma-t values, from 26.9 to 27.4 (0.5 sigma-t) in an interval of 20 m. Three empirical models will be considered in an attempt to explain this pattern:-

1. Oxygen consumption has occurred on a sigma-t surface.

This possibility, for the oceans in general, was explored by Seiwell and Seiwell (1938), who postulated that organic detritus sinking through water of increasing density will approach asymptotically some level of neutral buoyancy causing a stratum of maximum oxygen demand. If such a mechanism were operating in this case, there would have to be a distinct phosphate maximum coinciding precisely with the oxygen minimum, or at least some indication of nutrient regeneration over and above that of Chukchi or East Siberian Sea origin (see below). This is not the case here; the phosphate maximum is considerably higher. Also in situ nephthelometric measurements by Hunkins et al. (1969) show no exceptional particle accumulation in the pycnocline, although the data of Neshyba et al. (1969) studying forward scattering of laser light in water samples in the laboratory do imply some particulate accumulation at pycnocline Kinney et al. (1971) find a high value (55 m $_{r}$ /1) for particulate matter at the 55 m pycnocline. There is no high value at the depth of oxygen minimum. They find that diagnostically higher concentrations of particulate matterin specific layers is not clear from the available data.

Parr (1939) has suggested that there may be a serious error in the logic of the Seiwell hypothesis since the density of a particle is not constant but is subject to changes in relative density caused by physical contraction and expansion. Menzel and Goering (1966) find that the distribution of particulate carbon in water below 200 m is remarkably constant in time, space and depth. They also postulate that all of this material is refractory to decomposition. Thus the oxidation process proceeds rapidly

in the upper layers of the sea, but diminishes exponentially with depth. This seems likely and is assumed to be correct by Wyrtki (1962), who used the data of Riley (1951).

2. The layer is the product of dynamic forces operating at the boundary layer between two distinct water masses circulating in different directions.

Sverdrup et al. (1942) offer a mechanism for the formation of low oxyty layers in which a nearly horizontal internal boundary exists which separates currents flowing in opposite directions. To quote from him: "When dynamic equilibrium exists

$$\frac{A}{\rho} \cdot \frac{d^2s}{dz^2} = -R$$

where $\frac{A}{B}$ is the vertical coefficient of eddy diffusion and -R is oxygen consumption (respiration); since the consumption equals -R and is always positive, the curvature of s is positive when plotted against z. The curvature cannot remain positive at all depths, and therefore it is probable that s, the oxygen content, must be at a minimum near the boundary surface. Thus, a minimum in the vertical distribution of oxygen may indicate the presence of a boundary surface at which there are no currents"

Examination of the circulation patterns of the upper water mass in the Beaufort Sea and the Atlantic water mass underlying it (Fig. 21) indicates that in the northwestern Beaufort Sen the circulations are approximately in opposition - answering the requirements for Sverdrup's model. This is in fact a special case of the type of mechanism proposed by Wüst (1935) and Dietrich (1936) and now sophisticated by Wyrtki (1961), who summarized their view in the sentence, "the layers of relatively small replenishment by advective movement must be characterized by oxygen minima." In our instance it may be more useful to state that between two opposing circulations, the one over the other, there will be a layer of no motion in which advective movement is minimized. As there is also a very steep pycnocline at this depth, it is likely that vertical exchange is minimized. On this view the Beaufort Sea low oxyty layer represents a layer of no motion containing older water held in the shear between the upper water mass circulation and the circulation of the Atlantic core.

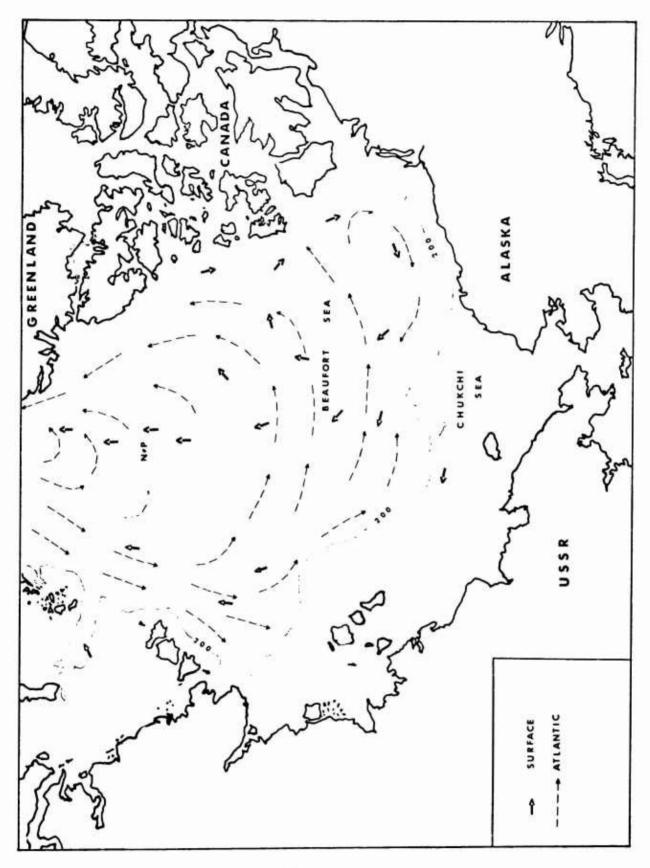


Fig. 21. The circulation of the surface water mass (heavy arrows) and the core of the Atlantic water mass (dashed arrows) in the Arctic Basin. (Simplified from Coachman and Barnes, 1962, 1963.)

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There are, unfortunately, very few available in situ current data on which to base such a model, but some of the NP-2 current data (Somov, 1955) do indicate vertical opposition of current in the region under consideration, although intertial oscillations and the difficulty of measuring absolute current from drifting ice make a proof difficult. There are no current data of sufficient quality that Richardson numbers and eddy diffusivity at layer depth might be determined in order to define a layer of no motion in the pycnocline.

The NP-2 data are the most synoptic available. There is definite evidence of a downward slope to the north in the isolines of nutrient concentration, oxyty, temperature and salinity. This agrees with the dynamic topography as calculated by Coachman and Barnes, with anticyclonic circulation in the Beaufort Sea gyral.

Thus, it is implied that the low oxyty water is drawn out from a zone of minimum horizontal and vertical movement along the isolines. This is considered to be a likely mechanism in this situation. Hunkins (personal communication) considers that such a layer of no motion is most likely in the region of opposition of circulation and finds evidence from C-14 data, deep current studies, and the distribution of oxygen, to support such a view.

One complication, however, and an alternate process, must be considered.

3. Oxygen utilization has occurred at shelf depth and the O2 minimum represents a "shelf bottom water" advected into the Arctic Basin.

Sverdrup (1929) found extensive areas of the East Siberian Shelf to be covered with a thin layer of water which was extremely low in oxygen; at his station 49(74°55'N 165°35'E) he found a layer with a minimum oxyty of 1.75 ml/l at 40 metres. He concluded that the layer is formed from relatively dense water lying for a more or less prolonged period in contact with the bottom, the oxygen being removed by respiration of benthic life. At some stations in slightly deeper water this layer shows as a distinct minimum in the oxygen curve when denser water with a higher oxyty intrudes beneath, raising it off the bottom.

This very low oxyty water, however, is of too low a density to be advected integrally into the main Arctic circulation and be detected in the Beaufort Sea, being about sigma-t 2.62. Kinney et al.(1970) find that Chukchi Sea bottom water and East Siberian and Laptev bottom waters

correspond fairly well with the high values of nitrate, phosphate, and silicate found in the nutrient maximum in the Beaufort Sea at 150 m.

Codispodi and Richards (1971) have described oxygen supersaturations caused by intensive production in the waters north of Bering Strait in summer. They find that up to 4.0 ml/l 0_2 is added to the surface waters in the Chukchi Sea over that present in the water in Bering Strait. On the basis of the oxidative ratio of Redfield (1963) of 0 : C:N:P=109:41:7.2:1(by weight) then 4.0 ml (0.35 mg.at/1) of oxygen released in photosynthesis will represent 0.14 mg.at/l of carbon fixed. This is indeed a high productivity and is confirmed in Dawson's (1965) data which show high carbon 14 fixation in the same waters. Zenkevitch (1963) using Uschakov's (1940) data, describes the spring bloom as developing a considerable biomass (18.8 to 115.1 mg/m³ of chlorophyll). This is considered to use up all available nutrients and to sink out of the euphotic zone to decay in lower layers. "A considerable development in zooplankton and a great scarcity of phytoplankton are characteristic of the summer period of plankton life in the Chukotsk Sea." It is this high local productivity which enables the Chukchi Sea to maintain a considerable summer whale population and historically a productive whale fishery. It thus appears that it is the biological cycle within the Chukchi Sea that causes the lowering of oxyty within the "Pacific water". Once the high productivity water leaves the surface, the oxidation process occurs rapidly and a characteristic profile of nutrients reflecting the water mass distribution, results. The NP-2 data show that the minimum of alkalinity lies at the nutrient maximum. This reflects the production of CO₂ in the regeneration process. It appears then that the maximum O₂ demand occurs in the "Pacific winter water"— about 150 metres in this case in the Beaufort Sea, and that the consumption probably took place rapidly over the Chukchi shelf.

The waters entering through Bering Strait and mixing and forming Chukchi Sea water are fairly well oxygenated. Frequently they are supersaturated. Codispodi and Richards (1971) find subsurface interlayers of high oxyty. Thus, the regenerative oxidation takes place, at least in part, with oxygen of recent photosynthetic origin which sinks from the surface waters before full equilibration with the atmosphere could take place.

The Atlantic water, on the other hand, having sunk over a broader and deeper front north of Spitsbergen is about 86% saturated, or 6.6 ml/l 0_2 . The addition of

oxidisable material on the Chukchi shelf further reduces this amount, leading to the characteristic "bump" in the oxyty curve at 200 m, right at the top of the Atlantic water (Fig. 19). It is interesting that the estimated primary productivity of 0.14 mg.at/l of carbon requiring 0.35 mg.at/l of oxygen (4.0 ml/l) to decay, for the Chukchi Sea, would reduce the oxyty of surface water to 5.0 ml/l and reduce the Atlantic water, initially at 6.6 ml/l, to 2.6 ml/l. The KRASSIN expedition of 1935 studying the oceanography and zoogeography of the Chukchi Sea found a low oxygen bottom water at 150 m in the northwestern part of that sea with an oxyty of 2.43 ml/l ((Zenkevitch 1963) citing from Uschakov (1945)). The data given by Zenkevitch are plotted together with our data and those of Somov (1955) in Fig. 22. This offers a clue to the origin of the low oxyty water. The comparison of vertical oxyty distribution with sigma-t distribution indicates that Chukchi minimum oxyty bottom water and Beaufort Sea minimum oxyty water are of the same density. Zenkevitch (1963) identifies the northwestern Chukchi Bottom water as Atlantic in origin. Thus the very top of the Atlantic water, with its higher temperature and salinity, intrudes up the continental shelf of the Chukchi Sea under the Chukchi/Pacific surface layer. The contact with the bottom lowers the oxyty because of benthic repiration. The Atlantic water contains only about 0.93 µg.at P/1, as phosphate when it sinks off Spitsbergen along the continental shelf, and it maintains this amount except where it intrudes upon the Chukchi shelf. The overlying Chukchi Sea water, with its high nutrient level maintained by continuous Pacific input plus local in situ regeneration of intense summer productivity, maintains a sink of material into the upper layer of the Atlantic water where it rests on the bottom. This increases the nutrient concentration in that layer reciprocally with the oxygen decrease.

The association of low oxyty layers with bottom waters is not uncommon: Richards (1961) cites several instances other than the usual bottom effect of lower oxyty in the lowest few metres; Soule (1940) showed that the low oxyty layer in the Labrador Sea is associated with the shelf; also, Thompson and Barkey (1938) found that waters deoxygenated by contact with the bottom occur at intermediate depths in some west Canadian fjords.

Trask (1953) demonstrated a relationship between the organic content of the sediment and the oxyty of the bottom water in the Gulf of Mexico. He found maximum organic content and minimum oxygen in the "area where the oxygen minimum layer impinges on the bottom (sides) of the basin of the Gulf of Mexico and (it) is consequently the zone of the lowest oxidation diffusion gradient." This situation seems to compare very well with that in the Chukchi Sea.

It is reasonable to consider models 2 and 3 as acting together; there are in fact opposed circulations, one above the other, in this part of the Arctic system, and it is therefore quite probable that the very low oxygen water on the shelf has arrived there from regions in which model 2 has already taken effect, to be further deoxygenated by contact with the bottom. The model 2 conditions are maintained over the deep water of the Canadian Basin to a diminishing degree in the western and northwestern extremes of the Beaufort Sea gyral. We can thus expect a tongue of low oxyty water to extend from the Chukchi Sea toward the Pole, tending to stream partially with the Transpolar Drift, but being partially deflected to the east by entrainment in the Beaufort Sea gyral.

Summary

Various proposed causes of low oxyty waters in the ocean are reviewed. The special circumstances surfounding the Beaufort Sea minimum oxyty layer are described and the observed profiles presented.

Three models are offered:-

- 1. A sinking detritus model in which particulate matter oxidizes in the pycnocline. The model fails because no special accumulations of detritus have been detected. The productivity of the overlying Beaufort Sea water is very low and thus a poor source of detritus. This type of process has never been really recognized as occurring in nature.
- 2. A circulatory model with opposing currents, one above the other, and a layer of no motion in between. The conditions for such a system are The oxycline in the upper (Pacific) present. water originates in the Chukchi Sea from highly productive water sinking under the surface layer. The sharp tongue of low oxyty in the very top of the Atlantic water is caused by this water being "older" due to the absence of horizontal motion where the pycnocline and the countercurrents coincide to minimize vertical and horizontal advection. This model is consistent with the observed distributions. But an ancillary process is also occurring.

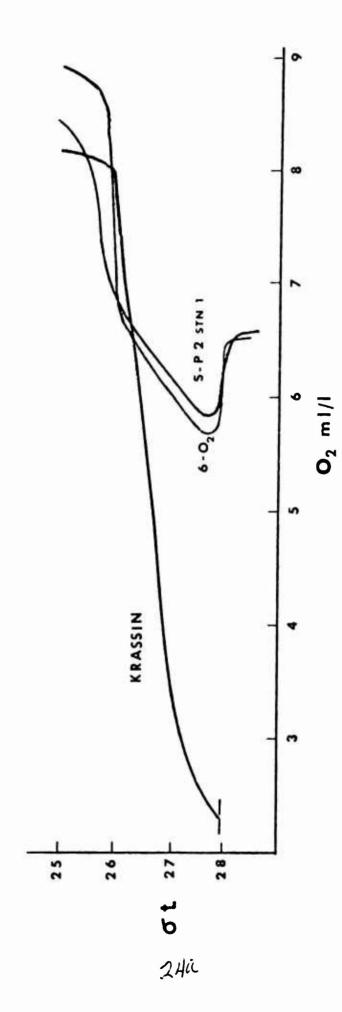


Fig. 22. Plot of oxyty against sigma-t for three stations; Krassin data from the Chukchi shelf, N-P2, and 6-02 from the Beaufort Sea.

A model involving shelf bottom water formed on the Chukchi shelf and advected into the Beaufort Sea. Soviet data from the KRASSIN expedition (1935) show a layer of very low oxyty formed on the bottom of the northern Chukchi Sea. This is shown to be Atlantic water intruding up the shelf to a depth of less than 150 m. The density of this water matches that of the Beaufort Sea low oxyty layer.

It is concluded that there is a tongue of low oxyty water extending out poleward from the northern Chukchi drawn along the Transpolar Drift, perhaps entrained somewhat into the Beaufort Sea gyral; it decays as it mixes away from the region of lowest oxyty which occurs where the surface layer of the Atlantic water mass, a rather stagnant layer in the circulation in this area of the Arctic Basin, impinges on the Chukchi shelf. This model is compared with a similar occurrence in the Gulf of Mexico described by Trask (1953).

These conclusions are reached from comparison with previously devised models from other oceans and not from synoptic data. They represent a prediction of conditions occurring about the "convergence" and sinking of Chukchi Sea water, and imply that the Chukchi Sea is surprisingly productive.

A final observation: it is the water of "Pacific" origin which contains the DSL of the Arctic. The DSL is thus associated with the water containing the highest organic content — it is not implied that the sound scatterers are responsible for significant oxygen demand but that the presence of nekton in such relatively high concentrations is indicative of the high productivity of the Chukchi Sea.

Postscript

In order to test the models proposed here, much more field work is required, although a more extensive survey of data available in other institutions would be very useful.

It is interesting to speculate on the universality of the phenomenon described, for this particular zone of low oxyty gives an opportunity of studying in miniature processes occurring elsewhere in the world ocean on a much larger scale. The Arctic Ocean is very stratified in its upper 300 metres; therefore biological regeneration and cycling occur at very shallow depths. Circulation is rapid for the most part, so that any minimum of advection shows

up in the oxygen distribution. The surface water is sigma-t 24 to 25; at 300 m, the density is about sigma-t 27.9. Such a gradient is extraordinary in waters of oceanic dimensions. The stable platforming of ice stations and the protracted periods of study which they allow make the Chukchi-Beaufort Sea low oxyty water an excellent subject for future study, in that the immediate causes of the observed profiles can be studied more intensively than is usual in oxygen distribution analysis from shipboard.

The following continuation of this study is proposed, assuming a drift station in the northwestern Chukchi Sea drifting northward.

- 1. Chukchi Sea productivity studies.
- 2. Profiles of nutrients through the "convergence" of Chukchi and Arctic surface water.
- 3. Current velocity and eddy diffusivity studies in the upper layers of the Atlantic water in the Arctic Basin.
- 4. Analysis of the regeneration process over the Chukchi shelf.
- 5. Study of the organic constituents of the sediments of the Chukchi shelf in order to ascertain whether this material is more concentrated where the minimum oxyty water intrudes upon the shelf.
- 6. Finally, from the data compiled, it would be possible to design an analogue model of the processes involved in the formation of the low oxyty water, from which the relative importance of the several causes could be 4ssessed.

IV. STUDIES ON THE PLANKTONIC COPEPODS OF THE BEAUFORT SEA

Introduction

The first work on the plankton of the Arctic Ocean was the result of the voyage of the "Fram", under Nansen, in 1893-1896, (Sars, 1900). In 1931, the "Nautilus" became the first submarine to be used for research in the north; zooplankton collections were made north of Spitsbergen and were reported on by Farran (1936). The first major zooplankton collections in the Eurasian Basin were made by the Russian "Sedov" expedition in 1937-1939 (Bogorov. The U.S.S. "Burton Island" made surface collections in the coastal and continental shelf areas of the Beaufort and Chukchi Seas in 1950 and 1951 (see Johnson, 1953, 1956; Hand and Kan, 1961), but it was not until the Russiam ice station NP-2 was occupied in 1950 and 1951, that the first year-long study of the vertical distribution of zooplankton in the Arctic Ocean was made. This was also the first time that plankton had been collected from depths greater than 300 m in the Arctic; until Brodskii and Nikitin (1955) reported this work, only the plankton of the upper layer of the Arctic Ocean had been known.

The submarines "Seadragon" and "Skate" made cruises in the Canadian Basin during which an automatic, multiple net sampler was used to collect the plankton of the upper 200 m. The results of these cruises were reported by Grice (1962), Mohr and Geiger (1962), and Geiger (1966).

In 1957 the American Drift Station Alpha repeated the type of survey made by the Russians on NP-2 (Johnson, 1963). Fletcher's Ice Island (T-3) was first occupied in 1952, and since then has provided a platform for oceanographic research. Marine biology in general, the epipelagic amphipods, and the pelagic polychaetes were studied on T-3 by Mohr, Barnard, and Knox respectively (1959). The results of comprehensive studies of the vertical distribution of plankton made from T-3 in the Canadian Basin have been published by Johnson (1963), Grainger (1965), and, most recently, by Harding (1966), and Harding and Dunbar (1968). In these latter studies, the distribution of the plankton has, for the first time, been related to the hydrography of the area. Of the zooplankton collections made in the Arctic, only three have been used to study the vertical distribution of these organisms to great depths in the Canadian Basin (Brodskii and Nikitin, 1955; Johnson, 1963; Harding, 1966; Harding and Dunbar, 1968).

The collection dealt with here was made on T-3 during the summer of 1966. It is unusual in that it is one of the very few collections by horizontal towing made below Arctic ice (Grice, 1962), and for the first time in the Arctic, "multiple horizontal tows" which provide simultaneous samples of plankton from a variety of depths, were used.

Materials and Methods

Zooplankton collections were made from thirteen stations occupied at T-3 during the summer of 1966, between June 25 and August 27. During that period, the ice island drifted along an erratic westerly track from a position at 75°46.3'N, 152°17'W to 75°38'N, 155°37'W; the overall distance covered being very small, about 400 miles north of the Alaskan coast (Fig. 1).

Most of the zooplankton collections made at these thirteen stations were horizontal tows using the drift speed of the ice island attained during periods of high wind. At these times, the ice island may drift at speeds of up to 0.5 knots relative to the water beneath it. Since wind speed and directions are never constant, and as no flow meter was used with the plankton nets, it is impossible to estimate the amount of water filtered by the nets.

Similtaneous collections were made from various depths using a multiple horizontal tow method. Six nets were hauled at the same time, the rings being suspended at the desired intervals from a heavily weighted cable (Fig. 5). Nets of mesh numbers 6 and 0 were used mounted on 0.5 and 1 m rings. (For detailed station list and sampling information, see Appendix 1.)

The samples were preserved in formalin and were sorted at the Marine Sciences Centre of McGill University during 1970 and 1971. The larger samples were split using a Fulsom Plankton Splitter, and one-half or one-quarter of the sample was counted while the remainder was searched for the rarer species only.

The plankton collections were made in 1966 and 1967 in conjunction with a study of sound scattering layers in the Arctic Ocean in cooperation with the Lamont-Doherty Geological Observatory. They were taken by Mr. William Hansen of the Marine Sciences Centre, McGill University.

CESERVATIONS AND RESULTS

Systematics 1.

Thirty-eight species of copepods have been identified during the course of this study. Of these, five need further clarification. In addition, there are nine unidentified specimens; of these, eight are sub-adult copepodites and therefore difficult to identify, and one is a mature female, referred to below as "Unidentified Species A". Copepodite stages were identified for all species except the smallest (Microcalanus pygmaeus, Oithona similis, Oncaea borealis, and Spinocalanus sp.). Nauplii, when caught, were not identified to species as the nets used in the sampling were of too large mesh sizes to collect nauplii adequately. Whenever possible, the copepodites as well as the adults were sexed. Sources used as aides to identification included Sars (1900, 1903, 1918, 1925), Brodskii (1950), Park (1970), Johnson (1963) and Grainger (1963).

The following is a systematic list of the species found:

Order Calanoida Family Calanidae Genus Calanus

C. hyperboreus (Krøyer) C. glacialis (Jaschnov) C. cristatus (Krøyer)

Family Eucalanidae Genus Eucalanus

4 E. bungii bungii (Giesbrecht)

Family Pseudocalanidae

Genus Pseudocalanus

P. minutus (Krøyer)

Genus Microcalanus

6 M. pygmaeus (G.O. Sars)

Genus Spinocalanus

S. abyssalis var pygmaeus (Farran)

S. magnus (Wolfenden)
S. sp.

Family Aetideidae Genus Aetideopsis

10 A. multiserrata (Wolfenden)

A. rostrata (G.O. Sars)

Genus Chiridius

C. obtusifrons (G.O. Sars) 12

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Genus Caidius
                    13 G. brevispinus (G.O. Sars)
                    14
                        G. tenuispinus (G.O. Sars)
Genus Pseudochirella
                    <del>1</del>5
                        P. spectabilis (G.O. Sars)
Genus Chiridiella
                    16
                        C. abyssalis (Brodskii)
Family Euchaetidae
Genus Euchaeta
                        E. glacialis (H.J. Hansen)
                       E. polaris (Brodskii)
Family Phaennidae
Genus Undinella
                   19 <u>U. oblonga</u> (G.O. Sars)
Family Scolecithricidae
Genus Scolecithricella
                   20
                        S. minor (Brady)
Genus Scaphocalanus
                   21
                        S. magnus (Th. Scott)
                        S. brevicornis (G.O. Sars
                   22
Family Centropagidae
Genus Centropages
                   23
                       C. hamatus (Lilljeborg)
Family Temoridae
Genus Temora
                   24
                       T. longicornis (Müller)
Genus Eurytemora
                   25 <u>E</u>. <u>sp</u>.
Genus Temorites
                   26
                       T. brevis (G.O. Sars)
Family Metrididae
Genus <u>Metridia</u>
                   27
                       M. longa (Lubbock)
                   28
                       M. lucens (Boeck) (pacifica?)
Family Heterorhabdidae
Genus Heterorhabdus
                       H. norvegicus (Boeck)
                   30 H. compactus (G.O. Sars)
Family Augaptilidae
Genus Haloptilus
                   31
                      H. acutifrons (Giesbrecht)
Genus Augaptilus
                   32 A. glacialis (G.O. Sars)
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Genus Pseudaugaptilus 33 P. polaris (Brodskii) Genus Pachyptilus 34 P. eurygnathus (G.O. Sars) Order Cyclopoida Family Oithonidae Genus Oithona 35 <u>0</u>. <u>similis</u> (Claus) Family Oncaeidae Genus Oncaea 36 O. borealis (G.O. Sars) 37 0. sp. Genus Lubbockia L. glacialis (G.O. Sars) 38 39 Unidentified Species A

This appears to be an unusually lengthy species list for the upper water of the Arctic Basin. Brodskii and Nikitin (1955) reported finding 48 species of copepods from the Russian drifting station NP-2 which was in much the same area in 1950 as T-3 was for this study. Harding (1966) has reported 45 species from T-3. These two studies, however, included samples from 4000 and 3000 m respectively, while the present study is complete to 300 m only. Comparable studies have reported 18 species from the upper 200 m of the Arctic Ocean (Grice, 1962) and 12 from T-3, 300 m (Grainger, 1965). Johnson (1963) found 36 species down to 2000 m at Station Alpha, and Zenkevitch (1963) cites 33 species of planktonic copepods as being common in the Chukchi Sea; this number is now known to be low - Grainger (1965) cites evidence from the literature to show that about 30 copepod species are known in the upper 300 m, 50 have been taken between 300 and 1000 m, and 20 from below 1000 m. Brodskii (1950) lists 39 species of calanoids from all depths of the central part of the Arctic Ocean, 12 of which are endemic to the Polar Basin, 8 also occur in the Norwegian and Greenland Seas, and 19 are also found in the Atlantic Ocean. To these should be added the five species which Johnson (1956) lists as being expatriates from the Bering Sea of the Pacific Ocean.

An explanation for the high number of species taken in the upper 300 m in this study may be that since the winds (and therefore the drift speeds of the ice island) tended to be fastest at night, many of the plankton tows were made during the night. During the middle of summer the reduction of light at night is minimal and vertical migration may be reduced or absent in some species (Bogorov, 1946); but for

at least part of the sampling period, the reduction of light was probably sufficient to induce vertical migration in most of the copepod species (Ligby, 1961). Previous studies on vertical migration in polar seas have been in ice-free areas, however, Hansen (personal communication) reports that in 1966, T-3 was surrounded by open water. In this case, some of the species found in the present collection may be expected to be well above their normal daytime vertical ranges. For instance, Lubbockia glacialis found by Harding (1966) only below 900 m was taken in six of the fourteen samples taken below 70 m with the number 6 nets. The method of sampling used in this study may also be of importance in this regard. A net towed for several hours at the same depth is more likely to catch the rarer species at that depth than a net hauled vertically through a large depth interval. This may be the explanation for the fact that many species (Aetideopsis multiserrata, Temorites brevis, Scaphocalanus magnus, Chiridius obtusifrons, etc.) were found 50 or 100 m above the depths at which they were found by Harding (1966) or Johnson (1963).

The five species mentioned above as being in need of taxonomic clarification are <u>Metridia lucens</u> (pacifica?), <u>Spinocalanus sp., Oncaea sp., and Eurytemora sp.</u> In addition, several comments are in order with regard to the taxonomy of certain other species.

Metridia lucens

Metridia lucens (Boeck, 1865) is a common Atlantic species and has been reported from East Greenland (Jespersen, 1939), northwest of Spitsbergen (Farran, 1936), Oslo Fjord (Wiborg, 1940) and Davis Strait (Jespersen, 1928). It was discovered in the Pacific and Giesbrecht (1895) and others noted differences in the morphology. Brodskii (1950) placed the Pacific form in a separate species as M. pacifica. Damkaer (1964, cited in Park, 1968) studied both Atlantic and Pacific specimens and could find no distinct morphological differences which would warrant the formation of a new species. It is important that this controversy in the literature be resolved as Johnson (1956) has listed M. pacifica as one of the "Pacific expatriates" (see below) found in the Chukchi and Beaufort Seas. If in fact M. pacifica M. lucens are one species, it becomes impossible to determine whether any one specimen has entered the Polar Basin from the Pacific or the Atlantic Ocean and the whole question of expatriatism for this species becomes more complex. It may be that as more biological work

is done in the Arctic Ocean, the mode of entry of this species will be clarified. As only one individual was collected, and it was not possible to examine the taxonomy in great detail, we have placed the specimen in the species <u>M. lucens</u>, especially as the validity of the Pacific species is doubtful.

Spinocalanus magnus (males)

Johnson (1963) reported finding two calanoid males which he recorded only as "Spinocalanus? males", since parts of the swimming feet were missing, and because the structure of the fifth legs was unusual in that they were uniramous which is not the case for other males of the genus. Harding (1966) found complete specimens and was able to assign the males to the species Spinocalanus magnus. In this study, many of these males were caught; mostly submature individuals (stages IV and V) and a few mature specimens. Morphological examination appears to confirm Harding's findings, although in most cases the swimming legs are not all present. Perhaps of greater significance is the observation that these males only occurred in samples which also contained large numbers of females of S. magnus and that although the mature males were considerably smaller than the stage VI females, the stage V individuals were less so; the stage IV males and females were the same size and were indistinguishable except for the presence of the partially formed fifthlegs in the young males.

Spinocalanus sp.

One species of Spinocalanus present in the collection could not be identified. It occurred in one sample from 250 m with large numbers of Microcalanus with which it was easily confused. The sample as a whole was not well preserved and in most specimens the swimming legs were damaged. The overall size of the mature females (0.8-0.9 mm) is smaller than the size ranges given by Brodskii for any Spinocalanus species. The smallest of them is S. longicornis (1.1 mm) and it may be that the present specimens belong to that species. For the time being they are listed as Spinocalanus sp.

Oncaea sp.

Two mature female specimens of the genus $\underline{\text{Oncaea}}$ were found in one haul from 300 m. That they are not $\underline{\text{O}}$ borealis is immediately obvious due to the lack of the

conspicuous dorsal hump found in that species. In addition, they are somewhat larger than <u>O. borealis</u> which Sars (1918) reported as measuring 0.70 mm at the most. These specimens both measure 0.91 mm (total length). Other <u>Oncaea</u> species known from the Arctic are <u>O. minuta</u> (which is much too small to be confused with these specimens) and <u>O. notopus</u> (Bogorov, 1946; Jespersen, 1939). <u>O. notopus</u> is cited by Sars (1900) as having a maximum size of 0.70 mm in Oslo Fjord. These two specimens may belong to a new species, or the size range given by Sars for <u>O. notopus</u> may be too small. It is not an uncommon phenomenon to find that Arctic representatives of species also found in subarctic or temperate regions are larger than their southern counterparts.

Eurytemora sp.

One mature female, found at a depth of 15 m, agrees with all the characteristics of the genus Eurytemora, but with none of the species descriptions in the current literature. Its overall length is 1.76 mm and the structure of the fifth thoracic leg is unusual in that the distal segment bears three, rather than two, spines; two apical (as is usual) and one lateral. The pterygoid processes of the terminal thoracic segment are obtuse compared with those of other species reported from the Arctic such as E. herdmani (Grainger, 1965; Johnson, 1956) and E. transversalis (Johnson, 1956). This specimen is therefore assumed to belong to a species new to science and will be fully described in a more appropriate publication in the near future.

The occurrence of a member of this genus in this collection is in itself unusual (see below).

Calanus hyperboreus

Grainger (1963) published length frequency histograms for the cephalothoracic length of <u>Calanus hyperboreus</u> in the eastern Canadian Arctic. The size range for mature females is given as 5.67 to 7.43 mm. Jespersen (1937) published a slightly larger range for the same species in Baffin Bay and Davis Strait of 5.54 to 7.70 mm. He was able to relate this variation to water temperature, the smaller animals being found in southeastern Davis Strait, and the larger ones in the colder waters of the Labrador Current and Baffin Bay. His conclusion was that the size of <u>C. hyperboreus</u> was inversly related to water temperature.

In this study, a number of small specimens were found which showed no morphological differences from the larger specimens. The size range for <u>C</u>. <u>hyperboreus</u> in the central Arctic is 5.35 to 7.50 mm.

Tidmarsh (personal communication) has found an even larger size range for this species in northern Baffin Bay and Kane Basin; from 5.12 to 7.68 mm.

In these three latter areas the water temperature is generally colder than in the area of Davis Strait, and yet contrary to what would have been expected from Jespersen's conclusions, the size range of <u>Calanus hyperboreus</u> has been extended only toward the smaller end of the range.

Genus Euchaeta

The genus <u>Euchaeta</u> was split by Scott in 1909 into two genera: <u>Euchaeta</u> and <u>Pareuchaeta</u>. The distinguishing characteristic was the shape of the inner bristle of the caudal rami. Vervoort (1957) examined representatives of many species of both genera over a wide geographical area and could find no constant morphological differences between them. He replaced <u>Pareuchaeta</u> in <u>Euchaeta</u>. For this reason the species in this collection are listed as <u>Euchaeta glacialis</u> and <u>E. polaris</u>, and are, in fact, identical with the species <u>Pareuchaeta glacialis</u> and <u>P. polaris</u> reported from the Polar Basin by Harding (1966), Grainger (1965), Brodskii (1950), Johnson (1963) etc.

Pseudochirella spectabilis

One mature male and one mature female of this species were identified from this collection, as well as stage IV and V individuals. The mature specimens fitted Brodskii's (1950) description in every detail except one. This one characteristic — the presence of five "massive spines" on the inner margin of the first basipodite of the fourth pair of swimming legs in the female — is important as it is a quick and easy means of making the identification. In this female specimen, however, there were nine of these spines on the fourth leg. Jespersen (1934) has noted variations in the number of these spines in other members of the genus.

Pseudaugaptilus polaris and Chiridiella abyssalis

Brodskii (1950) notes that the males of both of these species are unknown. A single mature male of each species occurred in this collection. A preliminary search

of the literature has not revealed descriptions of these males. If none should be found, the males of <u>Pseudaugaptilus polaris</u> and <u>Chiridiella abyssalis</u> will be described in a future publication.

2. Reproduction

The presence of a number of copepodite stages as well as mature individuals of any species indicates that it is breeding successfully in the area of collection. From the list below, it appears that all the species in the collection, except six, are breeding successfully in the Arctic Basin. Three of these exceptions (Calanus cristatus, Metridia lucens and Eucalanus bungii bungii) are expatriates from the Bering Sea; that is, they are strays from their usual range of distribution and successful reproduction (see below). Another, Temora longicornis, might be considered an expatriate from the Atlantic as it is known only from that ocean, although more samples in the eastern Canadian Arctic might link its previous known range with this finding from T-3. Two more, <u>Eurytemora sp.</u> and <u>Centropages hamatus</u> are members of brackish water, neritic genera. Although both are known on the coasts of the Arctic Ocean, these animals might be considered "expatriates" in that they are well out of their normal ranges in terms of salinity. They have not been reported from T-3 except where it has been in coastal areas. While the adults may survive in areas of higher salinity, successful reproduction would be doubtful.

The following is the list of stages recorded, per species:-

Aetideopsis multiserrata	M F	VI	V	IV	III	
Aetideopsis rostrata	M F	VI	V V	IA	III	
Augaptilus glacialis	M F	VI	V V		III	
Calanus cristatus	F		V			
Calanus glacialis	M F	VI	٧	IV	III	ΙΙ
Calanus hyperboreus	$_{\mathbf{F}}^{M}$	VI	V	IV	III	II

Centropages hamatus	r.:	VI					
Chiridiella abyssalis	N.	VI					
Chiridius obtusifrons	N. F	VI	V V	IV IV	III	II	
Eucalanus bungii bungii	M F	VI	v				
Euchaeta glacialis	M F	VI	V	IV IV	III	II	Ι
Euchaeta polaris	F	VI					
Eurytemora sp.	F	VI					
Gaidius brevispinus	M F	VI	V	IV	III	II	
Gaidius tenuispinus	M F	VI	V V	IV	III		
Haloptilus acutifrons	F	VI	٧	ΙV			
Heterorhabdus compactus	F	VI	٧	IV	III		
Heterorhabdus norvegicus	M F	VI	٧	IV	III		
Lubbockia <u>Elacialis</u>	F	VI					
Metridia longa	M F	VI VI	V V	IV	III		I
Metridia <u>lucens</u>	F	VI					
Microcalanus pygmaeus	M F	VI	j	uveni	les		
Cithona similis	F	VI	j	uveni	les		
Oncaea borealis	M F	VI	co	pulae	juve	niles	
Oncaea sp.	F	ΛI					
Pachyptilus eurygnathus	F	ΛI	٧				
Pseudaugaptilus polaris	M F	VI	V	IV	III		

Pseudocalanus minutus	M F	VI	V V	IV	III	ΙΙ
Pseudochirella spectabilis	M F	VI	٧	IV IV		
Scaphocalanus brevicornis	M F	VI	V V	IV		
Scaphocalanus magnus	M F	VI	٧	IV IV	III	II
Scolecithricella minor	M F	VI VI	٧	IV		
Spinocalanus abyssalis (var. pygmaeus)	M F	VI	V	IV		II
Spinocalanus magnus	M F	VI VI	٧	IA	III	
Spinocalanus sp.	M F	VI	j	uveni	iles	
Temora longicornis	M	VI				
Temorites brevis	M F	VI VI	V V	IA	III	
<u>Undinella</u> <u>oblonga</u>	M F	VI	V V			
Unidentified sp. A.	F	VI				

While other species were also caught only as mature individuals or in one or two young stages (<u>Lubbockia glacialis</u>, <u>Chiridiella abyssalis</u>, <u>Euchaeta polaris</u>, <u>Oncaea sp</u>., and <u>Unidentified Species A</u>), the limitations of the sampling methods must be borne in mind. Of these five species, only <u>Lubbockia glacialis</u> was taken in more than one sample. The others are all extremely rare, and it is not unusual to find only one or two individuals. The younger stages of <u>L. glacialis</u> are small enough to be missed by a number 0 or 6 net (even the mature individuals of this species were only captured with the number 6 nets) In fact, when interpreting the above results, the efficiency of large mesh plankton nets in sampling small size organisms or the smaller juvenile stages of some species should always be considered. In spite of this, Harding (1966) has shown that <u>L. glacialis Chiridiella abyssalis</u> and <u>Euchaeta polaris</u> do in fact breed successfully in the Arctic Ocean.

Of the thirty-nine species in the collection, four were caught throughout the depth range under consideration, and in sufficient numbers that some quantitative analysis might be made of their reproductive cycles and of the depth distribution of their reproductive stages. These species are Calanus hyperboreus, C. glacialis, Metridia longa and Euchaeta glacialis.

3. Breeding Cycles

There were five more or less distinct time periods during the summer of 1966 in which most of the samples were taken. These were June 25 to July 10, July 23 to 25, August 8 to 11, August 17 to 19, and August 27 to 28. Enough plankton samples were taken in each of these time intervals to make analysis of the reproductive cycles of each of the four species above possible. In presenting the relative numbers of growth stages, percentages rather than absolute numbers have been used in all cases, in order to avoid the bias introduced by differences in the number of samples or in overall towing times in each interval.

Calanus hyperboreus

Harding (1966) found that <u>Calanus hyperboreus</u> does not complete its development in one year in the Arctic, but may take two years or even longer to reach maturity. This phenomenen has been noted for other copepod species in Tanquary Fjord and the Arctic Ocean (Cairns, 1967, 1969). A slower development rate to maturity may be a method of conserving energy and diverting it to be used in the strenuous process of adaptation to life in the rigorous Arctic environment (Dunbar, 1968). Cairns (1969) notes the difficulty that he and other workers have encountered in following the development patterns of <u>Calanus</u> species, and contends that in Tanquary Fjord and the central Arctic Ocean <u>Calanus</u> hyperboreus and <u>C. glacialis</u> are opportunistic breeders, or have multi-year cycles, reproducing whenever environmental conditions will allow.

Table 1. Relative occurrence of the stages of <u>Calanus</u> hyperboreus in each of five sampling periods in 1966, expressed as percentages of the total copepodite population.

Stage	June 25 - July 10	July 23 - 25	August 8 - 11	August 17 - 19	August 27 - 28
I	_	_	-	-	-
II	0.12	0.3	0.1	0.01	-
III	1.7	4.0	1.3	1.0	0.5
IV	9.3	18.8	25.8	9.2	9.3
٧	25.2	35.3	37.9	49.3	46.6
VI F	62.4	40.5	34.9	40.5	43.6
M IV	1.2	1.1	-	0.01	-
N	2,416	899	779	7,276	2,136

Calanus hyperboreus is known to overwinter as stage III or IV (Grainger, 1959); in Arctic areas where this species has a two- or multi-year breeding cycle, subsequent winters must be spent as stage V or VI. The increase in numbers of stage IV and V Calanus hyperboreus during the first part of the sampling period shown in Table 1 and Fig. 23 reflects the maturation of the first year overwintered individuals.

Johnson's (1963) data indicate that spawning took place in late December on Drift Station Alpha; Cairns (1969) found that on T-3, C. hyperboreus spawned in early September in 1964; in the eastern Arctic, Grainger (1959) found that it occurred in May. Brodskii and Nikitin (1955) found the largest numbers of stage I present in June, indicating that spawning took place in the Arctic Basin in May in 1950 since Grainger's (1959) data indicate a three or four week development time from the first appearance of the nauplii to that of copepodite I. This variation in the time of spawning substantiates Heinrich's (1961) observation that Calanus hyperboreus and Metridia longa belong to a group of copepods which are capable of breeding in the absence of phytoplankton. These species do not appear to feed to any extent until stage II or III is reached.

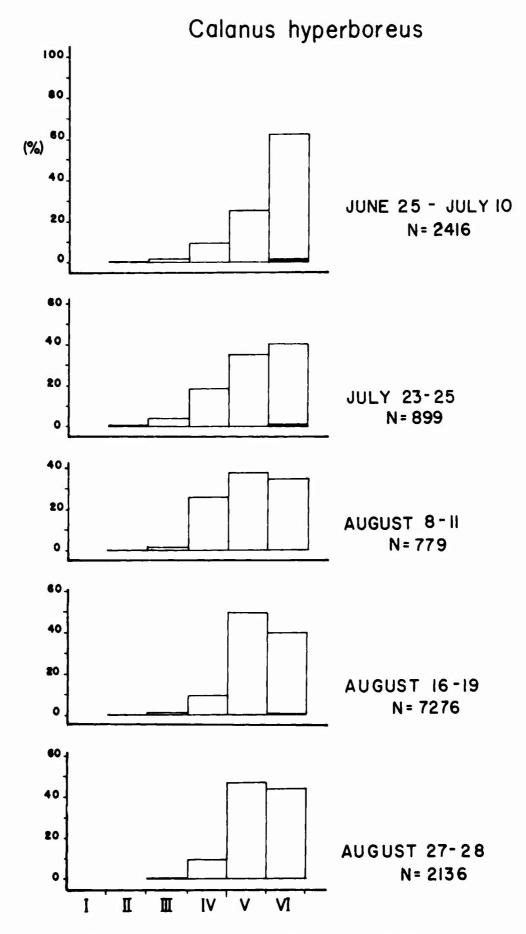


Figure 23. Relative occurrence of the copepodite stages of <u>Calanus</u> <u>hyperboreus</u> in each of five sampling periods in 1966. Shaded areas represent males.

The presence of higher numbers of mature females and males in June and July indicates that in 1966 spawning of Calanus hyperboreus occurred before sampling began, perhaps in late May as observed by Brodskii and Nikitin (1955). Although no stage I copepodites were caught, stage II was present throughout the period of sampling except in late August, by which time moulting to stage III appears to have occurred. Bogorov (1938) found that "biological spring" (the phytoplankton bloom) takes place in August in the Arctic Ocean. The development of C. hyperboreus to stage III and feeding in preparation for overwintering coincide Increases in the numbers of stage V and VI with the bloom. at this time reflect the two-year cycle of this species as the one-year-old individuals mature in preparation for a second winter and spawning in the following May.

Calanus glacialis

Many of the comments made above regarding two- or multi-year cycles also apply to <u>Calanus glacialis</u>.

Table 2. Relative occurrence of the stages of <u>Calanus</u> glacialis in each of five sampling periods in 1966, expressed as percentages of the total copepod population.

Stage	June 25 - July 10	July 23 - 25	August 8 - 11	August 17 - 19	August 27 - 28
I	-	-	-	•	_
II	-,	•3	•5	-	-
III	1.9	6.5	1.6	-	- I
IV	8.9	3.8	•5	,6	-
V	37.7	28.9	25.4	17.5	37.4
VI F	50.9	57.9	68.6	75.9	60.9
VIM	.5	2.6	3.2	•3	1.7
N	738	58 2	185	1553	174

The data presented in Table 2 and Fig. 24 show that stages V and VI of <u>C</u>. <u>glacialis</u> were dominant throughout the 1966 season. This species is known to overwinter as stage III (Grainger, 1965) during its first year and this is reflected in the presence of stage III in the first half of the sampling period only. The second winter is spent as stage V or VI as shown by the decrease in numbers of stage V and simultaneous increase in stage VI throughout most of the summer.

Heinrich (1961) has shown that <u>Calanus glacialis</u> breeds only in the presence of large amounts of phytoplankton. The appearance of increased numbers of males and the large numbers of females in August indicate that spawning occurred during the "biological spring". The stage I copepodites had not yet appeared before the sampling period ended.

Euchaeta glacialis

Unlike the three other species discussed here, Euchaeta glacialis is predatory, and is therefore not directly dependent on an abundance of phytoplankton for successful breeding. Johnson (1963) observed egg sacs and spermatophores associated with mature individuals in both winter and summer samples. This indicates that breeding may occur throughout the year and substantiates Brodskii and Nikitin's (1955) finding of stage I copepodites in nearly every month. Both of these reports note that the greatest number of stage I occurred in early June, leading to the conclusion that although breeding probably occurs all year round, there is a peak season not long before June. Heinrich (1961) points out that the fact that the various copepod species have different breeding cycles - all year round or with or without phytoplankton blooms - is useful to the community as a whole as it reduces interspecific competition for food.

Calanus glacialis

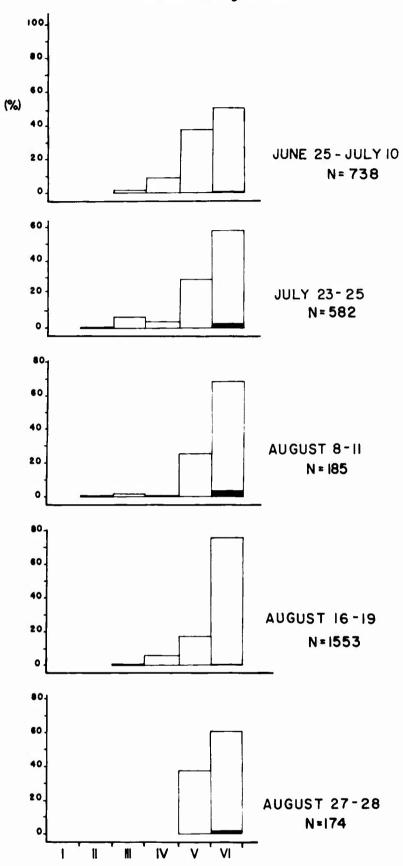


Figure 24. Relative occurrence of the copeopodite stages of Calanus glacialis in each of five sampling periods in 1966. Shaded areas represent males.

#20

Table 3. Relative occurrence of the stages of <u>Euchaeta</u> glacialis in each of five sampling periods in 1966, expressed as percentages of the total copepod population.

Stage	June 25 - July 10	July 23 - 25	August 8 - 11	August 17 - 19	August 27 - 28
I	1.3	1.0	_	-	-
II	43.0	23.2	2.4	1.0	3.5
III	18.5	66.4	65.4	60.0	26.6
IV F	4.8	1.1	1.2	1.2	1.3
IV M	2.7	0.7	1.2	0.5	0.9
V F	9.4	2.8	13.1	13.0	29.9
N M	12.9	3.0	14.1	22.5	34.6
VI F	7.2	1.3	1.5	1.8	3.3
VI M	0.3	0.5	0.9	<u>-</u>	-
N	1597	937	327	777	549

Table 3 and Fig. 25 present the 1966 data for this species. While the number of stage I copepodites found in late June and early July was small, the high percentages of stage II at this time indicate that a successful spawning did occur and that the majority of the offspring had already passed through stage I before sampling was begun.

Since E. glacialis is a carnivore, it is presumably able to continue its development during the winter months rather than overwintering at a single stage as do the other species discussed. Accordingly, the development to maturity seems to take only one year in this species, and early copepodites caught in 1966 would have been responsible for the generation spawned in 1967.

The data for the stages IV, V and VI are more difficult to interpret. The relatively small numbers of these stages may indicate that the June spawn of the previous year was not particularly successful. In this case, the

population may have been augmented by the year-round reproduction which has been noted by Johnson, and by Brodskii and Nikitin. Some of the mature animals represented here are probably those which spawned just before sampling began in late June 1966, and may be expected to die out during the remainder of the season.

Mileikovsky (1970) has found exactly the same type of year-round breeding cycle with a period of intense spawning in the spring for the predactious pteropod Clione limacina.

Metridia longa

Since the size of the stage I copepodites of Metridia longa approaches the sampling limits of number 0 mesh nets, only the data from the number 6 nets have been used here.

The data from NP-2 (Brodskii and Nikitin 1955) seem to indicate that \underline{M} . longa may breed during a large part of the year, even during the winter. This species like \underline{C} . hyperboreus, was found by Heinrich (1961) to breed independently of the phytoplankton bloom. Grainger (1959) found that at Igloolik in the eastern Canadian Arctic, nauplii of \underline{M} . longa appeared from March to July.

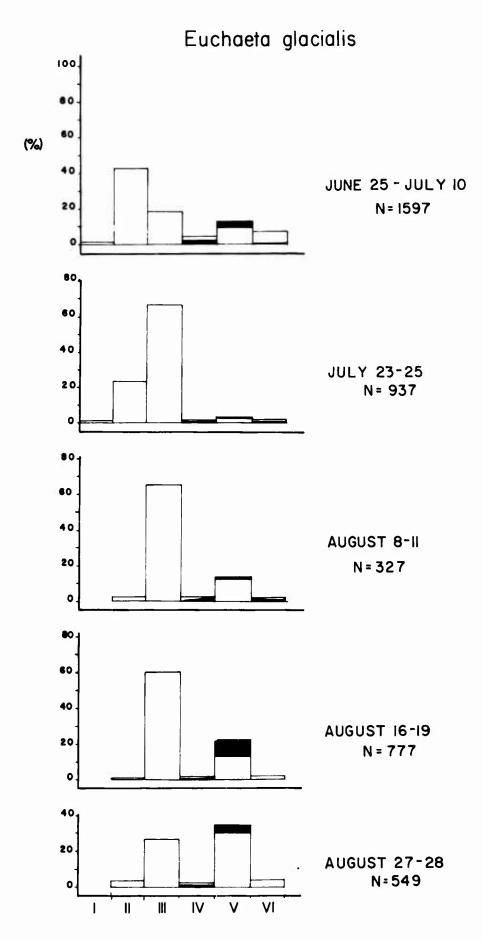


Figure 25. Relative occurrence of the copepodite stages of Euchaeta glacialis in each of five sampling periods in 1966. Shaded areas represent males.

Table 4. Relative occurrence of the stages of Metridia longa in each of five sampling periods in 1966 expressed as percentages of the total copepodite population. Data from number 6 nets only.

Stage	June 25- July 10	July 23 - 25	August 8 - 11	August 17 - 19	August 27 - 28
I	-	0.1	-	19.5	0.1
II	-	-	-	-	-
III	0.3	0.2	-	-	-
IV F	5.9	8.3	2.4	-	0.8
IV M	4.4	5.6	1.2	9.8	0.2
V F	12.2	18.0	18.0	19.5	5.4
V M	20.2	30.6	38.3	24.4	12.9
VI F	52.6	33.3	36,5	26.8	79.9
VI M	4.5	3.9	3.6	-	0.8
N	1539	1320	167	41	1306

The data presented in Table 4 and Fig. 26 show the appearance of a few stage I copepodites of Metridia longa in late July; in mid-August larger numbers. This would indicate that spawning began three or four weeks previously. (Grainger, 1959) in late June or early July, reached a peak in late July, and then decreased again. The large increase in mature females at the end of the sampling period may indicate that spawning may be expected to continue for some time. This increase is accompanied by a decrease in the numbers of stage V.

The data suggested that development of this species continues throughout the winter; the absence of stage II indicates that this stage may be expected to occur during the winter. Similar results were found by Grainger (1959) and Digby (1954).

One last interesting observation with respect to the development of both <u>Metridia longa</u> and <u>Euchaeta glacialis</u> is that while there were always more mature females than males, invariably the stage V males outnumbered the stage V females. A similar observation has been made by Tidmarsh (personal communication) for the eastern Arctic. We are at a loss to explain this phenomenon; data in the literature are of no help since no other authors appear to have sexed the copepodites of these species.

4. Depth Distribution of Reproductive Stages

Using the data from the samples taken with the 0.5 m number 6 mesh nets only, the depth distributions of the copepodite and mature stages for the four species discussed above have been worked out. Several weaknesses in method should be pointed out and borne in mind during the discussion:

- 1. There are no samples in the 1966 collection in the 101 to 199 m range, although there are samples between 200 and 300 m. This means that there are no samples from that part of the Arctic Intermediate Layer which is affected by the Pacific Winter Water. The depth range has been divided into 20 m intervals between 0 and 100 m, as well as one large interval from 200 to 300 m.
- There is only one sample in the interval from 0 to 20 m and this sample took a very small number of individuals: one <u>C</u>. hyperboreus, five <u>M</u>. longa, eighteen <u>E</u>. glacialis and no <u>C</u>. glacialis. Other workers have found this to be the most densely populated depth interval in the Arctic (see below).
- 3. Mature individuals of species as large as <u>C</u>.

 glacialis and <u>E</u>. glacialis may have escaped from the 0.5 m net, especially when it was towed at slow speeds for periods as long as 53 hours.
- 4. In all cases it should be remembered that the depth range sampled here does not necessarily represent the total depth range for these species or any of their stages.

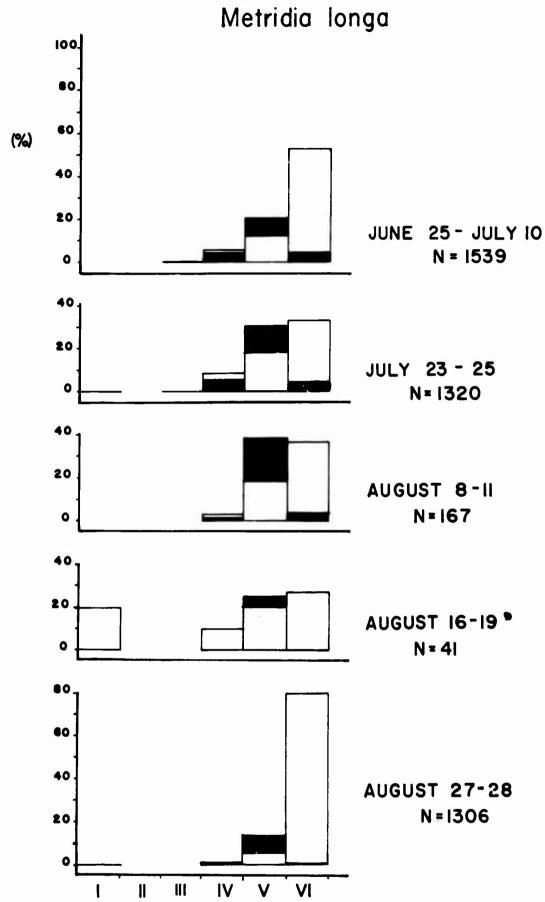


Figure 26. Relative occurrence of the copeopodite stages of Metridia longa in each of five sampling periods in 1966. Shaded areas represent males. Data are from 0.5 m, number 6 mesh nets only.

Calanus hyperboreus

Table 5. Relative occurrence of the copeopodite stages of Calanus hyperboreus in each depth interval.

Depth	F VI	M VI	V	IV	III	II	I	N
0-20 m	-	-	(1)*	-	-	-	-	1
21-40 m	27.1	-	41.2	26.5	4.9	0.3	-	716
41-60 m	33.3	-	51.5	14.0	1.2	-	-	606
61-00 m	56.5	-	38.6	4.7	0.2	-	-	889
81-100 m	54.5	_	37.7	7.4	0.4	-	-1	932
200-300 m	?8.4	2.5	17.2	1.7	0.1	0.1	-	1571
							·	

* only 1 individual caught.

The data presented in Table 5 and Fig. 27 indicate that the mature females of <u>C</u>. <u>hyperboreus</u> prefer the deeper waters of the range under consideration. While 27.1% of the animals in the 21-40 m range were sexually mature, 78.4% in the 200-300 m range were mature. The only mature males captured were in the deepest part of the range; this preference of the males for deeper waters has been noted for other species (Wiborg, 1940).

The immature stages, on the other hand, all seem to prefer shallower water, although the preference becomes less marked as the animals grow.

Calanus glacialis

Table 6. Relative occurrence of the copepodite stages of Calanus glacialis in each depth interval.

Depth	F VI	M VI	V	IV	III	II	I	N
0-20 m								0
21-40 m	44.8	2.0	35.0	14.8	3.0	0.4	-	540
41-60 m	74.1	11.1	14.8	-	-	-	_	27
61-80 m	82.9	1.7	14.9	0.6	-	-	-	175
81-100 m	76.9	2.2	16.5	4.4	-	-	-	91
200-300 m	58.0	1.5	31.8	0.7	8.0	0.4	-	274

The mature males and females of this species do not appear to have such a marked preference for deep waters as do the C. hyperboreus adults. Table 6 and Fig. 28 show that the highest percentages of mature females of C. glacialis occurred in the 41-100 m range with the maximum between 61 and 80 m. The depth of maximum occurrence of the males was slightly shallower, between 41 and 60 m. The stage V individuals do not appear to have a marked preference for any depth in the range studied. Stage IV copepodites of this species are found in the shallower layers (21-40 m) as were those of C. hyperboreus. The data for stages II and III are not sufficient to allow any conclusions to be drawn as to their depth distributions, but Harding (1966) who recorded all stages of both species found that the younger were distributed closer to the surface.

Calanus hyperboreus Ò ĺΟ 50 % E ۷I (m) 3 001 60. 80. 40. I۷ 20. Ш IINO STAGE I'S CAUGHT

Figure 27. Relative occurence of the copepodite stages of Calanus hyperboreus in each depth interval.

Shaded areas represent males.

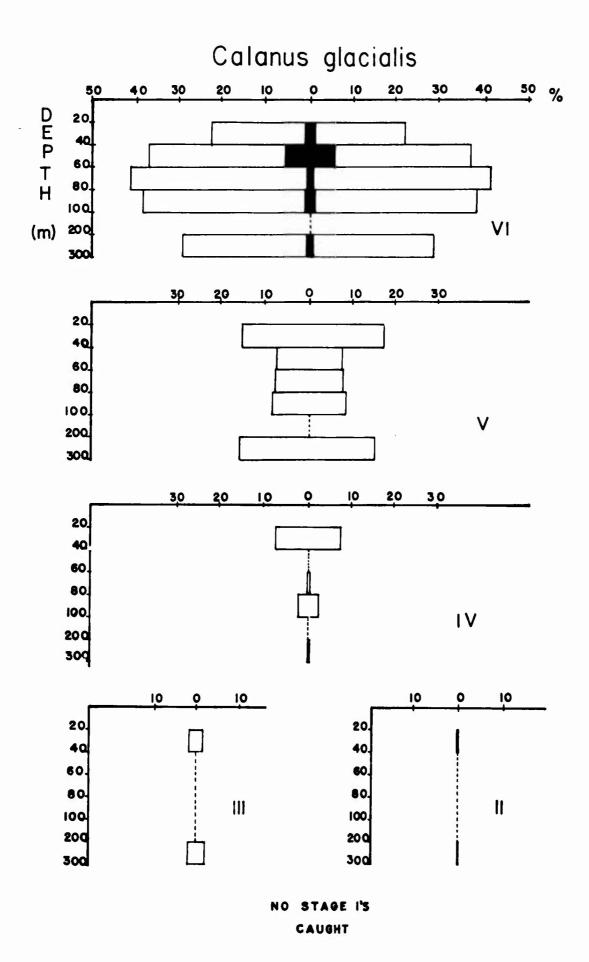


Figure 28. Relative occurrence of the copepodite stages of Calanus glacialis in each depth interval. Shaded areas represent males.

Metridia longa

Table 7. Relative occurrence of the copepodite stages of Metridia longa in each depth interval.

Depth	F VI	M VI	F V	M V	F IV	M IV	III	II	I	N
0-20 m	(3)*	-	(2)*	-	-	-	-	-	-	5
21-40 m	78.9	3.0	4.5	10.5	2.3	-	-	-	0.7	133
41-60 m	83.6	0.3	3.8	12.0	~	0.3	-	-	_	787
61-80 m	77.5	1.6	7.5	13.1	0.2	•	-	-	-	916
81-100 m	37.2	2.2	17.7	31.8	5.5	4.6	0.3	-	0.6	1749
200-300 m	30.2	9.8	15.0	21.8	14.5	8.8	4	-	-	788

^{*} only 3 (or 2) individuals caught — not included in percentage calculations since sample obviously was not representative.

The data shown in Table 7 and Fig. 29 present quite a different pattern from that observed for the preceding species. There is clear evidence here that the mature stage of Metridia longa seeks out the upper water layers. Between 77-84% of all the animals found in the upper 80 m were mature females. Data from Igloolik (Grainger, 1959) show that the centre of the population was deeper than 50 m there but they also show that the 50 m temperature is higher than it is at T-3 during the summer. M. longa is exhibiting a phenomenon often found in arctic-subarctic species; it is found at deeper levels in the more southerly latitudes or in areas of higher sea temperatures. It is well known to be a cold water species.

It can also be seen that the younger stages of $\underline{\mathbf{M}}$. longa are to be found in the deeper areas of the range under consideration, and if this range were extended, even greater numbers might be found. The explanation for this is that unlike other common species dealt with here, $\underline{\mathbf{M}}$. longa releases its eggs in deep water and development through the naupliar and early copepodite stages takes place there. This is substantiated by the findings of Grainger (1959) and Digby (1954).

It is apparent that the mature males prefer the deeper part of the water column under consideration. Wiborg (1940) made a similar observation in Oslo Fjord. Mature males of most calanoid species appear only briefly in the plankton and die quickly after spawning. Since Metridia longa was spawning during the sampling period, and is known to breed in deep water, this preference of mature males for deep water confirms the expected results.

Euchaeta glacialis

Table 8. Relative occurrence of the copepodite stages of <u>Euchaeta glacialis</u> in each depth interval.

Depth	F VI	M VI	F۷	MV	F IV	MIV	III	II	I	N
0-20 m	-	-	-	_	_	-	94.4	5.6	-	18
21-40 m	-	0.3	0.3	0.7	0.3	0.3	66.6	31.4	-	296
41-60 m	3.2	1.1	23.4	20.2	2.1	1.0	39.4	9.6	-	94
61-80 m	3.6	0.3	13.3	16.9	4.7	3.1	45.6	12.5	_	384
81-100 m	2.4	0.3	11.0	12.4	1.4	0.8	34.8	35.2	1.6	1107
200-300 m	8.6	0.3	9.5	13.7	4.6	2.6	25.9	33.3	1.5	1214

The data for the depth distribution of Euchaeta glacialis are more difficult to interpret than for the other species discussed. All the stage I encountered (30 individuals) were in the deepest part of the range under consideration. This would indicate that spawning took place in deep water, probably beyond the range of this study (see Table 8 and Figure 30).

Thorson (1949) has shown that for many marine invertebrates, the greatest amount of larval wastage is due to predation. Harding's (1966) results indicate that predacious chaetognaths (Eukrohnia spp.) and amphipods (Parathemisto spp.) are common in the upper 300 m. It is of obvious advantage to Euchaeta glacialis to breed in deep water to avoid as much predation pressure as possible; being a predator itself, there is no need for the young stages to be associated with an abundance of phytoplankton.

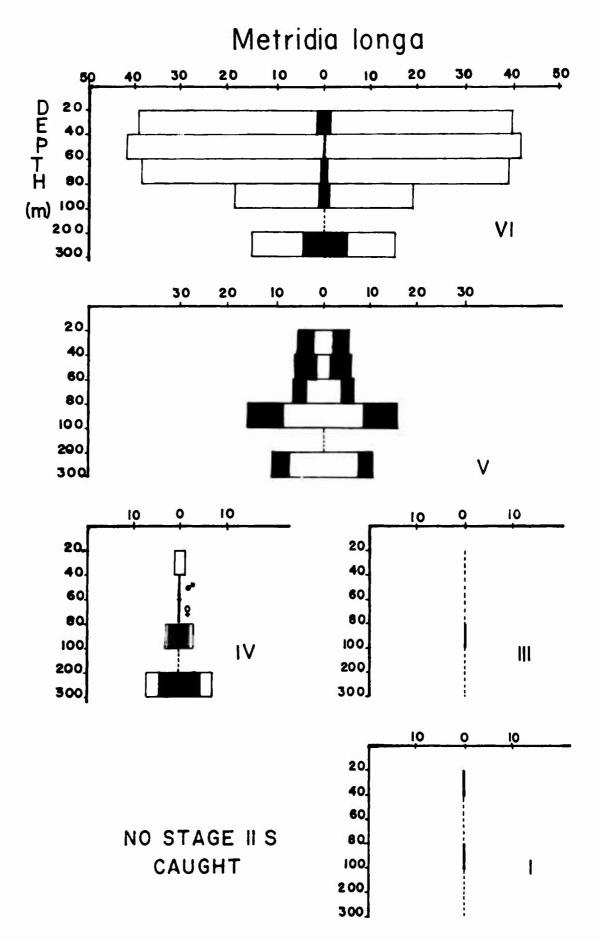


Figure 29. Relative occurrence of the copeopodite stages of Metridia longa in each depth interval. Shaded areas represent males.

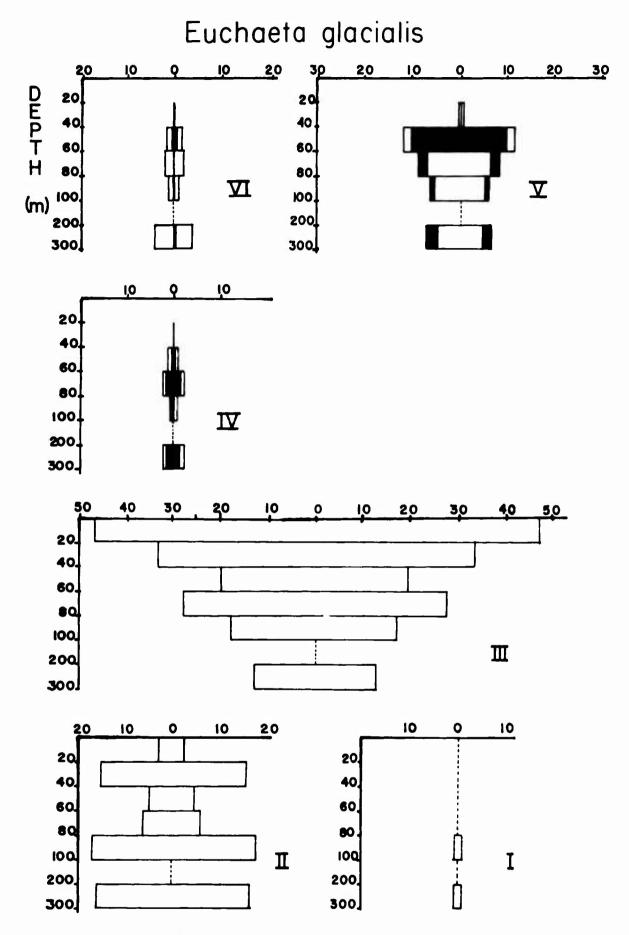


Figure 30. Relative occurrence of the copepodite stages of Euchaeta glacialis in each depth interval.

Shaded areas represent males.

Stage II is found throughout the range and probably occurred deeper as well.

Stage III showed a definite preference for the surface waters. These data for the early copepodite stages clearly show that spawning occurred in deep water, and that the animals gradually moved up to the surface layer as they passed through stage III.

The mature stages of <u>Euchaeta glacialis</u> were caught in very low numbers, perhaps because of an unsuccessful spawning in the previous season, as explained above. In any case, the representatives of stages IV, V and VI which were caught were found to be fairly evenly distributed with respect to depth. Slightly higher percentages for the deepest part of the range may indicate that some of these individuals are found in deeper water than was sampled here. The data for the older stages of <u>Euchaeta glacialis</u> for this depth range (0-300 m) are inconclusive. There is no obvious segregation of sexes with respect to depth.

5. Depth Distribution of Species

The depth range sampled in this study is known to contain the greatest density of zooplankton in the Arctic Ocean. This is to be expected in view of the trophic relationships between phytoplankton in the surface layers of the ocean and the zooplankton community. Harding (1966) found a distinct peak in the abundance of calanoids in the 175 to 300 m layer below T-3, and related this to the steepness of the temperature and salinity gradients through this layer. Johnson (1963) found that the three commonest species in his collections from the Polar Basin (C. hyperboreus, C. glacialis and M. longa) were all most abundant in the upper 200 m. Hopkins (1969) noted the "highest biomass concentration" in the 0-200 m layer and reported that 86% of this was made up by the calanoids. He also found that the genus Calanus constituted 45 to 54% of the zooplankton biomass in the upper 1500 m and that other significant contributions were made by Euchaela glacialis, the decapod Hymenodora, the amphipods Parathemisto and Cyclocaris, the chaetognath Eukrohnia, and the medusae Botrynema and Sminthea.

The variety of the sampling techniques used here makes it impossible to estimate biomass, or even the number of individuals per cubic metre. Even the data from the 0.5 number 6 nets are not reliable due to the great variation

in the lengths of towing times and in the speed of towing. Using the same depth intervals as in the previous chapter, a standard of comparison has been worked out for the 0.5 m, number 6 mesh net results, although its weaknesses are obvious. The total number of copepods caught within a depth interval was divided by the total number of hours of towing time in that interval, giving a number which represents the copepods caught per hour of sampling effort.

Table 9. Number of copepods caught per hour of sampling effort in the depth intervals sampled. Results from 0.5 m, number 6 nets only.

Depth/metres:	0-20	21-40	41-60	61-80	81-100	200-300
Copepods /hr.	8.8	36.8	29.6	119.5	241.6	57.9

There appears to be a large increase in the density of copepods in the 61-100 m region. This increase can be shown to be entirely due to one species, Microcalanus pygmaeus.

Table 10. Number of Microcalanus pygmaeus caught per hour of sampling effort in the depth intervals sampled. Results from 0.5 m, number 6 nets only.

Depth/metres:	0-20	21-40	41-60	<u>61-80</u>	81-100	200-300
Microcalanus pygmaeus /hr	4.3	20.6	15.9	93.6	201.5	0.71

Microcalanus pygmaeus represents 70.3 and 63.4% of the total numbers of copepods caught per hour in the 61-80 m and 61-100 m depth intervals respectively. Hopkins' (1969) work, however, indicates that the contribution of Microcalanus to the zooplankton biomass in the Arctic Basin is very small, although Microcalanus may well outnumber the two Calanus species at some depths. A comparison of the sizes of Microcalanus pygmaeus (0.7 - 0.8 mm) and Calanus hyperboreus (7 - 10 mm) or Calanus glacialis (3.4 - 4.3 mm) lends support to this observation.

Thus if the numbers of Microcalanus caught are disregarded, a fairly steady increase in the number of copepods is observed throughout the depth range under consideration.

Table 11. Number of copepods other than <u>Microcalanus</u> <u>pygmaeus</u> caught per hour of sampling effort in the depth intervals sampled. Results from 0.5 m number 6 nets only.

Depth/metres	0-20	21-40	41-60	61-80	81-100	200-300
Individuals/hr	4.5	16.2	13.7	25.9	40.1	57.2

Harding and Dunbar (1968) have shown that the abundance of zooplankton can be expected to decrease rapidly below 300 m, although this cannot be demonstrated by the present collection.

The number of species of copepods has been shown to increase with the depth in the upper layers of the Arctic Ocean. Most authors (Brodskii and Nikitin, 1955; Johnson, 1963; Grainger, 1965; etc.) have found the greatest number of species in the Atlantic Layer between 300 and 1000 m (Grainger, 1965). Harding (1966) reported a peak in the number of copepod species in his collections from T-3 in the 900 to 2000 m depth interval. Within the range of the present collection (0 to 300 m), the number of species increased steadily with depth.

Species lists for the water masses sampled are given below with an indication of the importance of each species. A species is called dominant (D) if it represents more than 15% of the total number of copepods collected, common (C) if it represents from 1 to 15%, rare (R) if it is found in numbers of less than 1% of the total and very rare (VR) for those which make up less than 0.01% of the total number of copepods taken.

Arctic S	Surface	Layer	(0-50 m)	1 ິ	species
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Calanus hyperboreus	34.8	D
Microcalanus pygmaeus	28.8	D
Calanus glacialis	14.5	C
Metridia longa	7.2	C
Euchaeta glacialis	7.2	C
Oithona similis	6.6	C
Spinocalanus magnus	0.2	R
Pseudocalanus minutus	0.2	R

Scolecithricella minor	0.2	R
Oncaea borealis	0.2	R
Spinocalanus abyssalis	0.1	R
Scaphocalanus brevicornis	0.1	R
Aetideopsis multiserrata	0.1	R
Temorites brevis	0.1	R
Eurytemora sp.	0.1	R
Oncaea sp.	0.1	, R
Temora longicornis	0.1	Ŕ
Metridia lucens	0.1	R

The Arctic Surface Layer is inhabited by at least 18 species of which 6 are common or dominant. These 6 constitute 99.1% of the copepod fauna in this layer. Grainger (1965) has reported that in his collections, 8 species comprised 99% of the total copepod fauna, namely the same 6 as above plus Pseudocalanus minutus and Oncaea borealis, neither of which occurred in large numbers in this collection. He also found, as will be shown below that the same species are common throughout the upper 300 m.

Some of the fauna in this surface layer may be transitory: the younger reproductive stages of such species as Calanus hyperboreus, Calanus glacialis and Euchaeta glacialis have been shown to prefer the shallower water layers. Other very rare species may be strays from deeper areas, although in many cases it is more likely that the depth ranges of such rare species are not well enough known, or that they are undergoing diurnal or seasonal vertical migrations. Of the 8 species found in this layer by Harding (1966) using number 0 nets, two, both rare, do not coincide with the list above. One important species added in the present list is Oithona similis, which was also found by Grainger (1965). Euchaeta glacialis is found to be of greater importance in the surface layer samples of this collection than was reported by Harding.

Pacific Summer Water Layer (50 - 100 m) 22 species

Microcalanus pygmaeus	71.3	D
Calanus hyperboreus	12.6	C
Metridia longa	6.c	C
Euchaeta glacialis	3.3	C
Oithona similis	3.0	C
Calanus glacialis	2.2	C
Scolecithricella minor	0.8	R
Scaphocalanus magnus	0.2	R

Chiridius obtusifrons	0.2	R
Oncaea borealis	0.1	R
Heterorhabdus norvegicus	0.1	R
Temorites brevis	0.1	R
Heterorhabdus compactus	0.1	R
Lubbockia glacialis	0.1	R
Pseudocalanus minutus	0.1	R
Spinocalanus magnus	0.1	R
Aetideopsis multiserrata	0.1	R
Aetideopsis rostrata	0.01	VR
Eucalanus bungii bungii	0.01	VR
Gaidius brevispinus	0.01	٧R
Spinocalanus abyssalis	0.01	٧R
Centropages hamatus	0.01	VR

In this water layer 22 species were caught and again the same six species were dominant and common. In this layer they make up 98.4% of the total number of copepods caught. As mentioned above, in this depth interval Microcalanus pygmaeus far outnumbers all the other species and overshadows a decrease in the importance of the other five which constituted 70.3% of the total copepod population in the Surface Layer, but only 27.1% in the Pacific Summer Water Layer.

Again, this list is much longer than Harding's (1966) for the 50-100 m layer (22 species to his 12). He did not find many Microcalanus, however, and the number 6 nets used here have uncovered a previously unknown concentration of this species.

Pacific Winter Water Layer (100 - 175 m)

The lack of samples from this water mass is unfortunate. Harding (1966) found the following 15 species from this water mass below T-3 in 1964.

Calanus glacialis

Metridia longa

Calanus hyperboreus

Luchaeta glacialis

Scolecithricella minor

Undinella obolonga

Aetideopsis rostrata

Chiridius obtusifrons

Scaphocalanus magnus

Gaidius brevispinus

Temorites brevis

Gaidius tenuispinus

Heterorhabdus norvegicus

Heterorhabdus compactus

Spinocalanus magnus

In all other cases, the numbers of species found in the various water layers were greater than those found by Harding, no doubt because he used only number 0 nets and vertical hauls. The 15 species above, therefore probably represent only the most likely species to be found in this layer. From the percentage data given for the other water layers, it appears that other species common in the 100 - 175 m layer probably include Microcalanus pygmaeus, Scaphocalanus brevicornis, Oithona similis, Oncaea borealis, Aetideopsis multiserrata and Spinocalanus abyssalis, since all of these occurred consistently in the water masses above and below the Pacific Winter Water Layer. The total number of species existing in this layer, then, is probably at least 21, and with the addition of some rare species, possibly about 26.

Intermediate Layer (175 - 300 m) 31 species

Five samples from this layer have yielded the greatest number of species found in one depth layer in this study:

Spinocalanus magnus	28.4	D
Scaphocalanus brevicornis		
Calanus hyperboreus	10.1	
	7.7	
Scaphocalanus magnus	2.5	Č
Gaidius brevispinus	7.5 4.5	Č
Metridia longa	4.4	Č
Temorites brevis		Č
Calanus glacialis	3.3 1.6	Č
Heterorhabdus compactus	1.3	
Microcalanus pygmaeus	1.2	Č
Heterorhabdus norvegicus	1.1	Č
Caiding tannianing	0.9	
Aetideopsis multiserrata	0.8	R
Aetideopsis rostrata	0.5	R
Spinocalanus abyssalis	0.4	R
Haloptilus acutifrons	0.4	R
Chiridius obtusifrons	0.3	
Augaptilus glacialis	0.2	
Pseudaugaptilus polaris	0.2	R
Undinella oblonga	0.2	R
Pseudochirella spectabilis	0.1	R
Oithona similis	0.1	R
Pachyptilus eurygnathus	0.1	R
Calanus cristatus	0.1	R
Euchaeta polaris	0.1	R
Oncaea borealis	0.1	R
Scolecithricella minor	0.1	
Lubbockia glacialis	0.01	
Chiridiella abyssalis	0.01	٧R
Unidentified sp. A.	0.01	

Thirty-one species were found in this water. The 6 species common or dominant in the other layers have lost their importance; from 175-300 m they represent only 25.1% of the total numbers of copepods. Spinocalanus magnus, Scaphocalanus magnus and Scaphocalanus brevicornis have replaced them in importance at this depth. These three species and the Aetideidae are known to be characteristic of the plankton community of deeper waters in the Arctic Ocean (Grainger, 1965). This layer contains a larger number of species than was found above it, and of these, more are common. The number of rare species can be expected to increase as further investigations are made.

The area of greatest faunistic change within the range considered in this study is the strong density interface at 50 m mentioned in the Introduction. Above 50 m, 18 species were found; 22 below 50 m. Of these 22, nine were not found above the interface, and four of the 18 species in the upper 50 m water were not found below it. Of these 13 (9+4) species limited by the density interface, most were common. By comparison, over the much larger distance between the 50 to 100 m interval and the 175 to 300 m layer. only three species disappeared and 11 new ones appeared. Of these 14 (3+11) species, six were rare or very rare. It appears that the sudden changes in density, salinity, and temperature at 50 m form a more effective barrier to some plankton species than do the greater, but much more gradual changes from 100 to 300 m between the Arctic and Atlantic water masses. This may not be true of other areas of the Arctic where the influence of the Atlantic water mass is much stronger.

Throughout the water column sampled, six species are very common: Calanus hyperboreus, Calanus glacialis, Metridia longa, Microcalanus pygmaeus, Euchaeta glacialis, and Oithona similis. In the lower levels (175-300 m) the importance of all except E. glacialis decreases, although they still occur in nearly all of the samples. Spinocalanus magnus, Scaphocalanus brevicornis and Scaphocalanus magnus appear as the important species of the deeper layers with Euchaeta glacialis. Ten species of the 39 in the collection occurred consistently (although not necessarily in large numbers) in most samples from the surface to 300 metres. These are:

Calanus hyperboreus
Calanus glacialis
Metridia longa
Microcalanus pygmaeus
Oithona similis
Oncaea borealis
Scolecithricella minor
Spinocalanus magnus
Temorites brevis
Euchaeta glacialis

These ten species include the six which are important in the upper 100 m. The remaining four also occur frequently over wide depth ranges, although they are less important numerically. Three others; Scaphocalanus brevicornis, Spinocalanus abyssalis and Aetideopsis multiserrata were found at all depths throughout the 300 m range, but they are rare in the upper 100 m, occurring in very small numbers, or as isolated individuals.

6. Zoogeography

Until 1955, work on the Arctic plankton had concentrated on the surface layer of 200 or 300 m. For this reason, the distributions, both vertical and horizontal, of all but the most common species are not well established in the literature. Many of the bathypelagic and abyssal species (Brodskii, 1950) in particular are extremely rare and have only been caught as isolated specimens, and it is impossible to draw conclusions about the ranges of the species from this information. In addition, the total lack of international cooperation in the standardization of collecting techniques makes the interpretation of results in the literature difficult. (See Bogorov, 1959, for discussion of this problem and some suggested solutions.) In the case of species of the genus Metridia, taxonomic confusion may also have made distributional questions difficult to resolve.

Most of the species in this material are not endemic to the Arctic Ocean. Characteristically, endemic species are found in the deepest layers of the Polar Basin where they have presumably been isolated by physical or physiological barriers. Most of the species are known from other oceans, and are successful over a wide range which includes the Arctic Ocean. Some are brought into the Arctic as expatriates where they eventually die without reproducing. Known distributions are given below with the authority or a reference for each species.

Arctic and Atlantic species

Aetideopsis multiserrata)
Calanus glacialis)
Calanus hyperboreus)- Harding, 1966
Chiridius obtusifrons)
Gaidius brevispinus)

Heterorhabdus norvegicus Metridia longa Metridia lucens Euchaeta glacialis Unidinella oblonga) }- }	Harding, 1966
Microcalanus pygmaeus Spinocalanus magnus Spinocalanus abyssalis Gaidius tenuispinus Scaphocalanus magnus Heterorhabdus compactus Haloptilus acutifrons Oithona similis) } }- }	Park, 1970
Pseudocalanus minutus Oncaea borealis Temorites brevis) }- }	Grice, 1962
Aetideopsis rostrata Augaptilus glacialis Scaphocalanus brevicornis) }- }	Brodskii, 1950
Pachyptilus eurygnathus) –	Sars, 1925
<u>Centropages hamatus</u> <u>Temora longicornis</u>	}-	Jespersen, 1939
Scolecithricella minor) –	Wiborg, 1940

All of these species are present in this collection. Temora longicornis is an Atlantic species which has not previously been reported from the central Arctic Ocean; the northern-most record was from 80°N, near Spitsbergen (Farran, 1936).

This list of 27 species is much longer than any found in the literature. Park's (1970) recent work on the calanoids of the very deep waters of the Caribbean revealed that several species from the Arctic are found there, and are apparently reproducing successfully. Some of these are likely to be bipolar species (see below), found in shallow waters at both poles and submerging to great depths in the intermediate and low latitudes.

It seems that the North Atlantic copepod fauna cannot successfully enter the Arctic Ocean (\underline{T} . longicornis is an exception here, and \underline{M} . lucens may well be); although there is a large flow of Atlantic water into the Arctic between eastern Greenland and Spitsbergen, most Atlantic

species disappear before this water submerges near Spitsbergen (Harding and Dunbar, 1968).

The 28 species listed above have been found at depths well above the Atlantic Water Layer in the Canadian Basin, and, in any case, the influence of this water has been very much weakened by the time it reaches this area. It is probable that all of these species are in fact typically Arctic, and have extended their ranges southward, rather than the opposite case. Dunbar and Harding (1968) and Briggs (1970) have put forward the idea that the Arctic Ocean has been populated from the Pacific and that the North Atlantic Ocean, being younger, derived much of its planktonic fauna in turn from the Arctic. This theory is supported by the evidence that the Atlantic is not known to possess an endemic boreal "epipelagic" fauna (Ekman, 1953; Briggs, 1970).

It should also be noted that the six most abundant species are included in this group. They are most successful in the Arctic Ocean and may therefore be considered as having the centre of their distribution there.

Arctic and Pacific species

Chiridiella abyssalis Eucalanus bungii bungii	}-	Hardin $\hat{\epsilon}$, 1966
Calanus cristatus Gaidius brevispinus Scaphocalanus magnus Metridia lucens Pseudaugaptilus polaris))-)	Morris, 1970
Calanus glacialis Pseudocalanus minutus Scolecithricella minor) }- }	Park, 1968
Spinocalanus magnus Spinocalanus magnus Spinocalanus abyssalis Aetideopsis rostrata Gaidius Tenuispinus Heterorhabdus compactus Temorites brevis)))-)	Brodskii, 1950
Oncaea borealis Cithona similis	}-	Grice, 1962

This list of 19 species is shorter than that given above for Arctic-Atlantic distributions, but it does indicate that the communication between Pacific and Arctic planktonic faunas may be greater than previously thought. Harding's list included only six species in this Arctic-Pacific category, but his work was prior to that by Morris (1970) and Park (1968) in the North Pacific. This matter will be discussed at length in a later publication.

Bipolar Species

The phenomenon of submergence of planktonic species in lower latitudes is well known, and allows for the bipolar distribution of some of them. The following copepod species are found in both the Arctic and Antarctic Oceans:

Microcalanus pygmaeus Spinccalanus magnus Scaphocalanus magnus Heterorhabdus compactus Heterorhabdus norvegicus Temorites brevis)))-)	Brodskii, 1950
Oithona similis Augaptilus glacialis Gaidius tenuispinus Haloptilus acutifrons Pachyptilus eurygnathus Scaphocalanus brevicornis) }- }	Harding, 1966

All of the above, except <u>H. norvegicus</u>, have also been found in the very deep waters of tropical seas (Park, 1970; Harding, 1966), offering good evidence that tropical submergence is indeed the means by which bipolarism has developed.

Neritic Expatriates

Two species of calanoids were found in this collection which are normally found only in the brackish waters of coastal areas. They are <u>Centropages hamatus</u> and <u>Eurytemora sp.</u>; both members of neritic genera of which members have been found in the coastal areas of the western Canadian Arctic. It is interesting that these animals manage to survive in waters of comparatively high salinity long enough

to reach T-3, which was at least 400 miles from the coast of Alaska during 1966. Centropages hamatus occurred at 55 m, and Eurytemora sp. at 15 m.

Endemic Arctic Species

There are three species in this collection which do not fit into any of the categories discussed above and must be considered to be endemic to the Arctic Basin.

Lubbockia glacialis Euchaeta polaris Pseudochirella spectabilis

All three were found in the deepest layer of the water column sampled (175-300 m), as would be expected from the discussion of the characteristics of endemic species at the beginning of this section. These were not isolated findings; each species was found in more than one sample and more than one individual of each occurred. They have been shown to reproduce in the Arctic Basin. Harding's (1966) list of endemic copepods is much longer (it includes these three); his samples were taken over a much greater depth range and almost all of the species he lists as endemic came from the Arctic Deep Water (900 m to bottom).

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APPENDIX I

Plankton Tow List

Ice Island T-3, 1966

Station 2

June 25-27, 1961 75°46.3'N 152°17'W

Multiple Horizontal Tow

Length of tow	Net No.	Diameter	Mesh Size	Depth	Comments
52hr.54 min.	1 2 3 4 5 6	0.5 m 0.5 m 0.5 m 0.5 m 0.5 m 0.5 m	6 6 6 6	300 m 250 m 200 m 100 m 70 m 30 m	

Station 3

July 7, 1966 75°35.4'N 151°20'W

Boat Tows (Horizontal)

Length of tow	Net No.	Diameter	Mesh Size	Depth	Comments
0.5.	4	4 -	0	4 -	
0.5 hr.	1	1 m	0	1 m	
	2	1 m	0	3 m	
	3	1 m	0	15 m	

Station 4

July 23-25, 1966 75°50.8'N 151°01'W (start) 75°45.0'N 151°42'W (end)

Multiple Horizontal Tow

Length of tow	Net No.	Diameter	Mesh Size	Depth	Comments
48 hrs.	1 2 3 4 5 6	0.5 m 0.5 m 0.5 m 0.5 m 0.5 m	6 6 6 6	300 m 230 m 200 m 100 m 67 m 30 m	

Station 5

August 8, 1966 75°58.8'N 153°07'W

Multiple Horizontal Tow

Length of tow	Net. No.	Diameter	Mesh Size	Depth	Comments
4 hrs.	1 2 3 4 5 6	0.5 m 0.5 m 0.5 m 0.5 m 0.5 m	6 0 6 6 6	4 m 10 m 12 m 20 m 25 m 30 m	net failed net failed net failed net failed

Station 6

August 8-9, 1966 75°58.8'N 153°07'W

Multiple Horizontal Tow

Length of tow	Net No.	Diameter	Mesh Size	Depth	Comments
4 hrs.	1 2 3 4	0.5 m 0.5 m 0.5 m 0.5 m	6	4 m 10 m 12 m 20 m	net failed net failed net failed
	5	0.5 m 0.5 m	6 0	25 m 30 m	

Station 7

August 9, 1966 75°58.8'N 153°07'W

Multiple Horizontal Tow

Length of tow	Net no.	Diameter	Mesh Size	Depth	Comments
4 hrs.	1 2 3 4 5 6	0.5 m 0.5 m 0.5 m 0.5 m 0.5 m	6 0 6 6 6	4 m 10 m 12 m 20 m 25 m 30 m	net failed net failed net failed net failed net failed

Station 9

August 10-11, 1966 75°58.8'N 153°24.8'W (start) 75°57.4'N 153°38'W (end)

Multiple Horizontal Tow

Length of tow	Net No.	Diameter	Mesh Size	Depth	Comments
6 hrs.	1 2 3 4 5	0.5 m 0.5 m 0.5 m 0.5 m 0.5 m	6 0 6 6 0 6	25 m 40 m 45 m 45 m 55 m	net failed

Station 10

August 11, 1966 75°57.4'N 153°38'W

Multiple Horizontal Tow

Length of tow	Net No.	Diameter	Mesh Size	Depth	Comments
4 hrs.	1 2 3 4 5	0.5 m 0.5 m 0.5 m 0.5 m 0.5 m	6 0 6 6 0 6	65 m 70 m 75 m 80 m 85 m 90 m	

Station 11

August 16-17, 1966 75°29.7'N 154°35'W (start) 75°28.7'N 154°47'W (end)

Multiple Horizontal Tow

Length of tow	Net No.	Diameter	Mesh Size	Depth	Comments
27.5 hrs.	1 2 3 4 5	0.5 m 0.5 m 0.5 m 0.5 m 0.5 m	6 6 0 6 6	35 m 45 m 55 m 65 m 75 m	net failed

Station 12

August 17, 1966 75°28.7'N 154°47'W

B.K.G.

Length of tow	Net No.	Diameter	Mesn Size	Depth	Comments
0.5 hr.	1	1 m	0	40 m	22 min tow + 8 min. up
					and down.

Station 14

August 19, 1966 75°28.8'N 154°48'W

B.K.G.

D. N. G.			Mesh		
Length of tow	Net No.	Diameter	Size	Depth	Comments
0.5 hr.	1 2 3 4	1 m 1 m 1 m	0 0 0	55 m 25 m 15 m 30 m	net failed

Station 15

August 27-28, 1966 75°38'N 155°37'W

Multiple Horizontal Tow

Length of tow	Net No.	Diameter	Mesh Size	Depth	Comments
11 hrs.	1 2 3 4 5	0.5 m 0.5 m 0.5 m 0.5 m	6 6 0 0 6	30 m 45 m 60 m 75 m 90 m	net failed

Station X

July 10, 1966 75°40.1'N 151°07'W

Boat Tows (Horizontal) Mesh

Length of tow	Net No.	Diameter	Size	Depth	Comments
20 min.	1 2	0.5 m 0.5 m		15 m 30 m	

APFENDIX [1

OCCURRENCE OF THE SPECIES IN THIS COLLECTION

	Arctic Ocean	Atlantic Ocean	Pacific Ocean	Antarctic Ocean
Calanus hyperboreus Calanus glacialis	+	+		
Calanus cristatus	+ +	+	+ +	
<u> </u>	+		1 +	
Pseudocalanus minutus	+	+	+	}
Licrocalanus pygmaeus	+	+	+	+
spinocalanus abyssalis	+	+	+	+
Spinocalanus magnus	+	+	+	+
Aetideopsis multiserrata	+	+] .]	
Aetideopsis rostrata	+ +	+	+	+
Chiridius obtusifrons Gaidius brevispinus	+	+	+	
Gaidius tenuispinus	+	+		+
Pseudochirella spectabilis	+	,	`	`
Chiridiella abyssalis	+	+		1
Euchaeta glacialis	+	+	1	ľ
Euchaeta polaris	+			
Undinella oblonga Scolecithricella minor	+	+		
Scolecithricella minor	+	+	+	
Scaphocalanus magnus	+ +	++	+	+
Scaphocalanus brevicornis Centropages hamatus	+	+	1	7
Temora longicornis	+	+		
Eurytemora sp.	+			1
Temorites brevis	1 + 1	+	+	+
Metridia longa	+	+	i	i
Metridia longa Metridia lucens	+ + + + +	+	+	
Heterorhabdus norvegicus	+	+	1	+
Heterorhabdus compactus	+	+	+	+
Haloptilus acutifrons	+	+	l	+
Augaptilus glacialis	+	+		+ }
Pseudaugaptilus polaris	+	++	ł	
Fachyptilus eurygnathus	+	+		
Oithona similis Oncaea borealis		▼		T
Lubbockia glacialis	+	•		
Oncaea sp.	+			
				,

APPENDIX III

RAW DATA, STATIONS 2, 3, 4, 5, 6, & 7. 1967

Station 2-0₂
25 April 1967
Lat. 79° 20' Long. 174° 02' W

Depth (Metres)	Temp.	°/00	02 <u>m1/1</u>	PO ₄ -P <u>ug-at/1</u>	SiO ₂ ug-at/l
3		30.59	8.72	0.89	5.51
10	-1.65	30.61	8.70	0.88	5.44
20	-1.66	30.61	8.71	0.91	5.46
30	-1.6 8	30.61	8.69	0.92	5.44
40	-1.70	30.61	8.68	0.92	5.45
50	-1.68	30.63	8.60	1.10	6.24
60	-1.38	31.56	8.01	1.31	10.20
70	-1.23	31.99	7.59	1.49	13.24
80	-1.24	32.07	7.49	1.64	16.00

Station 3-0₂
28 April 1967
Lat. 79.33' Long. 174.23' W

Depth (Metres)	Temp.	°/00	$\frac{0}{m1/1}$	$P0_{\mu}-P$ $\mu g-at/1$	SiO ₂ ug-at/l
80	-1.26	32.05	7.41	1.62	16.7
90	-1.30	32.20	7.20	1.67	22.0
100	-1.34	32.41	6.75	1.75	23.9
110	-1.39		No s	ample	
120	-1.41	32.72	6.60	2.04	34.2
130	-1.46	32.83	5.48	2.09	35.3
140	-1.48	32.97	6.39	2.11	39.0
150	-1.56		No s	ample	
160	-1.56	33.26	6.29	2.13	40.3

Station 4-0₂
29 April 1967
Lat. 79°32' Long. 174°18' W

Depth (Metres)	Temp.	°/00	$\frac{0}{m171}$	PO ₄ -P ug-at/1	SiO ₂ ug-at/l
160	-1.48	33.21	6.40	2.13	36.0
170	-1.43	33.36	6.22	2.12	37.0
180	-1.31	32.99	6.10	2.10	35.2
190	-1.12	33.79	5.87	2.00	30.1
200		34.01	5.73	1.71	20.0
210	-1.03	34.18	5.58	1.22	18.5
220	-0.96	34.31	6.80	1.13	12.0
230	-0.84	34.40	6.25	1.13	10.7

Station 5-02

1 May 1967

Lat. 79°40' Long. 173°46 W

Depth (Metres)	Temp.	°/00	$\frac{0}{m1/1}$	P04-P <u>ug-at/l</u>	SiO ₂ ug-at/l
230			6.30	1.14	9.8
240	-0.64	34.46	6.32	1.03	10.0
250	-0.49	33.68	6.35	1.00	10.5
260	-0.38	34.56	6.39	0.98	10.0
270	-0.24	34.60	6.42	0.96	9.4
280	-0.08	34.64	6.42	0.95	9.4
290	0.04	34.67	6.50	0.92	9.4
300	0.13	34.72	6.50	0.92	9.3

Station 6-0₂

3 May 1967

Lat. 79°57' Long. 174°24' W

Depth (Metres)	Temp.	°/00	Sigma-t	02 <u>m1/1</u>	PO ₄ -P ug-at/1	SiO ₂ ug-at/l
3 10 20 30 40 50 60 70 80 90 110 120 130 140 150 160 170 180 190 220 230 240 250 260 270 280 290 300	-1.66 -1.65 -1.65 -1.67 -1.31 -1.22 -1.30 -1.55 -1.56 -1.59 -1.56 -1.59 -1.13	30.57 30.61 30.61 30.61 31.56 31.56 31.59 32.59 32.69 32.69 33.33.33.34 34.45 34.54 34.54 34.54 34.54 34.54 34.54 34.54 34.54 34.54 34.54 34.54 34.54 34.54 34.54 34.54 34.54	24.61 24.63 24.63 24.65 25.15 25.40 25.88 26.18 26.32 26.44 26.61 26.85 27.77 27.76 27.77 27.78 27.77 27.86 27.91	8.72 8.72 8.72 1.72 1.72 1.72 1.72 1.73 1.74 1.75	0.90 0.91 0.91 0.91 0.93 1.06 1.77 1.84 1.98 2.04 2.07 2.04 2.07 2.01 1.70 1.13 1.06 1.99 0.97 0.95 0.95 0.93	4.7 3.0 5.0 10.5 10.5 10.5 10.5 10.5 10.6 10.6 10.5 10.6 10.5 10.6 10.

Station 7-02

7 May 1967

Lat. 79°38' Long. 172°14' W

5 8.75 0.91 30 -1.67 30.57 8.69 0.91 40 -1.67 30.60 8.75 0.94 50 -1.68 30.64 8.71 0.93 60 -1.35 31.43 8.34 1.00 70 -1.20 31.61 7.57 1.34 80 -1.24 31.89 7.14 1.57 100 -1.32 32.31 6.72 1.75 120 -1.55 32.63 6.41 1.90 140 -1.56 32.89 6.37 2.04 150 -1.60 33.05 2.07 160 -1.57 33.16 6.19 2.05 170 -1.42 33.30 6.01 2.04 180 -1.35 33.44 5.99 2.02 190 -1.21 33.67 5.75 1.75 220 -0.90 34.29 5.29 1.14 250 -0.58 34.52 6.48 0.98 300 0.14 34.73<	