

# Physical Oceanographic Results of the "Calanus" Expeditions in Ungava Bay, Frobisher Bay, Cumberland Sound, Hudson Strait and Northern Hudson Bay, 1949-1955<sup>1</sup>

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## ABSTRACT

Results of the physical oceanographic work of the "Calanus" expeditions of 1949-55 are presented in summary. Bathymetric maps are given for Ungava Bay, Frobisher Bay and north-east Hudson Bay. Temperature, salinity and density profiles are used to show the direction of flow of water, without dynamic calculations. Temperature-salinity correlation diagrams show the presence of Atlantic water below 100 metres, well developed in Cumberland Sound, less so in Ungava Bay and Hudson Strait (but still present), and very slight in northern Hudson Bay. In Frobisher Bay the entry of Atlantic water, if it occurs, is masked by tidal turbulence. Inversions of density, giving temporary negative stabilities, are recorded at a number of stations, concentrated in the regions of large tidal ranges; association of these inversions with the state of the tide is indicated. Stability conditions of the water in general are presented; the winter régime in northern Hudson Bay offers no reason to doubt that a normal vertical exchange of water occurs. Special hydrographic conditions in certain inlets are described. The dominance of the whole hydrodynamic pattern by the tides, especially in the eastern part of the area under study, is emphasized.

## INTRODUCTION

THE "CALANUS" EXPEDITIONS of 1947 and 1948, the first two years of operations, were not concerned to any significant degree with physical oceanography. Such material as was obtained has already been published (Dunbar, 1951). The expeditions of 1949 and 1950 worked within the limits of Ungava Bay with the exception of a few days spent in the Button Islands in the eastern end of Hudson Strait in both years, and a section (Section V) across Hudson Strait from Wakeham Bay to Big Island made in 1950. During the winters of 1948-49, 1949-50 and 1950-51 the ship was beached in Frenchman's Cove at Fort Chimo, on the Koksoak River. In the 1951 season one section (Section VI) was made from the mouth of the Korok River to Akpatok Island, and the remainder of the season's work was done in southeast Baffin Island, principally in Frobisher Bay. The *Calanus* was beached at Frobisher Bay airfield for the 1951-52 winter. The 1952 season was cut short owing to engine trouble, and the hydrographic results were restricted to a few stations in Cumberland Sound. The ship was drawn up on the marine railway at Churchill for the winters of 1952-53 and 1953-54. The working seasons of 1953 and 1954 were spent in the northern part of Hudson Bay

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and the northwestern end of Hudson Strait. Stations occupied by Mr. A. W. Mansfield in April, May and June, 1955, working through the ice, have also been incorporated into this report.

The hydrographic sections are shown on the accompanying maps (Fig. 1, 2 and 3). For other stations referred to in the present paper, see the station lists already published (Dunbar and Grainger, 1952; Grainger, 1954; Grainger and Dunbar, 1956).

#### METHODS

The *Calanus* is a 43-ton diesel ketch equipped with echo-sounder, trawl gear, dredges, plankton gear and the usual hydrographic equipment. During most of the field work Bergen Nautik reversing water samplers were used, with Negretti and Zambra deep-sea thermometers. Unprotected thermometers were not used,

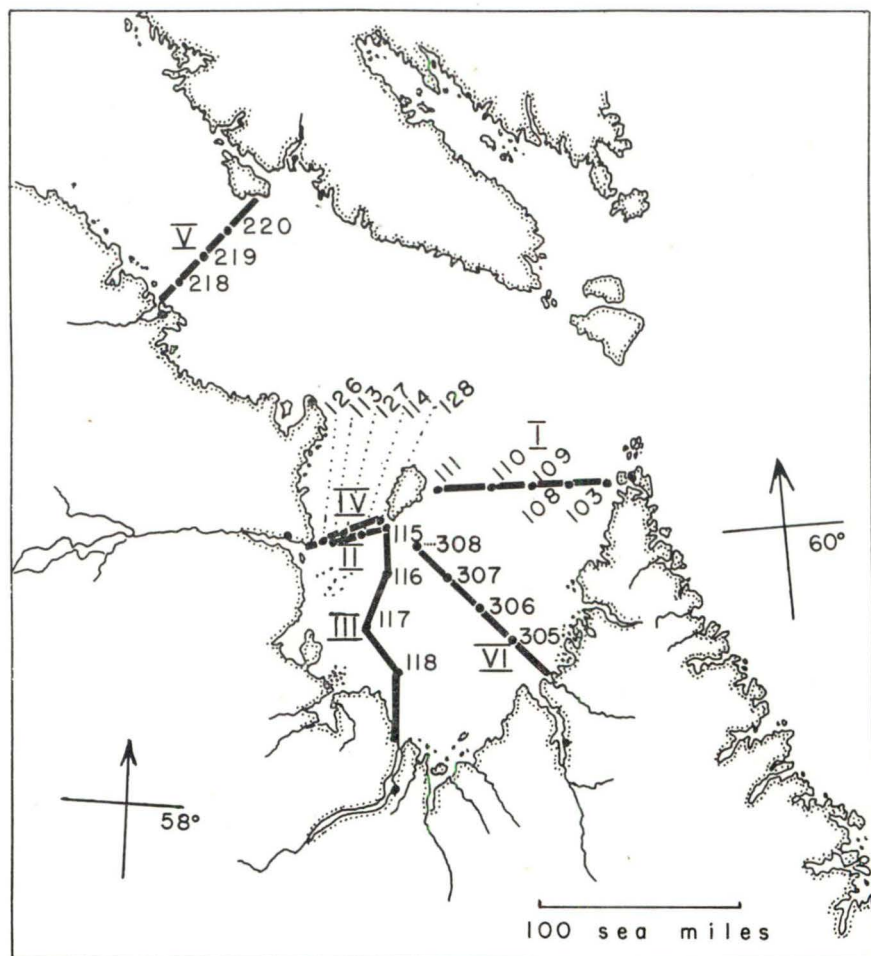


FIG. 1. Hydrographic sections in Ungava Bay and Hudson Strait (Sections I-VI).

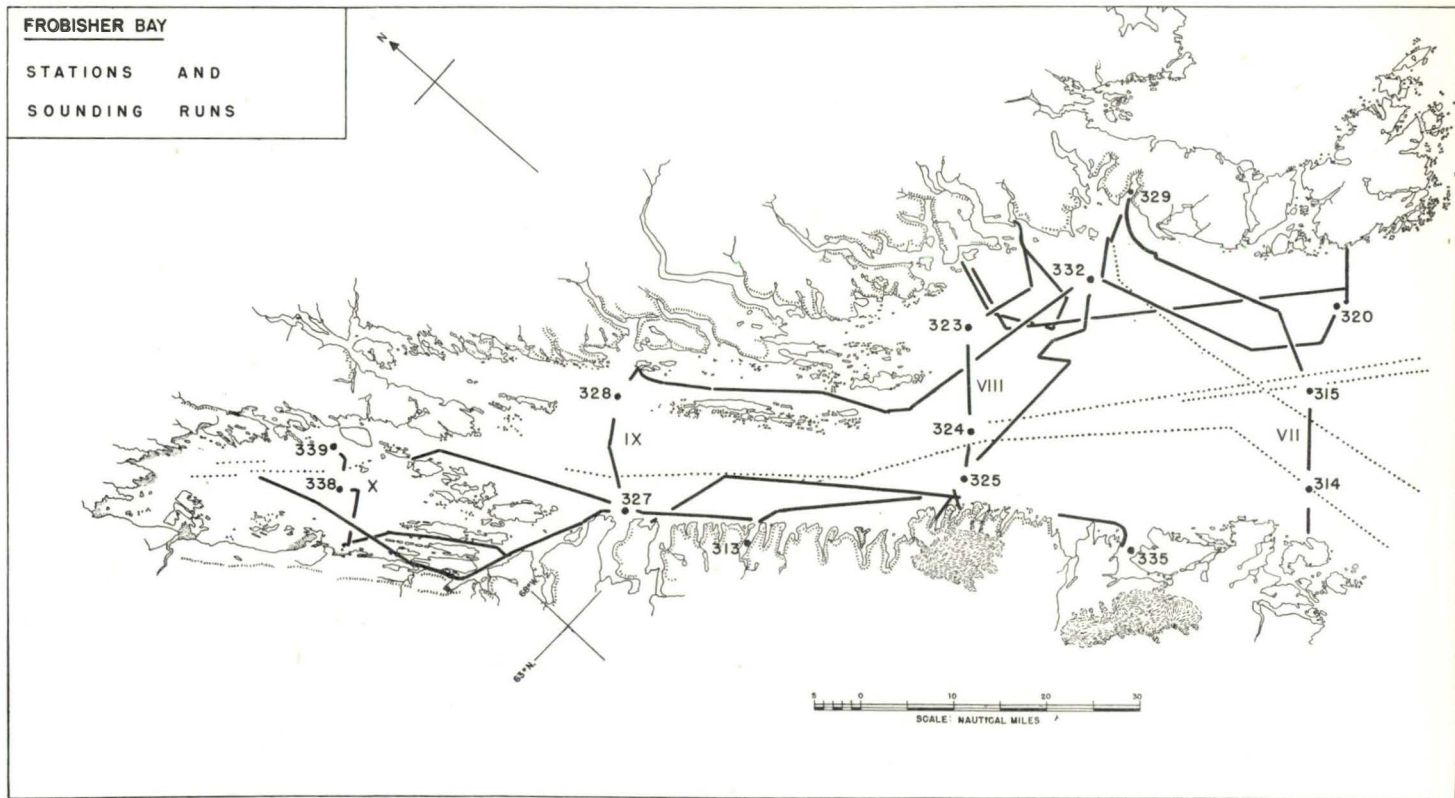


FIG. 2. Sections (VII-X) and hydrographic stations in Frobisher Bay, 1951. Solid lines: sounding runs made by the *Calanus*. Dotted lines: sounding runs taken from U.S. Hydrographic Office Chart No. 5854 (1944), corrected to 1950.



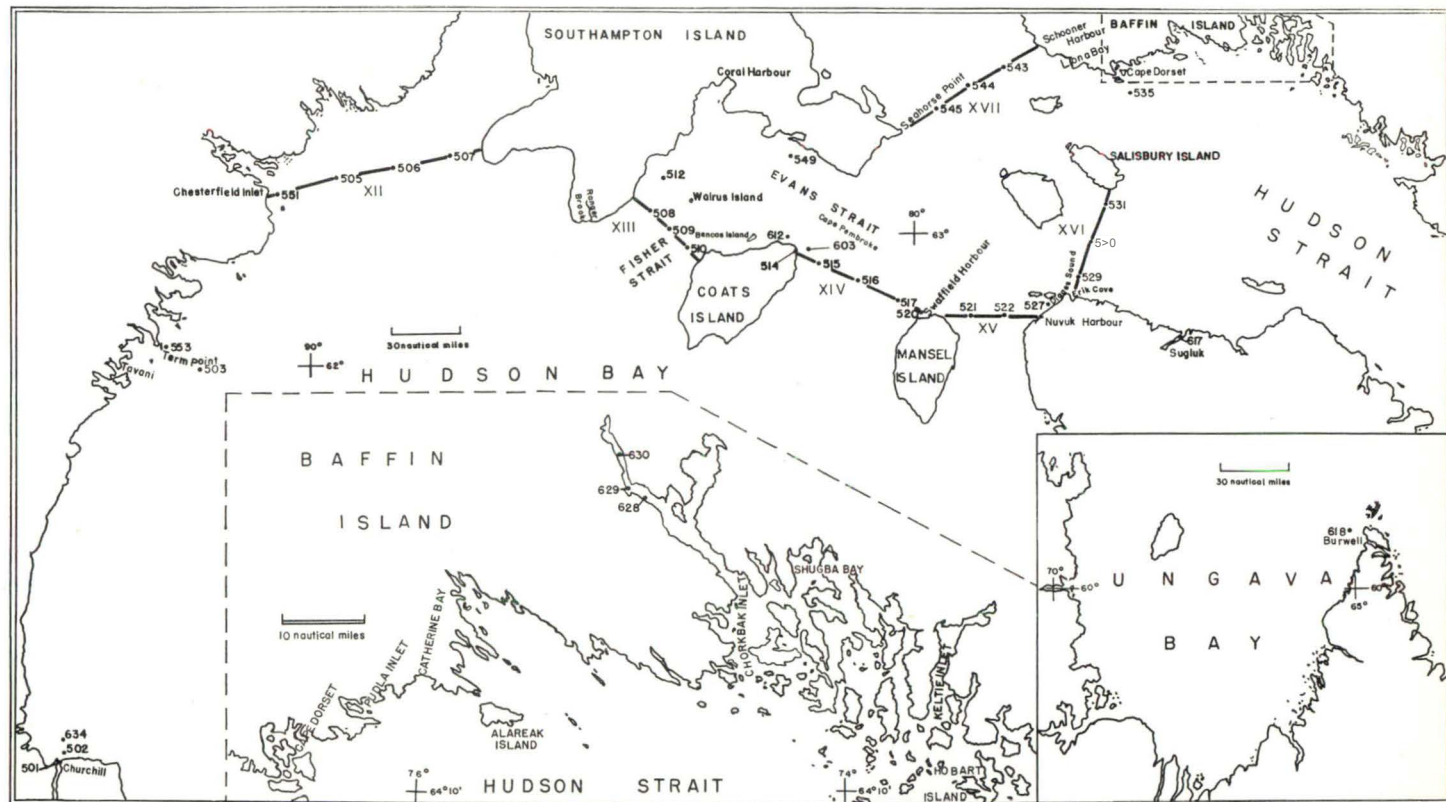


FIG. 3. Hydrographic stations and Sections (XII-XVII) in northern Hudson Bay and western Hudson Strait, 1953-54; together with chart showing position of Station 618 (1954) in Ungava Bay.



and there may consequently be small errors in the depths of observation. These errors, however, were kept down to a minimum by making hydrographic observations only in fairly calm weather; wire angles were usually normal to the surface and were very seldom less than  $80^\circ$ .

The water samples were preserved in 200–250 ml. glass bottles with bakelite screw tops, up to the end of the 1952 season, after which Danish citrate bottles were used. Both types of bottle are safe against evaporation for the periods of time involved. Titration for chlorinity was done in the Fisheries Research Board of Canada Oceanographic Laboratories at St. Andrews, N.B., through the kindness of Dr. H. B. Hachey. Oxygen and phosphate concentrations were determined in the field, but are not included in the present paper.

Dynamic calculations of horizontal water movement have not been made, for two reasons: (1) the dominant and masking influence of the tides in the areas under study, particularly the eastern part, and (2) the impossibility of finding a motionless horizontal reference level in these shallow and turbulent coastal waters.

#### BATHYMETRY

The general bathymetry of the Canadian eastern Arctic is fairly well known, but detail in certain areas has still to be filled in. The *Calanus* made sounding runs in Ungava Bay, Frobisher Bay, and the region between Foxe Channel, the western end of Hudson Strait, and Coats and Mansel Islands, in all of which the soundings were incomplete. The results of this work, together with soundings published since 1950 by the Canadian Hydrographic Service, are given in Fig. 4, 5 and 6.

The western and southern portions of Ungava Bay are shallow, generally less than 100 m. deep (Fig. 4). There is a channel over 200 m. deep which enters the bay in the northwest and skirts the western and southwestern shores of Akpatok Island. Although soundings are not yet quite extensive enough for certainty, this channel probably continues to the south of Akpatok Island, and certainly runs northward again in the eastern half of the bay. There are depressions in this channel which exceed 300 m. in depth. There is some water over 400 m. deep west of Killinek Island off the extreme northern tip of Labrador, and in fact the 400-m. contour forms the northern boundary of Ungava Bay. Akpatok Island thus forms the highest part of a *massif* which is separated from the mainland by a channel or "moat" of over 200 m. depth, a finding which is in agreement with the remarkable geological difference between the island and the mainland surrounding it.

The bottom of Ungava Bay is irregular, apparently lifted into ridges and heavily loaded with boulders, giving the impression of a terrain recently glaciated, probably with numerous eskers and lateral moraines, and with too short a lapse of time since the retreat of the ice to allow sedimentation to exert any great smoothing effect. It offers, in consequence, almost no good trawling grounds and even makes the use of the dredge somewhat hazardous. The bottom material, apart from rock, is heavy glacial mud with sand.

Frobisher Bay (Fig. 5) contains the deepest water the *Calanus* has so far worked in. The southwestern half of the bay is by far the deeper, containing inside a deep threshold at the mouth of about 300 m. sill depth a trough of over 600 m. maximum depth which lies very close to the steep southwestern shore and extends to the inner group of islands. In the outer part of the bay, outside the outer islands, this deep water gives way fairly steeply towards the northeast, and the bottom finally forms a flat shelf (the *Calanus* Shelf) which gradually shallows off toward the northeast shoreline. The *Calanus* Shelf offers excellent trawling bottoms consisting of sandy mud with shells and fine gravel, but the fauna itself is not rich.

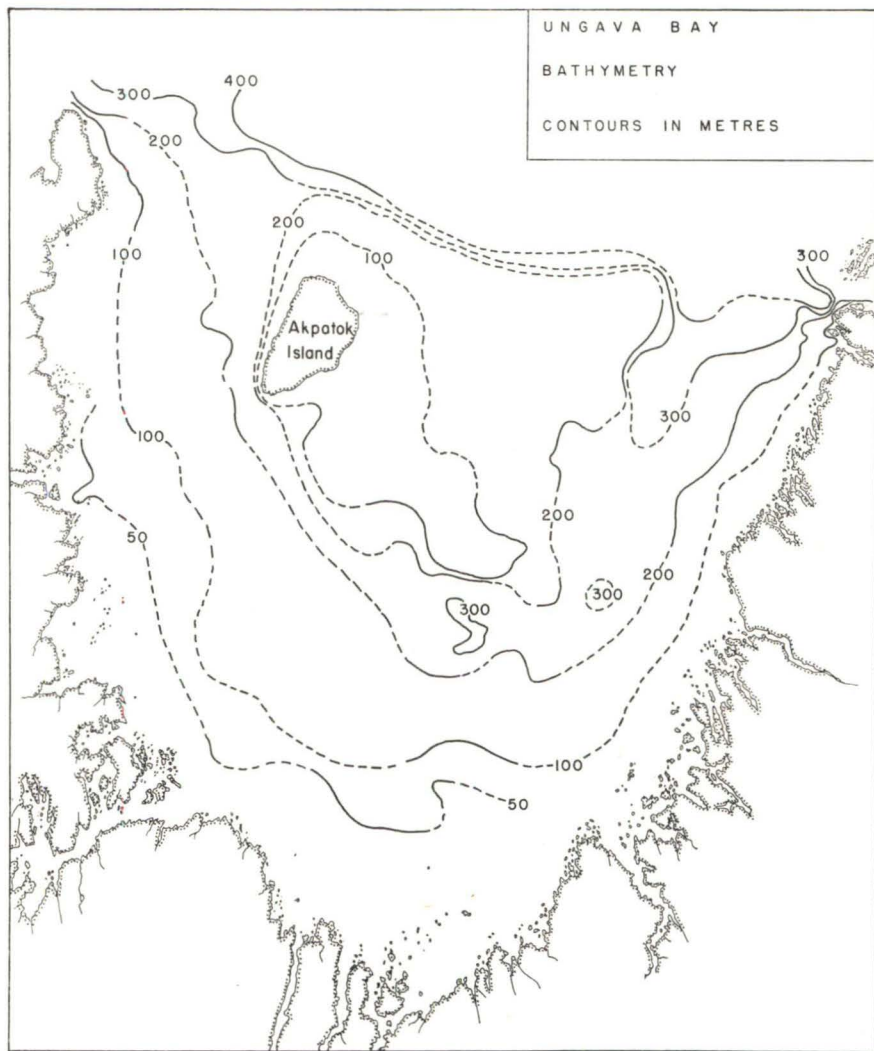


FIG. 4. Bathymetry, Ungava Bay, based on published data and *Calanus* observations.

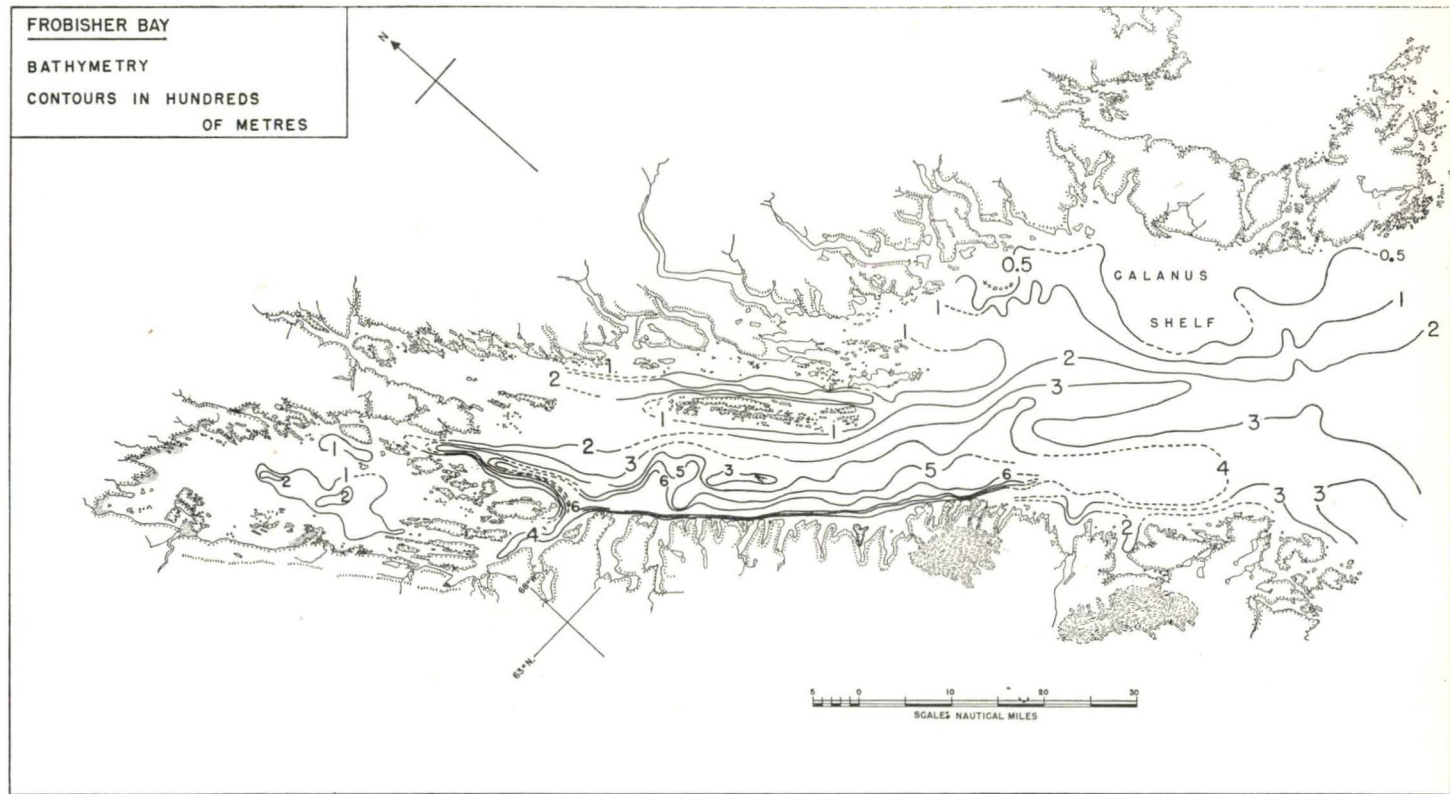


FIG. 5. Bathymetry, Frobisher Bay.



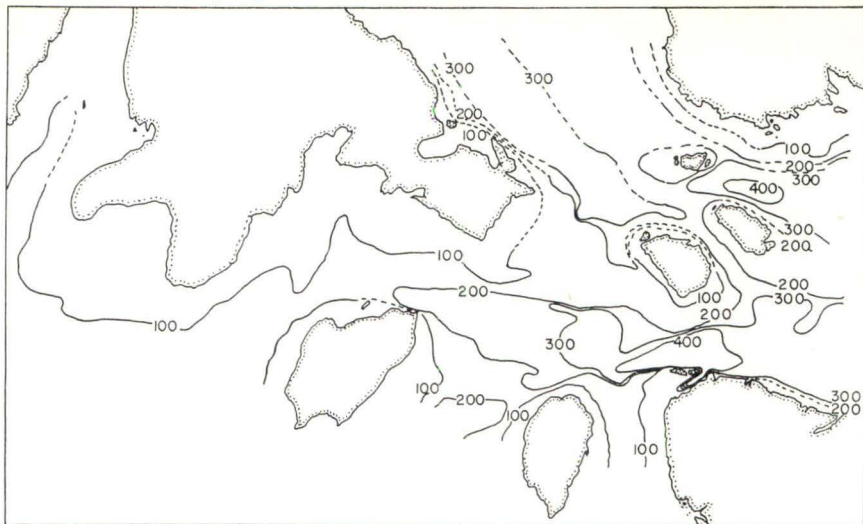


FIG. 6. Bathymetry, northern Hudson Bay and the western entrance to Hudson Strait. Depths in metres.

The outlet from Hudson Bay, between the Coats, Mansel, Salisbury, Mill and Nottingham islands, has been poorly sounded until quite recently, and there has therefore been doubt about the presence or absence, and position, of a possible shallow threshold between Hudson Bay and Hudson Strait. Such a threshold would have had considerable bearing on our understanding of the circulation within Hudson Bay. It now appears, however, as shown in Fig. 6, that there is no threshold between northwestern Quebec and southwestern Baffin Island (Foxe Peninsula), the channels being over 300 m. deep south of Nottingham Island and just under 300 m. north of the island. The shallowest water in the whole area shown in Fig. 6 is between Southampton Island and the mainland of Quebec, across Coats and Mansel Islands, and even here the sill between Coats and Mansel is almost 200 m. deep, or not much less than the deepest water within Hudson Bay. There is therefore very little to hinder free exchange of deep water between Hudson Bay and Hudson Strait.

#### PROFILES OF SECTIONS

##### UNGAVA BAY (Sections I-IV and VI; Fig. 7-11)

In some of these as in certain other sections described in this paper there are instances of density inversions shown by aberrations of the profiles. These are discussed under a subsequent heading.

The Ungava Bay sections were run on the following dates:

Section I, July 16, 1949; Section II, July 21, 1949; Section III, July 21-22, 1949; Section IV, August 23-24, 1949; Section VI, July 24, 1951.

Figures 8 and 10 show a southerly current through Sections II and IV, which

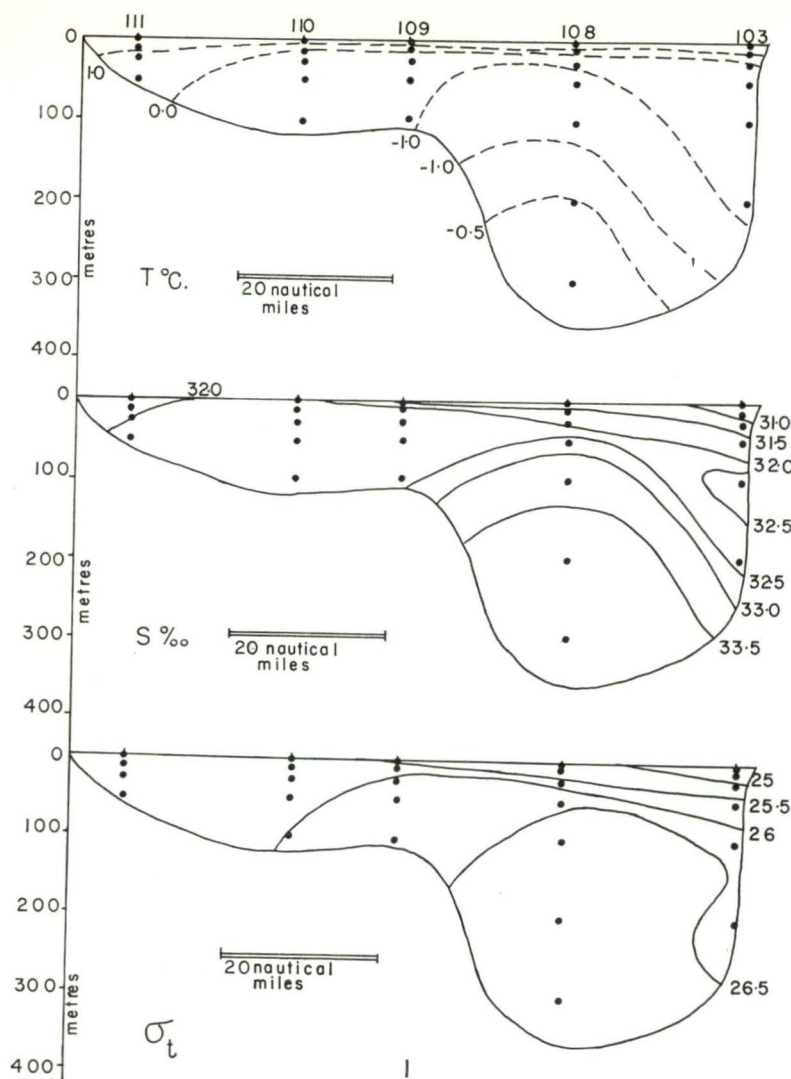


FIG. 7. Temperature, salinity and density profiles, Section I.

...e close together but which were occupied a month apart. The southerly current between Payne River and Akpatok Island is developed differently in the two sections, Section II showing a more strongly developed current in the western part, Section IV in the deeper water against Akpatok Island. Section IV shows a weak northward movement between Stations 126 and 127, possibly an eddy development. Sections III and VI indicate that this southward movement is not continued round the southern tip of Akpatok; instead it flows further to the south and apparently weakens considerably. It can be seen, turned in an eastward direction, between Stations 117 and 116 in Section III, and between Stations

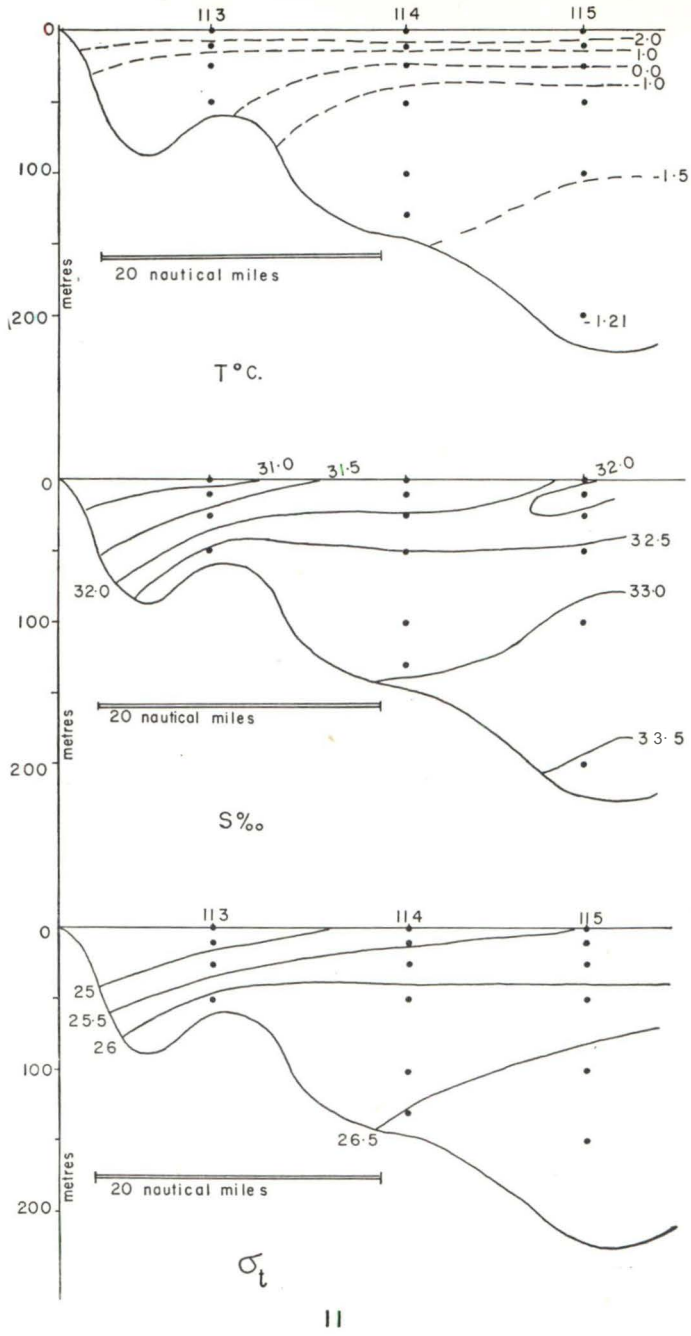


FIG. 8. Temperature, salinity and density profiles, Section II.



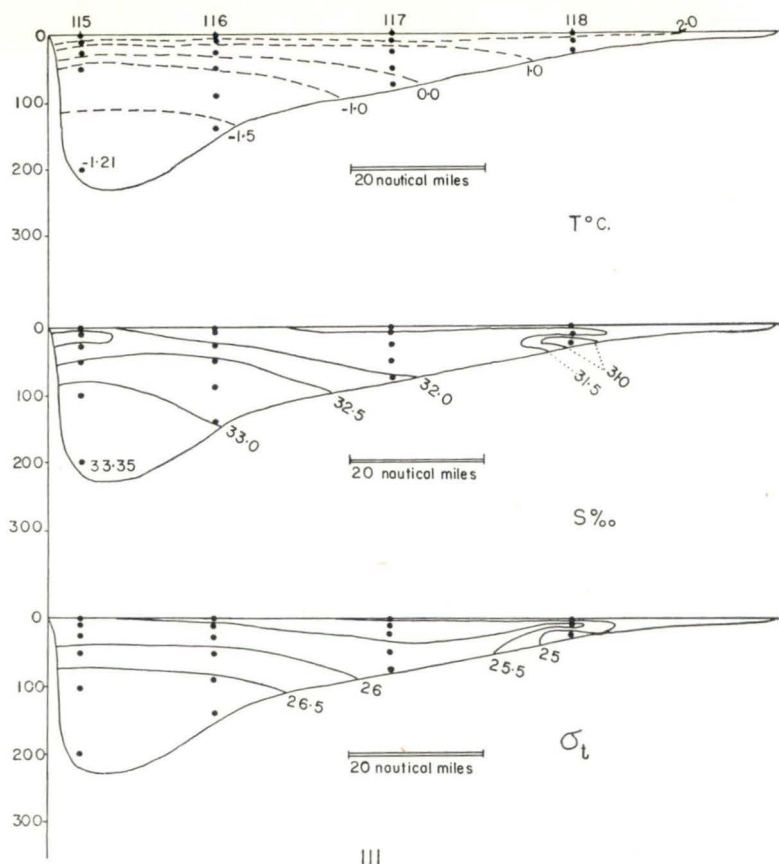
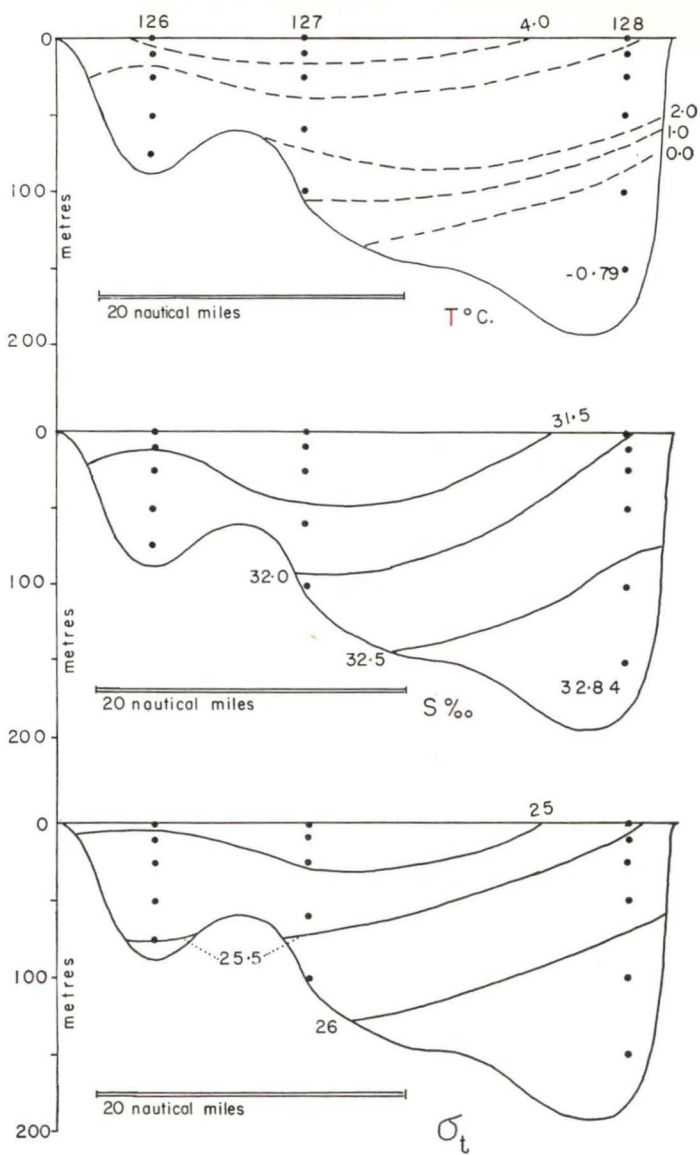


FIG. 9. Temperature, salinity and density profiles, Section III.

307 and 306 in Section VI, where it has turned farther round toward the northeast.

Section I presents a much more vigorous picture in which clearly new water has entered the bay. The southward set shown in Sections II and IV is again apparent in Section I, between Akpatok Island and Station 109 in the surface layers, and between Stations 109 and 108 as a subsurface current. This current is also seen close to Akpatok Island in Section VI (occupied two seasons later than the other Ungava Bay stations), and it may possibly be represented in the weak currents setting southwest between Stations 305 and 306 in Section VI, and west between Stations 117 and 118 in Section III. Alternatively, and perhaps more probably, these weak countercurrents represent clockwise eddies in these two sections themselves. At all events, the water which enters the bay on both sides of Akpatok Island makes its exit in the deep channel close to the Labrador shore, the northward-going current being shown strongly developed in Section I (Fig. 7), between Station 108 and the mainland, and also between Stations 108



IV

FIG. 10. Temperature, salinity and density profiles, Section IV.

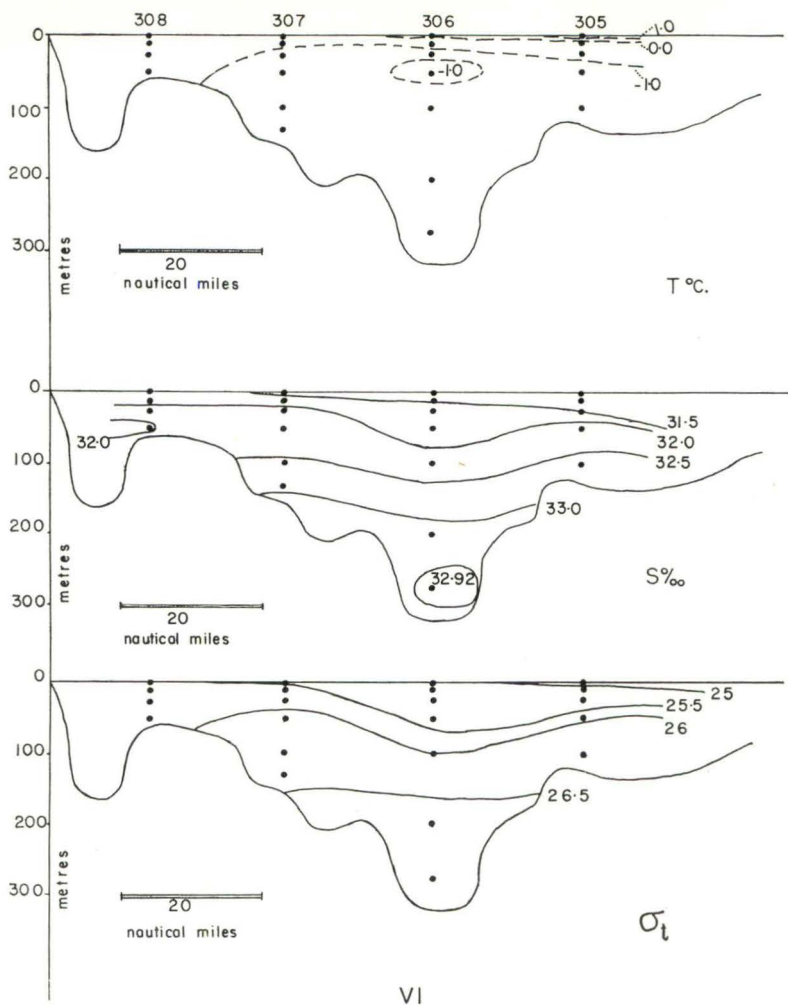


FIG. 11. Temperature, salinity and density profiles, Section VI.

and 109 as a shallow surface current over-riding the southward current deeper down.

The details of the movement of these currents are not shown by the present material. Sections III and VI indicate a complicated play and counterplay of water, with the development of eddies, a situation which is to be expected in a region of such fierce tidal intervention. The possible correlation of undulant profiles, such as are shown in Sections III and VI, with tidal action, has been discussed by Bailey (1955), quoting Riis-Carstensen (1936) and Kiilerich (1939).

#### HUDSON STRAIT (Section V, Fig. 12)

Section V, across Hudson Strait from Wakeham Bay to Big Island, is straightforward except for the density inversions in deep water, and shows the already



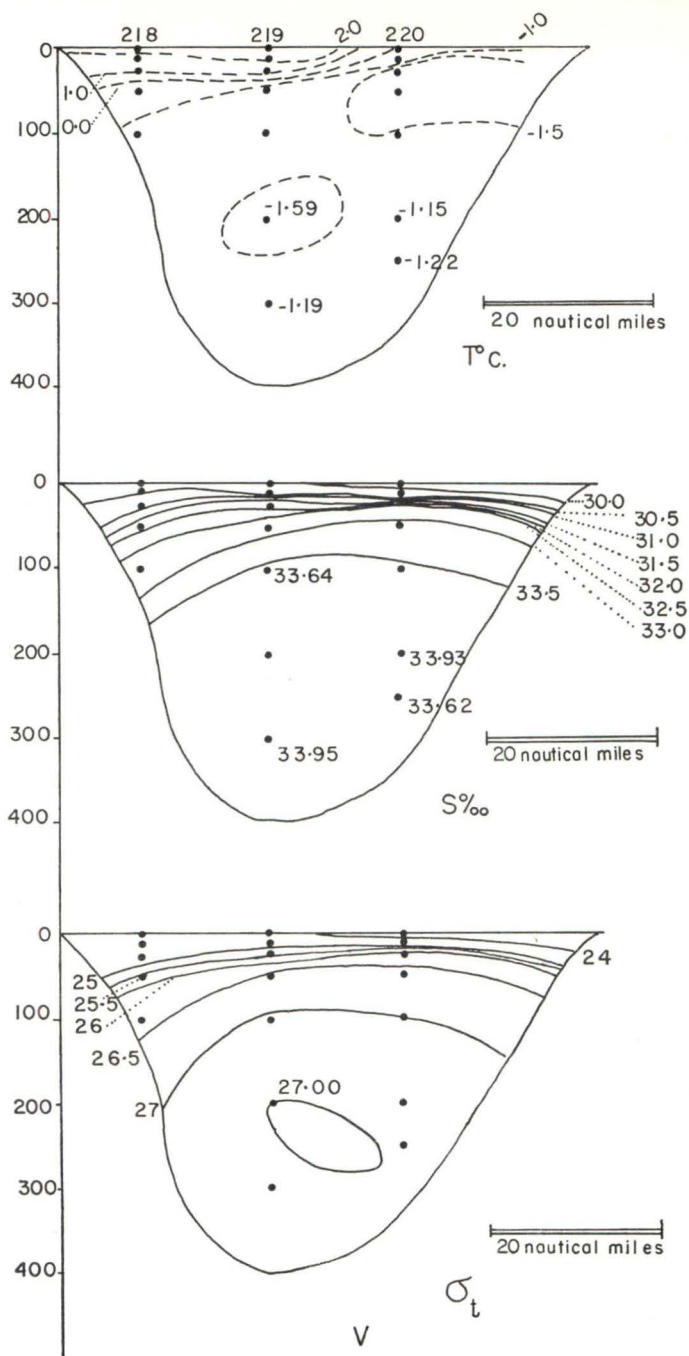


FIG. 12. Temperature, salinity and density profiles, Section V.

familiar pattern of movement in the strait. There is a northwesterly set along the Baffin Island coast, and a southeasterly set along the Quebec shore. The observations were made on the night of July 30–31, 1950. The rise in temperature at 200 m. and below, accompanied by high salinities, is characteristic of Hudson Strait, Ungava Bay and Cumberland Sound, and is subsequently discussed under Temperature–Salinity Correlation.

#### FROBISHER BAY (Sections VII–X, Fig. 13–16)

These sections were run on the following dates: Section VII, August 8, 1951 (Station 320 on August 11, 1951); Section VIII, August 13, 1951; Section IX, August 19, 1951; Section X, August 30, 1951.

Frobisher is a narrow bay with a maximum tidal range at its head of 36 feet. Turbulent conditions, and a hydrodynamic situation dominated by the tides, are therefore to be expected. Section VII, for instance, at the mouth of the bay, shows water entering the bay at the surface on the southwest side and leaving it on the northeast side, the reverse of the normal expected movement. The dominant movement shown by the isopycnals over the section as a whole is outwards from the bay. This can only be explained by the fact that at the time of the observations the tide was flooding at Station 314 and ebbing at both 315 and 320. Similarly in Section VIII, the dominant movement is into the bay, and here Stations 323 and 324 were occupied during the flood tide, Station 325 during the ebb, one hour after high water.

Section X obeys the same rule; both Stations, 338 and 339, were occupied during the ebb tide, and the isopycnals show water leaving the bay. Section IX, however, is an apparent exception to this pattern; both Stations, 327 and 328, were occupied on the ebb tide according to the tide tables, and yet the section shows marked movement inwards. Station 327 was made 2 hours after high water, and this time is in agreement with the actual observation of the time of high water before leaving anchorage on the southwest shore. Station 328, estimating from the tide tables, was occupied 5 hours and 40 minutes after high water. If the assumption of the dominance of tidal currents in Frobisher Bay is correct, this anomaly must be left for the time being as unexplained. The tides of Frobisher Bay have not been given much study up to the present, in fact the very nature of the tidal wave in this region is not certain, and it may well be that the very uneven bottom configuration at the level of Section IX causes local aberrations in the tides. Apart from this one section, however, the agreement between the state of the tide and the slope of the isobaric surfaces is striking. A similar interpretation could well apply to the undulant profiles in Ungava Bay, described above.

As Trites (1956) has pointed out, the dynamics of inshore and partly enclosed waters are not properly understood. Studying the circulation in Chatham Sound, B.C., Trites found an association between the state of the tide and certain aspects of the behaviour of the water; and the reversal of the geopotential slope by the ebb and flow of the tide, in inlets, is illustrated and discussed by Sverdrup, Johnson and Fleming (1942, pp. 557–558).

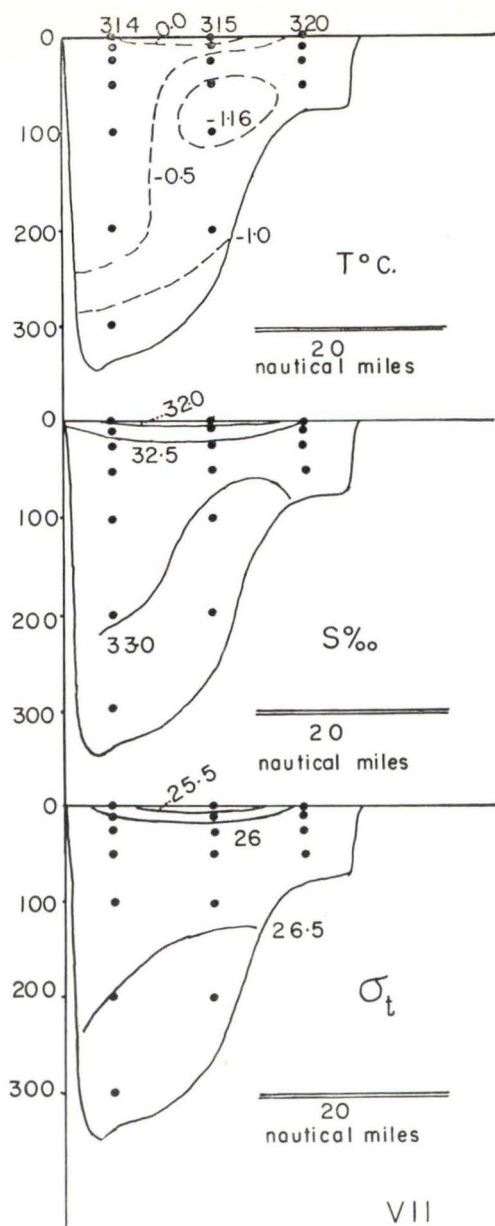


FIG. 13. Temperature, salinity and density profiles, Section VII.

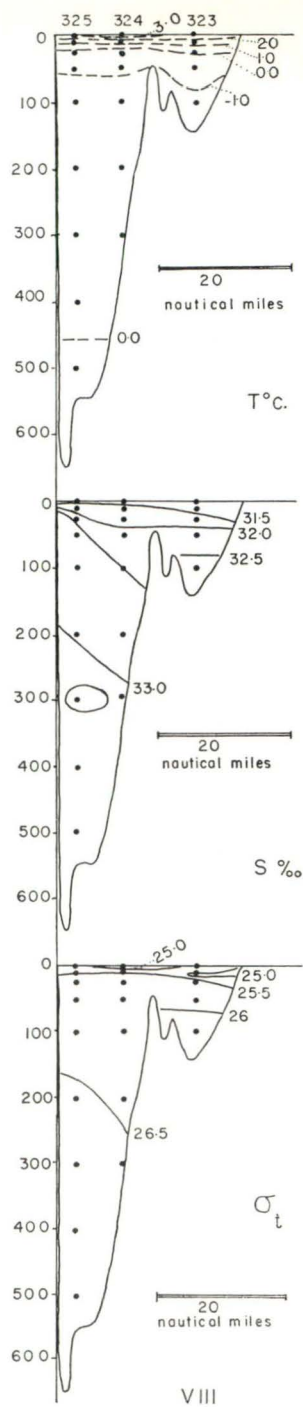


FIG. 14. Temperature, salinity and density profiles, Section VIII.



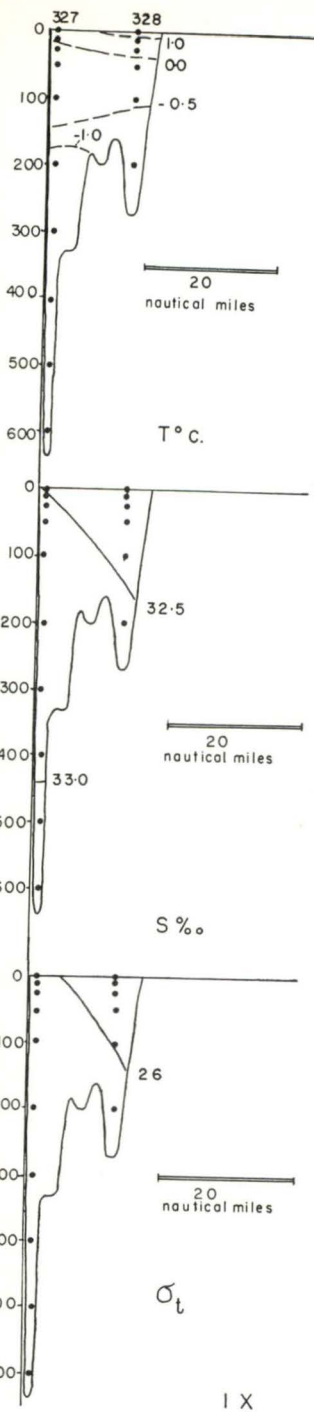


FIG. 15. Temperature, salinity and density profiles, Section IX.

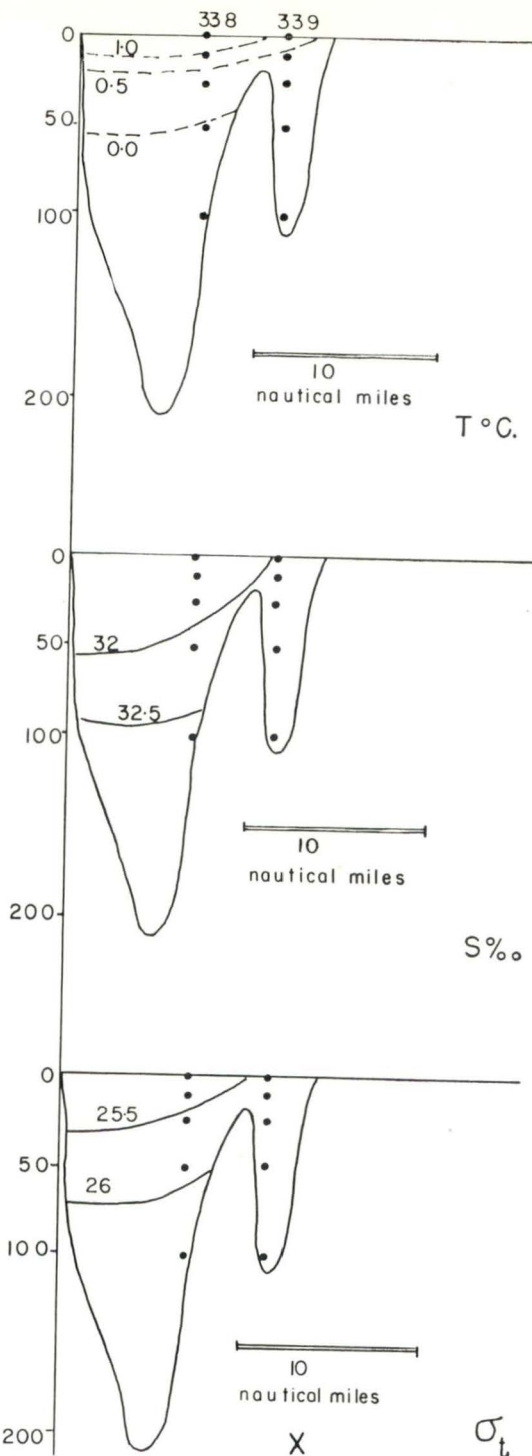


FIG. 16. Temperature, salinity and density profiles, Section X.

## CUMBERLAND SOUND (Section XI, Fig. 17)

Section XI shows water flowing both in and out of the sound, at different levels, for the most part very weakly. This again may be associated with the

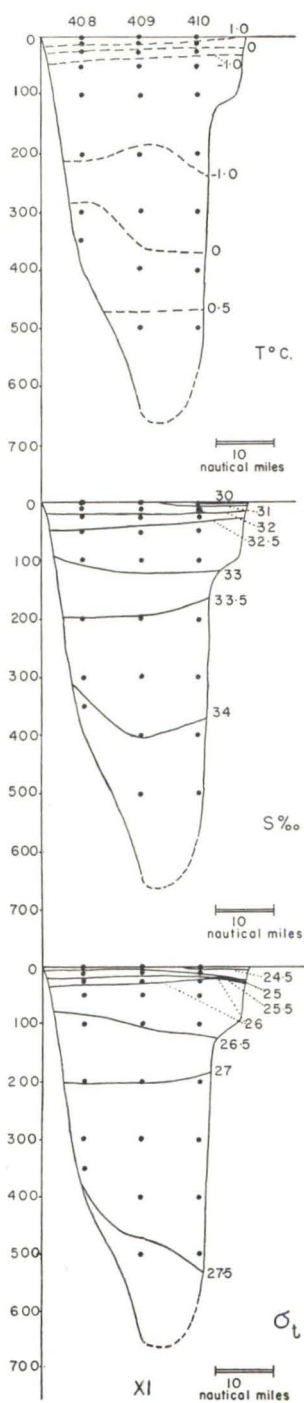


FIG. 17. Temperature, salinity and density profiles, Section XI.

ide, for Stations 408 and 410 were occupied over slack water, the former at high water and the latter at low water. The 300- and 350-m. samples at Station 408 were taken during the end of the flood, about half an hour before high water, while the 10-, 25- and 50-m. samples were taken half an hour after high water. These times are in agreement with the slopes of the isopycnals at the depths mentioned. Similarly, the indication of inward flow between Stations 409 and the northeast shore agrees with the state of the tide (beginning to flood) at the time of taking the 0-, 10-, 25- and 50-m. samples at Station 410. The section was run on the night of July 30-31, 1952.

NORTHERN HUDSON BAY AND WESTERN HUDSON STRAIT (Sections XII-XVII, Fig. 18-23)

All these were run in the 1953 season. The dates of observation are as follows: Section XII, July 24; Section XIII, July 25; Section XIV, August 3 (Station 520 on August 4); Section XV, August 5; Section XVI, August 11; Section XVII, September 2.

Section XII shows the expected southward set between Station 506 and the

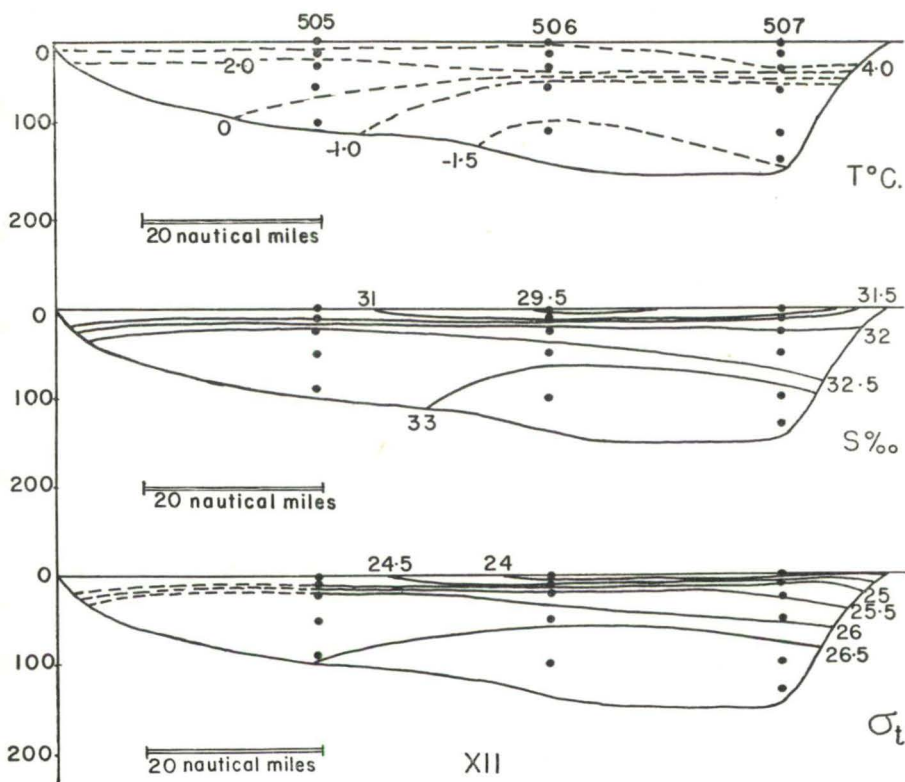


FIG. 18. Temperature, salinity and density profiles, Section XII.

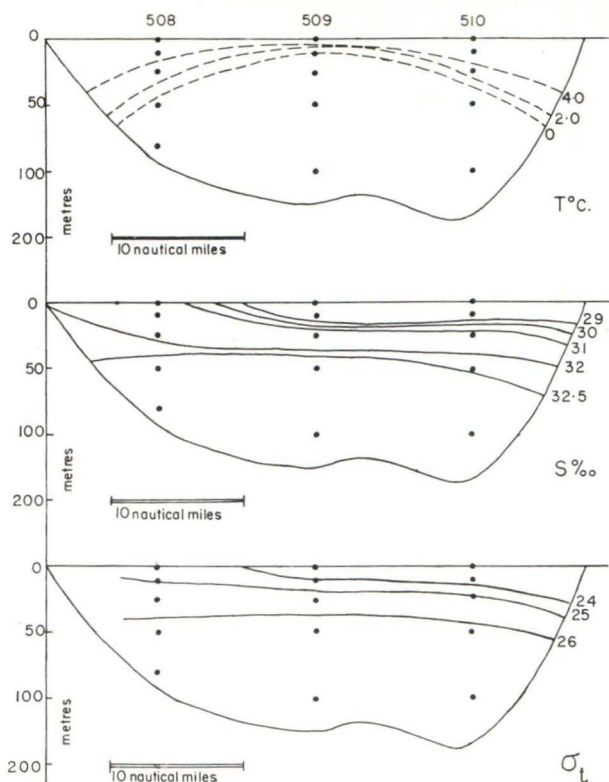


FIG. 19. Temperature, salinity and density profiles, Section XIII.

mainland coast; it is well developed below 50 m. between Stations 506 and 505, but of uncertain strength farther west, owing to the absence of an inshore station. A weak northward movement is indicated between Station 506 and Southampton Island, below 25 m.

Section XIII, between Southampton and Coats Islands, shows only north-easterly movement in Fisher Strait. Whether this is a permanent condition is uncertain. In an earlier paper (Dunbar, 1951) I suggested that there might be a southwesterly set in this region, based on the drift-bottle results of the *Loubyrne* expedition of 1930 (Hachey, 1935). The present results, however, and the statements in the Arctic Pilot, Vol. III (British Admiralty, 1947), indicate that such a southwesterly current is not normal. The point is not unimportant, since it has considerable relevance to the fate of the water which flows southward past Seahorse Point, eastern Southampton Island (see below).

A weak movement into the bay, however, is shown in Section XIV, between Station 516 and Coats Island. Taken together with the previous section, this



indicates a clockwise rotation round Coats Island. At the eastern end of Section XIV there is a northerly current leaving Hudson Bay, between Station 517 and Mansel Island. In Section XV, unfortunately, there is no station close enough to Mansel Island to demonstrate whether or not a similar circulation occurs round that island as round Coats. A southward set along the east coast of Mansel Island, which would be implied by such a rotary current, is, however, described in the Tide Tables for 1957: "... Captain Balcom of the Government steamer *N. B. McLean* reports a predominant southward set along the eastern side of Mansel Island". For the rest, Section XV shows a northward set between Station 521 and the Quebec coast, but only below 25 m.

Between the Quebec coast and Salisbury Island, Section XVI shows only water moving to the east, out of Hudson Bay, with the exception of an indication

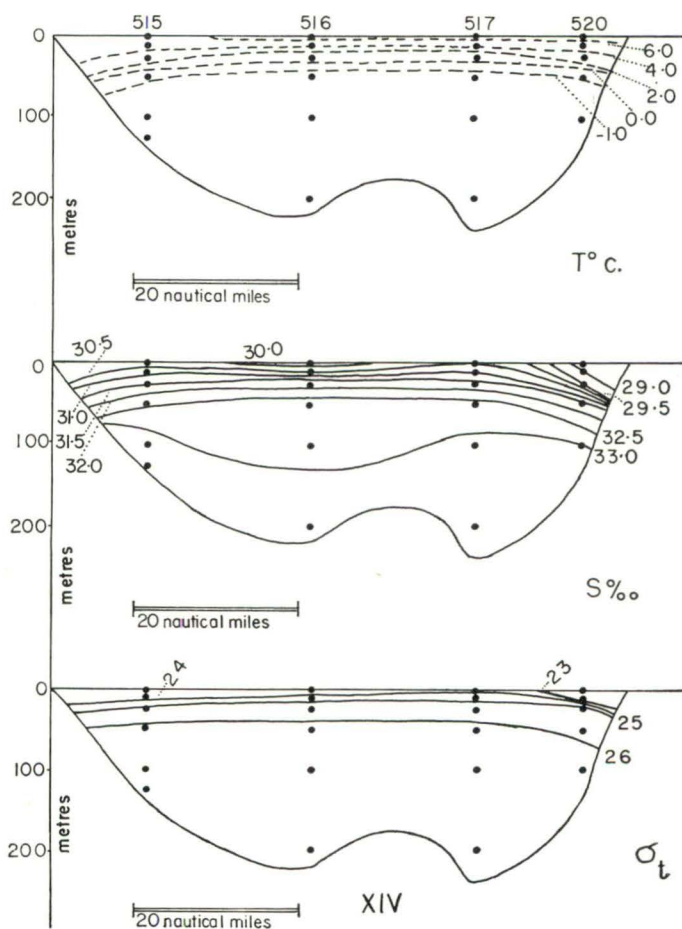


FIG. 20. Temperature, salinity and density profiles, Section XIV.

of westward movement at the 200-m. level at Station 531, close to Salisbury Island, where the 26.7 isopycnal surface curves downward.

In Fig. 23, Section XVII is presented from the northwest or Foxe Basin side, with Baffin Island on the left and Southampton Island (Seahorse Point) on the right. There is a well-developed current setting into Foxe Channel along the Baffin Island coast between that coast and Station 544, and a lesser current setting out of Foxe Channel along the Southampton Island coast. This latter current was also found, by various methods of measurement, by the H.M.C.S. *Labrador* expedition of 1955 (Campbell and Collin, 1956). In view of the fact that there is little evidence of a westerly set in Fisher Strait (see above), this water must find its way elsewhere, probably joining the water leaving Hudson Bay through Section XVI.

The surface currents demonstrated by Sections XII-XVII are shown in Fig. 24, together with the distribution of temperature and salinity at the surface

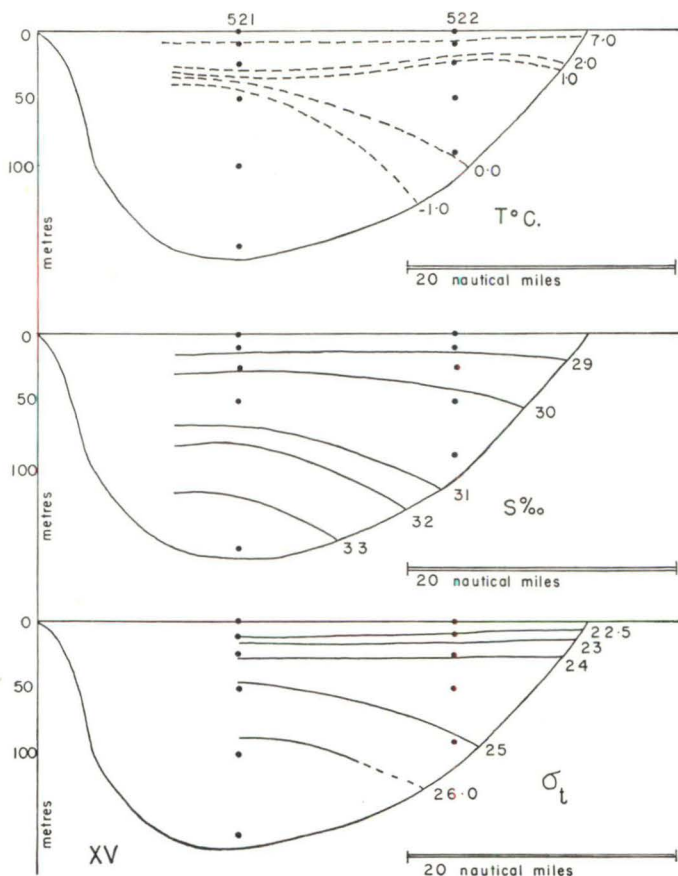
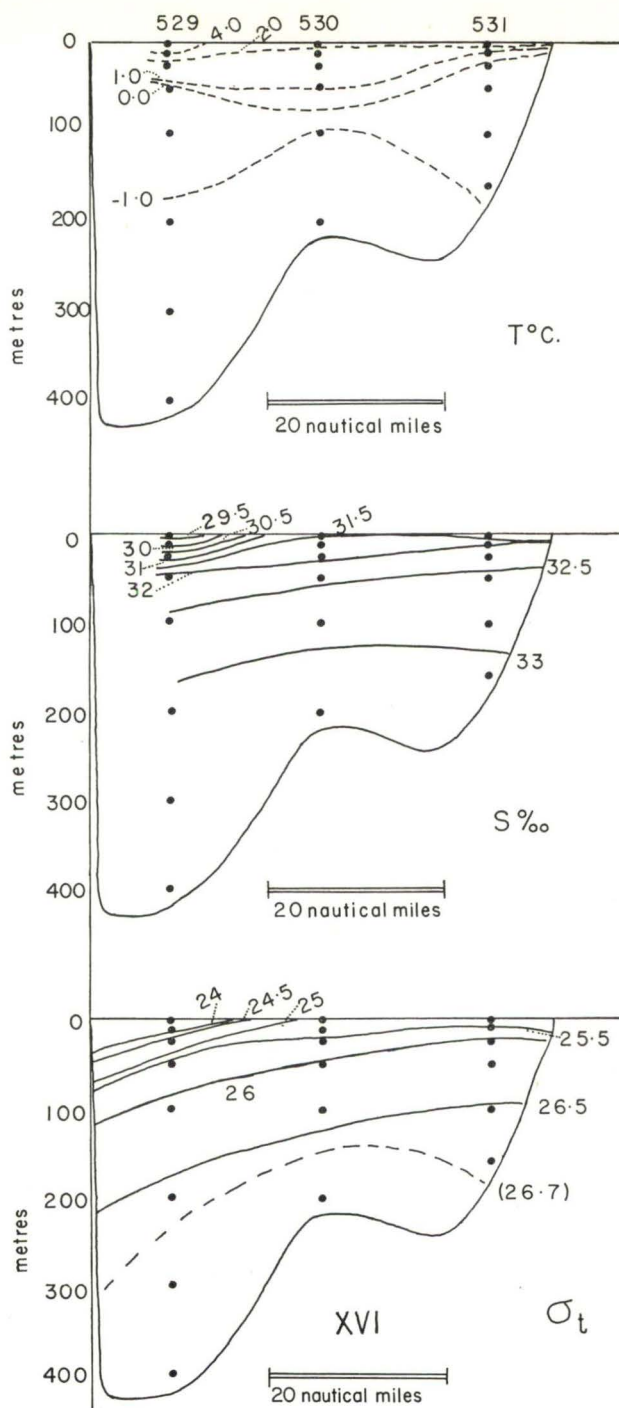


FIG. 21. Temperature, salinity and density profiles, Section XV.



22. Temperature, salinity and density profiles, Section XVI.

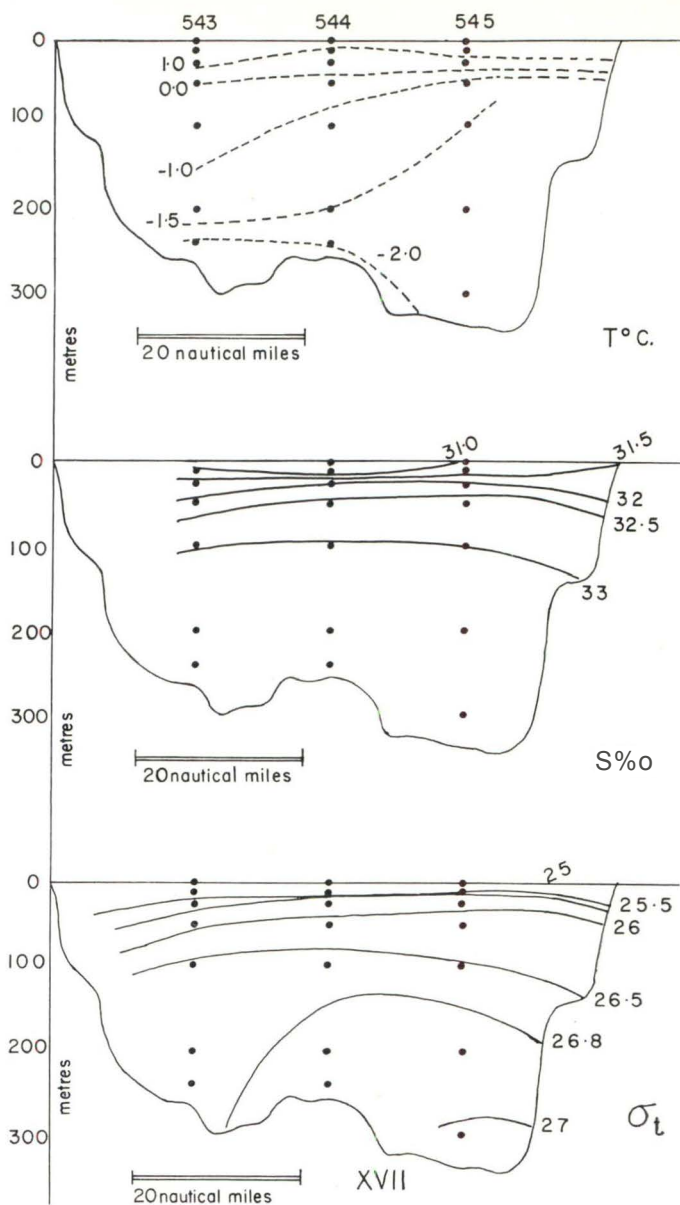


FIG. 23. Temperature, salinity and density profiles, Section XVII.



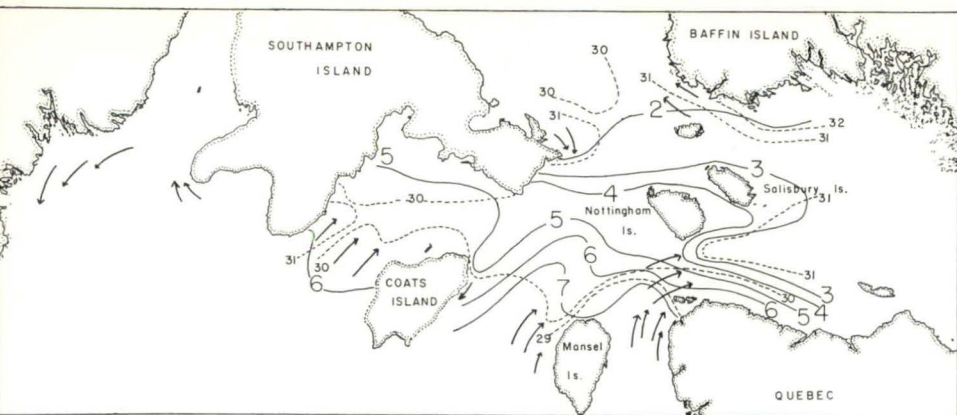


FIG. 24. Surface temperatures, northeast Hudson Bay, late July to early September, 1953. Arrows show surface currents as indicated by Sections XII to XVII.

in this region, for late July to early September, 1953. The strong warming and refreshing effect of the outflow from Hudson Bay is well shown. The chart is more detailed than the *Loubyrne* figures for 1930 (Hachey, 1931) and shows a somewhat greater extension of the warmer surface water towards the northeast, although the season of observation of the two expeditions is the same.

#### TEMPERATURE-SALINITY CORRELATION (Fig. 25-32)

The chief interest that attaches to the T-S correlation figures is the presence or absence of a turn-up of the curves in the deeper water, indicating the intrusion of a water of origin different, or partly different, from that of the remainder of the water, which consists of Arctic water considerably diluted in the upper 50 m. by land drainage run-off and melting ice. This turn-up occurs commonly at 100 m. and below in Ungava Bay (Fig. 25), mid-Hudson Strait (Fig. 26) and Cumberland Sound (Fig. 28), but it is almost entirely absent from Frobisher Bay (Fig. 27) and Hudson Bay and the western end of Hudson Strait (Fig. 29). Similar T-S curves are recorded from the Labrador Current (Bailey and Hachey, 1951a), but not from the Labrador fjords or the inshore regions of that coast (Nutt and Coachman, 1956; Nutt, personal communication). In the Labrador Current this rise in temperature in the deeper water is caused by admixture either of the deeper water of the Canadian Current (Baffin Island Current), or of water from West Greenland, or of Labrador Sea water. In Cumberland Sound, Hudson Strait and Ungava Bay, the intrusion of water direct from the Labrador Sea core water is improbable. Whether the influence comes from the West Greenland current, part of which turns westward towards the Canadian coast in the region of the Holsteinsborg Ridge, or from the Baffin Island Current, is uncertain; in either case part of the water probably comes ultimately from the West Greenland side. The temperature levels reached by the upturned portions of the curves

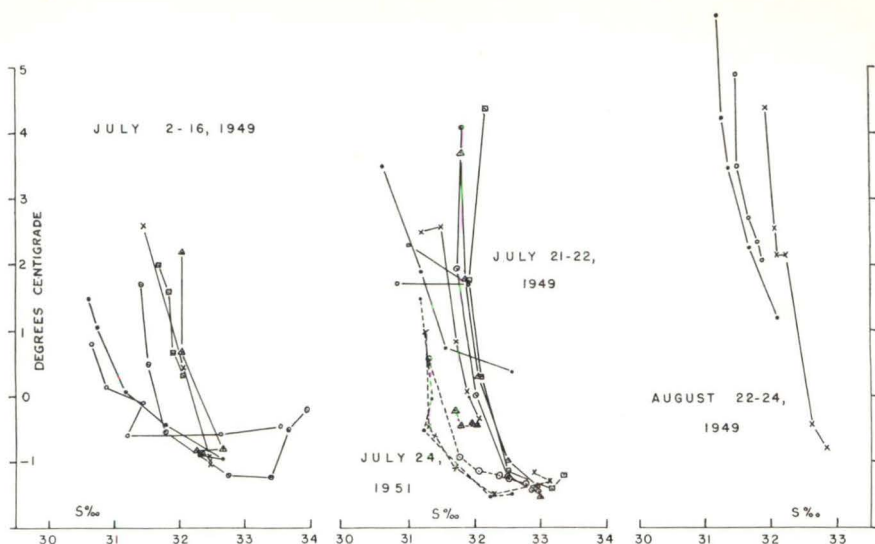


FIG. 25. Temperature-salinity curves, Ungava Bay.

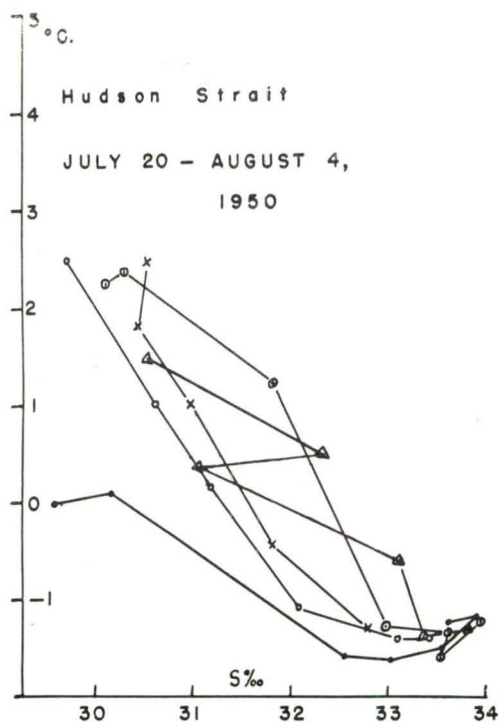


FIG. 26. Temperature-salinity curves, mid Hudson Strait, 1950, from Stations 208A, 218, 219, 220 and 221.

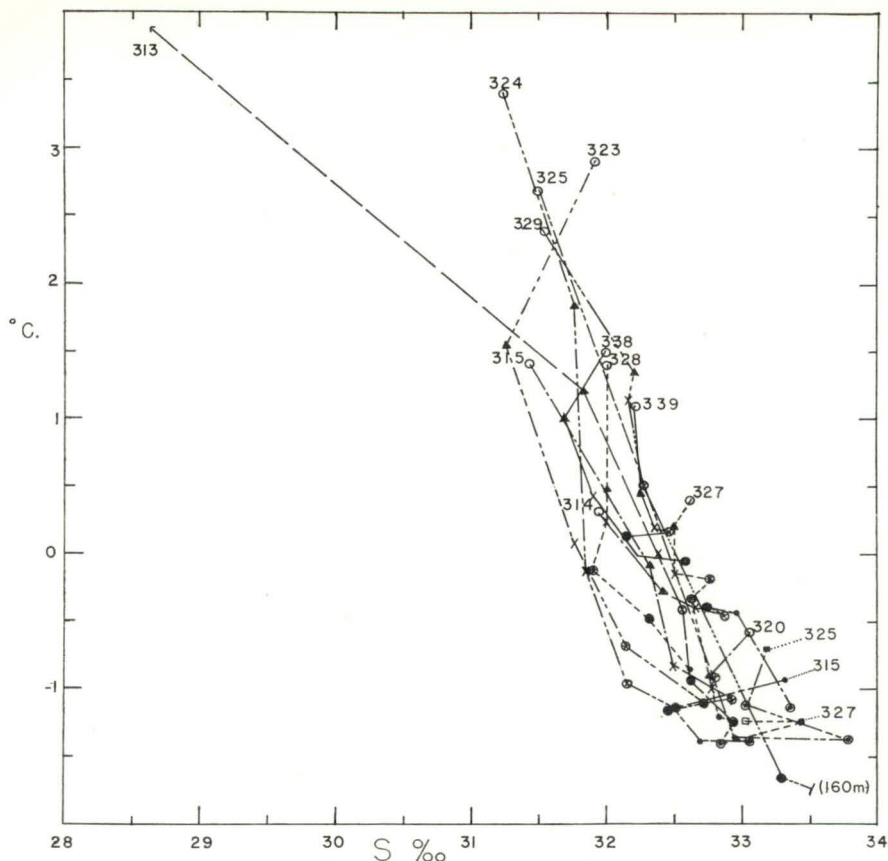


FIG. 27. Temperature-salinity curves, Frobisher Bay, 1951. Numbers are station numbers. Depth symbols as in Fig. 28.

(between  $-1.0$  and  $0.0^{\circ}\text{C}.$ ) are low, indicating that the proportion of West Greenland water is not overwhelming; the effect is more marked in Cumberland Sound than elsewhere in the region studied here.

The almost complete absence in Hudson Bay of this intrusion from the Atlantic region is not surprising, but it is interesting in view of earlier discussions of a possible marine climatic change in Hudson Bay owing to Atlantic influence (Dunbar, 1951; Bailey and Hachey, 1951b). On the present evidence such Atlantic influence is very slight, perhaps intermittent. Figure 29 shows minor upturnings at four Stations, 516, 521, 527 and 544. Figure 31 (1954) shows one at Station 612. The rises in temperature are all quite small, and the shapes of the curves as a whole are not the same as in Cumberland Sound and Ungava Bay. Whether these can be interpreted as the last depauperate traces of Atlantic water is a matter of opinion. Since the Atlantic influence elsewhere appears only below the 100-m. level, and is most marked still lower down (as in Cum-

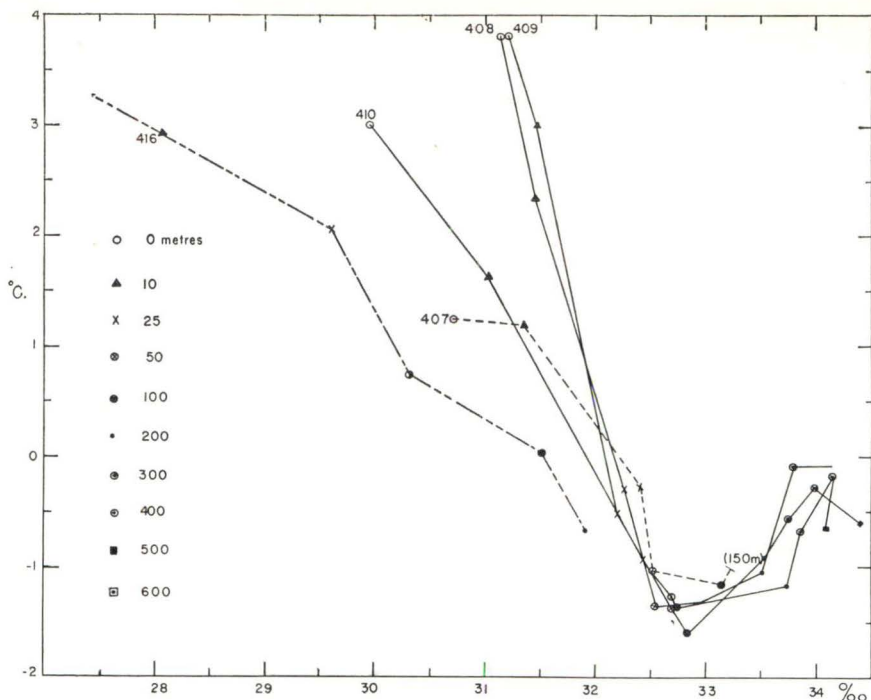


FIG. 28. Temperature-salinity curves, Cumberland Sound, 1952. Depths symbols apply also to Fig. 27, 29 and 31.

berland Sound), the very shallowness of Hudson Bay may exclude much of the Atlantic water.

From Fig. 27 it appears that the Atlantic intrusion is as slight in Frobisher Bay as it is at the exit from Hudson Bay. This, in view of the strong effect at the mouth of Cumberland Sound and the considerable influence in Hudson Strait and Ungava Bay, requires to be accounted for. The upturning appears at three stations only, 315, 325 and 327, and at all three they are associated with density inversions (see below), so that they cannot be considered as indicative of the Atlantic effect. The Cumberland Sound section (Fig. 28) shows increase in temperature, without density inversion, between 100 and 400 m.; the threshold at the mouth of Frobisher Bay has a sill depth of about 300 m. There should therefore be no obstacle to the entry into the bay of large quantities of the warmer water below 100 m.

A possible explanation of this anomaly can be found by examining the positions, on the T-S graph, of the 100- and 200-m. datum points. These are compared, Frobisher Bay with Cumberland Sound, in Fig. 30—Stations 329 and 416 have been omitted, since they lie in small fjords of special hydrographic conditions (see below). The separation of the two sets of datum points is quite clear, the more so if the 100-m. points of Frobisher are compared with those from Cumberland, and the same for the 200-m. points. Apparently the turbulence



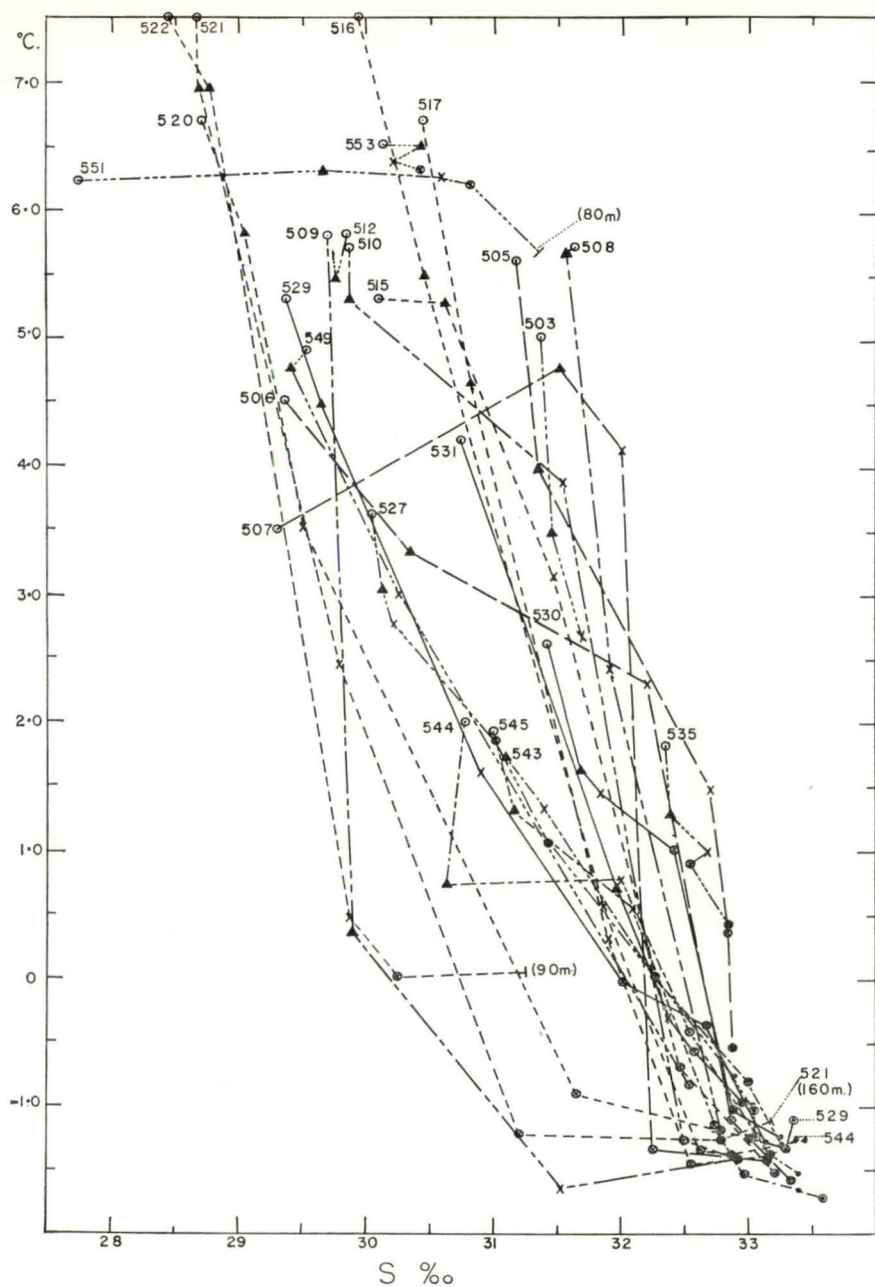


FIG. 29. Temperature-salinity curves, northeast Hudson Bay, 1953 (Sections XII to XVII and isolated stations). Depth symbols as in Fig. 28.

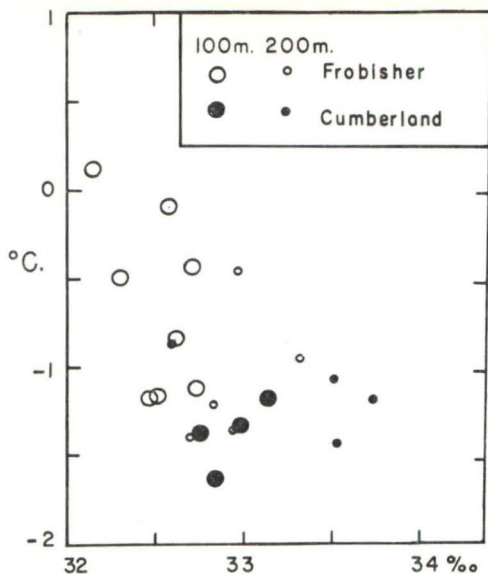


FIG. 30. Temperature-salinity correlation for samples from the 100- and 200-m. levels in Frobisher Bay and Cumberland Sound. See text.

of Frobisher Bay, resulting from the shape of the bay and from its strong tidal currents, effects a mixture of the upper and lower water so that at the 100- and 200-m. levels there is freshening and warming when compared with the comparatively undisturbed water entering Cumberland Sound. This masks the upturnings of the T-S curves characteristic of Cumberland Sound.

It was stated above that part of the warmer water in the Cumberland Sound section (and this applies to all the examples of rise in temperature below 100 m. demonstrated here) might come from the West Greenland Current. It might also come, in whole or in part, from the warmer Atlantic layer of the Arctic Sea itself, by way of the Baffin Island Current. The upturning in the T-S curves is characteristic of the material collected by H.M.C.S. *Labrador* in Baffin Bay, the channels through the Arctic Archipelago, and the Beaufort Sea (Bailey, 1955).

The T-S curves for Ungava Bay in 1949 (Fig. 25) are grouped by dates in order to show the seasonal warming of the water. Summer warming, in turbulent areas, can reach down as far as 100 m., as here demonstrated, and if the working season is long, as it is in Ungava Bay, this has to be taken into account in all comparative studies. It will be noted that there is no turn-up in the August 22-24 curves from Ungava Bay, taken from Section IV. This appears to be a space rather than a time effect, since the turn-up is well developed at Station 618 (Fig. 31), occupied on August 21, 1954, just west of Port Burwell. Section IV is west of Akpatok Island. It should also be noted that at only one station do the August 22-24 (1949) curves reach below 100 m., and then only to 150 m. In general, however, there appears to be a significant difference in this respect

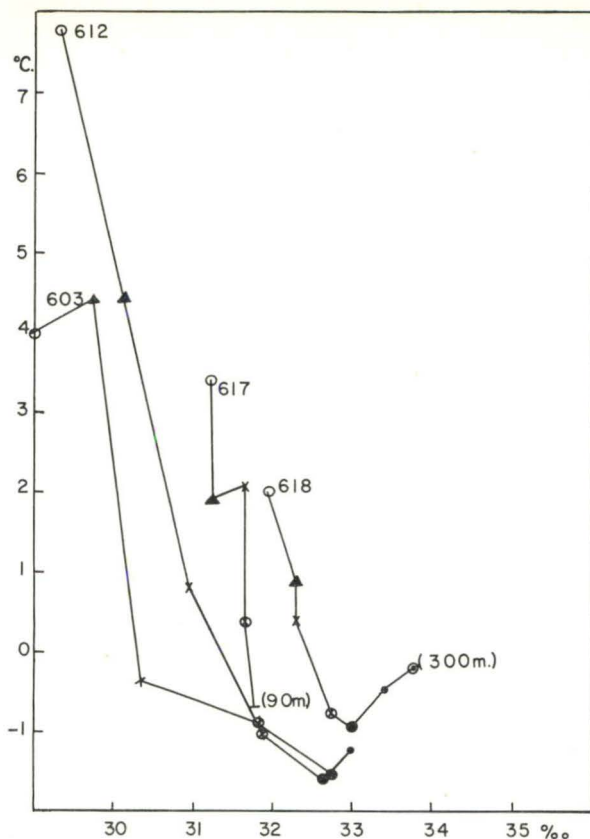


FIG. 31. Temperature-salinity curves for two stations in northeast Hudson Bay (603, 612), one in Sugluk inlet (617), and one in northeast Ungava Bay (618), 1954.

between water east and west of Akpatok, the Atlantic influence being more strongly developed in the northeastern part of Ungava Bay than elsewhere within the bay.

There are three more points to be observed concerning the T-S correlations from Hudson Bay. In Fig. 29, the different types of line (dotted, full, etc.) represent the several hydrographic sections. There is a separation of the curves involving a salinity of approximately 2‰ in all but the bottom right-hand corner of the Figure, which might be thought to be significant of some major dichotomy of water type. This separation, however, on inspection, turns out to exist in the upper 50 m. only (with one exception—90 m. at Station 522), and can therefore safely be put down either to local turbulence in the upper layers, or to the dynamic pattern of the movement of the water itself, or to coastal effects. For instance, five of the stations which show the shift to the left—520, 522, 521 (Section XV and the eastern end of Section XIV), 527 and 529—are all at the northeastern

corner of Hudson Bay, in the main outgoing current, where lower salinities and densities are to be expected.

The second point is the surprisingly high temperature from surface to bottom (80 m.) shown at Station 551. Station 551 is close to the western end of Section XII, but whereas that section was run on July 24, 1953, Station 551 was occupied on September 11 of the same season, some 7 weeks later. The same high temperatures are shown at Station 553, farther down the coast, to a depth of 50 m. Whatever the causes of these temperatures, they would be expected to be quite important biologically; further work along this coast is clearly needed, particularly in connection with (1) the known existence in Hudson Bay of relics from a warmer climate (Dunbar, 1955a) and (2) the experiment already under way to introduce species of Pacific coast salmon into streams draining into southwestern Hudson Bay. The high temperatures are most probably the result of intense insolation coupled with wind-mixing.

Finally, there is the question of long-term changes in the marine climate of Hudson Bay. Bailey and Hachey (1951b) and Dunbar (1951) have suggested the possibility of an increasing Atlantic influence in Hudson Bay, on the basis of a comparison of the *Loubyrne* 1930 results with those of the *Haida* in 1948. This is illustrated in Fig. 32, in which polygon A encloses all datum points from the

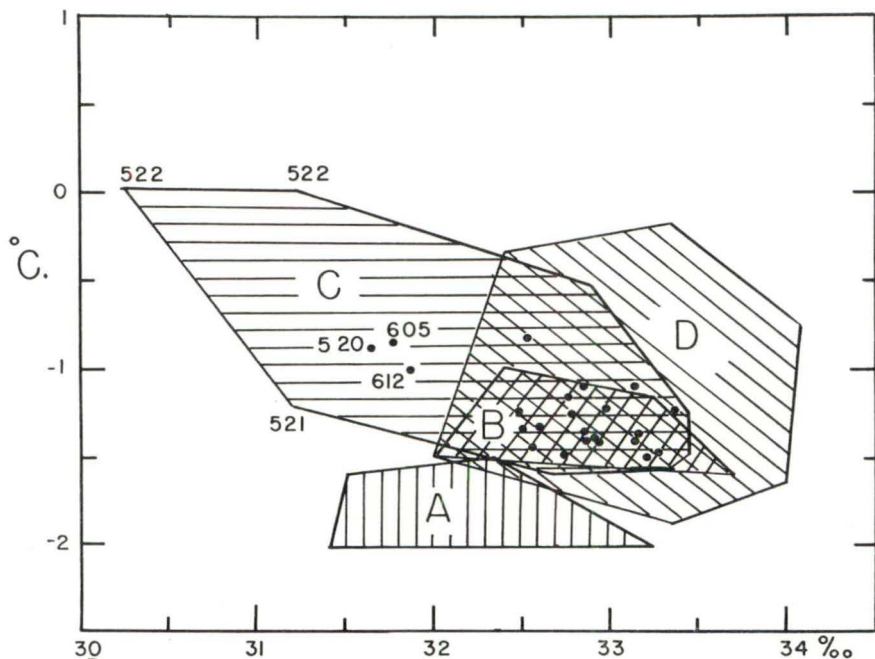


FIG. 32. Polygons enclosing temperature-salinity datum points for *Loubyrne* observations, 1930, in Hudson Bay (A); *Haida*, 1948, Hudson Bay (B); *Calanus*, 1953-54, Hudson Bay (C); and Arctic water in general, from Dunbar (1951). In all cases observations from depths less than 50 m. are omitted.



1930 expedition from 50 m. down to the bottom, and polygon B encloses the equivalent observations from 1948. For comparison, polygon D represents the Polar, or Arctic, water of the eastern Arctic in general, taken from the upper 200 m. in various regions supposedly outside the influence of Atlantic water (see Dunbar, 1951). Although the extreme low temperatures recorded from several stations in 1930 have been questioned, as possibly due to instrumental difficulties, nevertheless the general low level of the 1930 temperatures as compared with 1948 must be considered significant, and moreover, the differences in salinities between the two years' results are even more striking. Polygon C in Fig. 32 encloses the *Calanus* results from the 1953 and 1954 seasons, again with all observations from depths less than 50 m. excluded. These come from the north Hudson Bay only, between the islands, and not from the main body of the bay, but the *Calanus* stations nevertheless fall in regions covered by both the *Loubyrne* and the *Haida*. The datum points in polygon C which fall significantly outside the *Haida* 1948 polygon, marked by the station numbers, are all from 50 m. depth with one exception, a 90-m. observation at Station 522. It is reasonable to ascribe these lower salinities and higher temperatures to local and temporary conditions, and since the bulk of the *Calanus* observations fall within the *Haida* range, it can safely be stated that there is here no evidence of climatic change since 1948.

#### DENSITY INVERSIONS

Inversions of density in the sea have not yet achieved scientific respectability; and it must be stated from the start that any forces tending to invert must also tend to bring about mixing and therefore an approach to uniform density. This is undoubtedly a correct view to take, but it must nevertheless be admitted that the dynamics of turbulence are by no means fully understood and that the time scale involved in the mixing process is not known. Moreover, density inversions are nothing new; they have appeared in the results of several oceanographic expeditions, and it is not unreasonable to suspect that they would have appeared far more frequently had they not been quietly obliterated by a stroke of the pen, on the assumption that they were mistakes of one sort or another. Such instabilities, in fact, have usually been looked upon as fictitious, attributed to faulty thermometers, to errors in thermometer readings, sample labelling, titration, or the working up or filing of results.

The earliest instance of density inversion of which I am aware is in the late nineteenth century, from the results of the cruise of the *Vitiaz* in the Okhotsk Sea (Makaroff, 1894). That was before the days of standardized oceanographic method, and might be disqualified also on the grounds of thermometer error. The next is from the results of the *Michael Sars* expedition of 1910, in the north Atlantic (Helland-Hansen, 1930, and quoted in Sverdrup, Johnson and Fleming, 1942, p. 417). Spilhaus, Ehrlich and Miller (1950) have recorded inversions of density in the waters just south of Cape Cod, and have given evidence of some correlation of the times of observed instability with the times of lunar transit. In his extensive study of the Faroe-Shetland Channel, Tait (1957) found more

or less persistent instabilities; he writes: "One effect of turbulence which is encountered in the Faroe-Shetland Channel is inversion of density in the vertical column, and yet another, in at least one particular case, is the suggestion of a horizontal sub-surface tortional current through the body of the oceanic water-mass." That density inversions might be set up by tortional currents appears to be a new idea, and might have considerable relevance to the problem of the inversions found by the *Calanus* expeditions.

The observations of the H.M.S. *Challenger* off the Labrador coast in 1932 contain five stations with density inversions (British Admiralty, 1932), and the *Haida* in 1948 also recorded five inversions, at its Stations 3, 11, 13, 14 and 25. One of these stations was off the Labrador coast, two were in Hudson Strait and two off the coast of Coats Island. Four of them were between the surface and 10 m. depth. Finally, Dr. Carsola (personal communication) states that density inversions of short duration are common in shallow water observations in progress (1954-55) at the U.S. Navy Electronics Laboratory at San Diego.

In the instances recorded by the *Calanus*, titrations have been repeated where possible, and the methods used on board ship have been strictly examined and seem to preclude the possibility of other errors. Had there been errors in titration, it might be expected that although the salinities showed inversion, the temperatures would not. Of the total 27 instances used here (see below: some did not depend on depth observations taken simultaneously, and have been excluded), there are found to be eight involving temperature inversions as well as salinity inversions, two in which the temperature was the same at the two levels involved, and 17 in which there was no temperature inversion. Of those 17, however, there was a temperature inversion in eight instances at the level immediately above or below the density inversion. Copies of the raw data can be examined upon request to the author.

Unstable conditions of the type discussed here were recorded at 24 stations by the *Calanus* expeditions of 1949 to 1953. There were two inversions at Station 221 and three at Station 327. In the record given in Table I, only cases of inversion which involve "simultaneous" measurement of temperature and sampling of the water at the two depths involved are included; that is, where the depth levels were spanned by a single string of samplers, closed and reversed in series. The actual time difference between observations 100 m. apart is about 30 seconds, and between other vertical distances in proportion. There were a few instances of inversion, mentioned below, which were based on measurements made many minutes apart following separate lowerings of the wire. These have not been included in the statistical treatment.

The figures in the last column of Table I are measures of stability, in these cases negative stability, calculated from the formula

$$E = 10^5 (d\sigma_t/dz)$$

(Sverdrup, Johnson and Fleming, 1942), where  $d\sigma_t$  is the difference in density between the two depth levels concerned, and  $dz$  the difference in depth in metres



TABLE I

Station	Date	Depth of Inversion	Time of observation	Time of high water	Time before or after high water	Stability (see text)
		<i>m.</i>	<i>EST</i>	<i>EST</i>	<i>hr. min.</i>	
103	16/7/49	100-200	0315	2330	3 45 after	-290
118	22/7/49	10-25	0545	0530	0 15 "	-5730
220	31/7/50	200-250	0140	2053	4 47 "	-480
221	4/8/50	10-25	1100	1230	1 30 before	-6870
221	4/8/50	200-250	1020	1230	2 10 "	-660
201C	29/8/50	50-80	1100	0900	2 00 after	-600
305	24/7/51	10-25	0920	1230	3 10 before	-533
306	24/7/51	200-275	1415	1240	1 35 after	-267
308	24/7/51	25-50	2120	0055	3 35 before	-280
309	28/7/51	100-150	1930	1600	3 30 after	-180
314	8/8/51	50-100	0840	1020	1 40 before	-240
315	8/8/51	50-100	1125	1020	1 05 after	-680
320	11/8/51	10-25	1420	1247	1 33 "	-200
325	13/8/51	300-400	1548	1517	0 31 "	-610
327	19/8/51	50-100	1116	0820	2 56 "	-240
327	19/8/51	300-400	1030	0820	2 10 "	-70
327	19/8/51	500-600	1045	0820	2 25 "	-340
328	19/8/51	25-50	1353	0820	5 33 "	-250
329	21/8/51	10-25	1022	0956	0 26 "	-133
339	30/8/51	50-100	0750	0530	2 20 "	-520
410	31/7/52	400-500	0420	2228	5 52 "	-90
508	25/7/53	50-80	1625	1229	3 56 "	-100
509	25/7/53	50-100	1845	0060	low water	-240
512	8/9/53	10-18	1430	1238	1 52 after	-750
535	17/8/53	25-50	1134	1513	3 39 before	-360
543	2/9/53	200-240	0715	0624	0 51 after	-125
544	2/9/53	200-240	1105	0632	4 33 "	-100

With the exception of the inversions in the upper layers at Stations 118 and 21, the indices of instability are not large compared with the positive stabilities found normally in these waters in summer. The force required to produce the instabilities must nevertheless be considerable. The most obvious, in fact the only, force that could reasonably be expected to play a part in this phenomenon is to be found in the large tidal ranges and currents which characterize the bottle-neck region of Ungava Bay, Hudson Strait, and Frobisher Bay. Accordingly, the distribution of the times of observation of the inversions with respect to the state of the tide was first compared with hypothetical distributions in which the same number of stations were modally arranged about points from 3 to 3 hours after or before high water, on the hypothesis that the inversions tended to occur close to the time of strength of tide, whether the tide was rising or falling. Agreement with these distributions was unsatisfactory. The stations at which inversions occurred were then arranged on a tidal clock, the period of the clock being 12½ hours (Fig. 33).

Preliminary published notice of this analysis has already been given (Dunbar, 1955b). Three instances of inversion based on "non-simultaneous" observations were included in that preliminary report by oversight, and they have here been removed. Figure 33, then, shows the distribution, with respect to the state of the tide, of 17 stations at which inversions were observed in Ungava Bay, Hudson Strait and Frobisher Bay, 1949-51, compared with the remainder of the stations

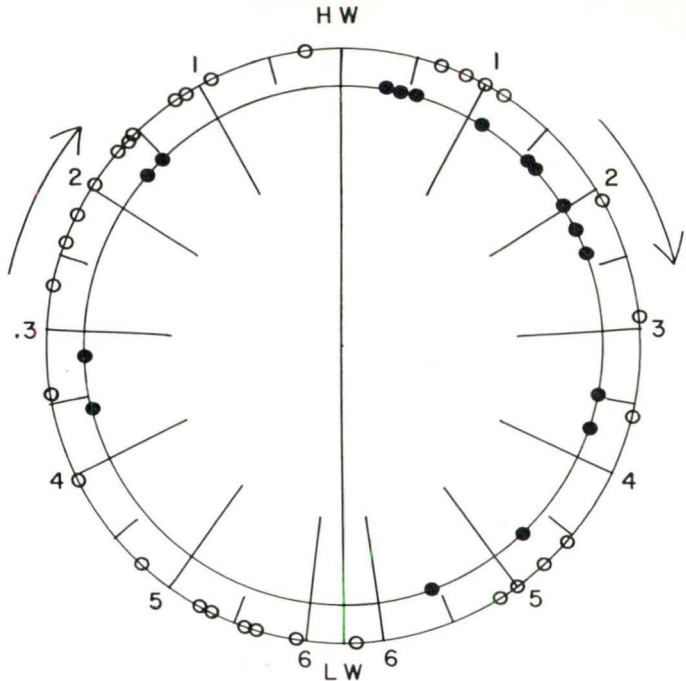


FIG. 33. Tidal clock showing the state of the tide at the time of occupation of stations with density inversions (black) and without density inversions (open circles), in Ungava Bay, Hudson Strait and Frobisher Bay, 1949-51. HW—high water; LW—low water. Figures are hours.

occupied during the same seasons and in the same area. The total number of stations is 48.

To test the agreement of these stations on the tidal clock with an even distribution, ten classes of radial scatter, each consisting of a sector subtending an angle of  $36^\circ$  at the centre of the clock, were set up, and the degree of association was tested by the  $\chi^2$  method. Comparing the radial scatter of all stations with the equally distributed radial pattern for the same total number of stations gave a  $P$  value of .57. For the stations without inversions, the  $P$  value was .56. These are both close to an equal scatter, as would be expected. The  $P$  value for the stations with density inversions, on the other hand, is .08, which is fairly close to disagreement with the equal scatter at the 5% level. Moreover, a comparison of the means (standard error of the difference between the means) of the inversion and non-inversion stations gives a  $P$  value of .01 (difference of the means is 2.78 times its standard error), which is evidence of significant disassociation. It is, furthermore, immediately apparent that of the 17 inversion stations 13 lie on the ebb tide and over one half lie in one quadrant in the first three hours after high water.

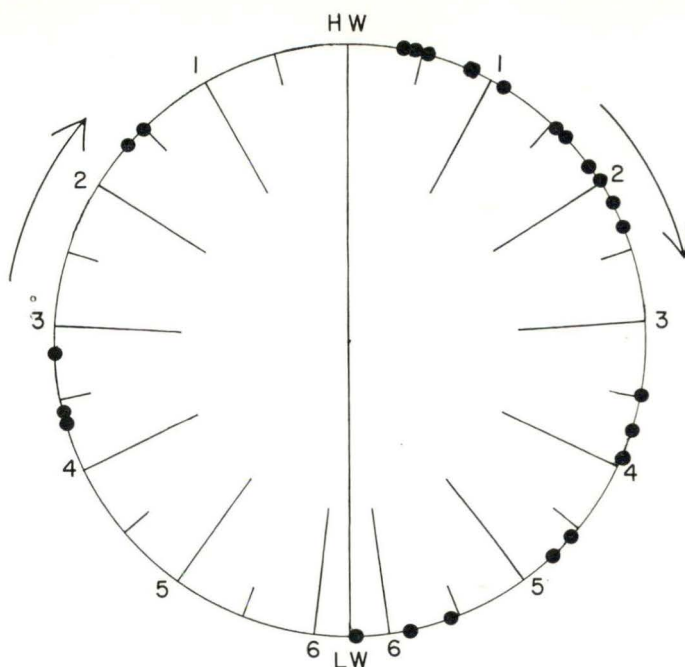


FIG. 34. The same as in Fig. 33, but showing the stations without density inversions omitted and seven stations with density inversions added, from the 1952 and 1953 seasons (Stations 410, 508, 509, 512, 535, 543 and 544).

In the years 1952 and 1953, seven more observations of instability were made, as shown in Table I, one at the mouth of Cumberland Sound, one off Cape Dorset, two in Foxe Channel and three in Fisher Strait. These are added to the earlier observations in Fig. 34. When this distribution is compared with an even scatter of the same number of stations (24), again by  $\chi^2$ , the value of  $P$  is a little less than .04 (about .038), again good evidence of disassociation from the even scatter. In this Figure, all but five of the stations lie on the ebb tide, and 11 of the 24 lie in the first three hours after high water.

On the hypothesis that the inversions are associated not only with the state of the tide but with the force of the tidal wave, it is interesting that in spite of the large number of hydrographic stations occupied in 1953 in northern Hudson Bay, there should be so few instances of instability as compared with the observations in Hudson Strait, Ungava Bay and Frobisher Bay. In fact, of the seven instances from the 1953 season, only three can be said to come from Hudson Bay itself. This is in keeping with the smaller tidal ranges within Hudson Bay than in the rest of the area studied here. There were no instances of instability recorded from the few stations in Hudson Bay occupied in 1954.



The inversions at Stations 543 and 544 have been included in Table I. The temperatures from which the densities are calculated at these two stations, at 240 m., are  $-2.08$  and  $-1.99$  respectively; values which are of the order found by Hachey (1931) in Hudson Bay in 1930, and also by H.M.C.S. *Labrador* in Foxe Basin in 1955 (Campbell and Collin, 1956). These very low temperatures may be caused by thermometer inaccuracies; and where they have been met in the *Calanus* work the temperature has been measured again at the same depth with a different thermometer. In the case of Stations 543 and 544, the second thermometer readings were  $-1.39$  and  $-1.57$  respectively. Unfortunately salinity samples were not taken together with the second temperature measurements. However, if the higher temperature value had been used together with the salinity from the first observation in each case, the densities would have been lower, so that the density inversion would have been more marked, not less so.

There are nine stations at which instabilities appear but at which these may be artifacts because the observations at the two depths concerned were not made at the same time (with a single string of samplers). These instances are set out in Table II, in which the first seven represent instabilities between the surface and 10 metres, the remaining two being from various depths lower down.

TABLE II. Time of observations, before (+) or after (-) high water.

Station	Hours	Minutes
227	+0	15
323	+3	30
327	-3	15
338	-1	10
508	-3	56
544	-4	00
549	-3	24
219	-2	15
553	-3	45

Although these instances are not taken as valid for present purposes, it is at least interesting, if not more than interesting, that eight out of the ten occur on the ebb tide.

It must be admitted that the level of accuracy possible at present in the calculation of the state of the tide at all stations may not be as great as could be desired. The tide datum points are too far apart to admit great accuracy in the tracing of the progress of the tidal wave. However, by checking the times calculated from the tide tables against observations on shore as soon as possible before or after occupying hydrographic stations, it has been possible to gain considerable confidence in the estimates; the errors are probably of the order of considerably under one hour in some cases, much less in others. Errors of this order would not disturb the general pattern of the results.

The conclusion is that there is a turbulent effect associated with the tide

particularly with the ebb tide, whose time scale is not known but which results in frequent finding of density inversions when the column of water is sampled in the standard way at standard depths, in areas where the tidal range is large and the tidal currents are consequently strong. Such turbulence would be expected to have important biological effects, among others, and indeed such effects have already been recorded in the vertical distribution of the microplankton (Bursa, personal communication). Such instabilities are also extremely interesting from the physical point of view, and would repay further and much more detailed investigation. As already mentioned, the tortional current effect recorded by Tait (1957) in the Faroe-Shetland Channel might be a profitable line of attack on the problem.

The maximum tidal ranges involved (at springs) are as follows: Head of Frobisher Bay (Frobisher's Farthest), 36 feet; Port Burwell, 22.5 feet; Koksoak River entrance (Ungava Bay), 45 feet; Leaf Basin (Ungava Bay), 54.5 feet; Lake Harbour (southern Baffin Island), 35 feet; Wakeham Bay, 30 feet; Nottingham Island, 15.75 feet.

One further point of interest is that in Frobisher Bay some of the inversions were found at depth levels between 300 and 600 m. In view of the fact that the distribution in depth of tidal currents in inlets is little known (e.g. Pickard, 1953b), this might have a possible value in the study of tides as such.

#### VERTICAL STABILITY

Since some time has been devoted here to the study of negative stabilities, it might be proper to give some account of the general stability conditions in the regions covered by the present series of expeditions. Table III sets out the values of the approximate stability index  $E$  for a number of stations from the whole geographic range from northwest Hudson Bay to Cumberland Sound, representative of the stations occupied in the 1947-54 seasons. (One 1947 station, No. 41 in Ungava Bay, is included in this series.)

It will be seen first that with two exceptions the negative stabilities given in Table I are all small compared with the general range of positive stabilities shown in Table III. This has already been referred to above.

Five other points which should be mentioned here are shown in Table III. (1) The order of stability everywhere in this area is considerably higher than is found in temperate regions, for instance in the North Atlantic. This is characteristic of northern, especially Arctic, waters in summer. (2) The upper 50 m. in Hudson Bay are somewhat more stable than elsewhere in the area, and to some extent this greater stability extends down to 100 m. (3) Stabilities in Hudson Strait, Ungava Bay, Frobisher Bay and Cumberland Sound are of the same order throughout. (4) The contrast between the Hudson Bay stations and the rest is not very great, except at the 25- to 50-m. level. (5) The columns of equal density between the surface and 10 m. at Station 115, and between 25 and 100 m. at Station 109, point to mixing processes, probably the result of density inversion some short time before the measurements were made.

TABLE III. Stabilities,  $10^8(d\sigma_t/dz)$ , for sample stations in the area covered (1947-1954)

Depth	Stn: 505 Date: 24/7	509 25/7	603 24/7	612 10/8	516 3/8	521 5/8	530 11/8	545 2/9	220 31/7	309 28/7	208A 20/7	115 21/7	128 24/8	307 24/7	234 31/8	41 17/8	108 16/7	109 16/7	618 21/8	314 8/8	324 13/8	409 31/7	
<i>m.</i>																							
0	3000	5800	6000	10400	6600	900	1900	1600	4800	12000	8400	0	1900	4400	1200	−100	1500	6300	3400	4100	5600	2600	
10	8470	9130	5330	6200	10200	8800	934	5200	13930	2800	3270	1666	266	1533	600	133	1533	2530	333	1330	1133	5460	
25	720	4520	4640	3280	2680	5200	1920	2320	1600	160	3000	1600	480	1040	1800	1240	3320	0	1600	720	1240	1680	
50		240	1580	1200	400	2560	900	400	800	180	1680	1060	900	200		480	1020	0	440	−240	500	240	
100				290	470		320	340	300			150				240	170		300	200	170	540	
200								160									230		260	340	280	160	
300																						150	
400																						310	
500																							
	North and northeast Hudson Bay						West Hudson Strait		Mid-Hudson Strait			Ungava Bay										Frobisher Bay	Cum-ber-ld. Sd



## WINTER RÉGIME IN NORTHERN HUDSON BAY

That Hudson Bay below about 50 m. might be dynamically dead was suggested by Hachey (1931) as a result of the 1930 observations. Later, working on the *Haida* 1948 material, Bailey and Hachey (1951b) found that this was in fact not the case, which is confirmed by the *Calanus* findings reported here (above) for the north and northeastern part of the bay. Another possibility which arose out of the same observation, namely the very high stability of the Hudson Bay water in summer, was that the normal winter vertical exchange of water might be inhibited, and that this might be related to the supposed low biological productivity of the bay. This low productivity was deduced from the lack of commercially valuable fishes, and it is now known that Hudson Bay, in terms of plankton production, is not greatly different from neighbouring bodies of water. The evidence available at present, given here, suggests that this second possibility is also not realized, and that on the contrary the behaviour of the Hudson Bay water in winter, at least in the upper 50 m. (all that we have material from), is normal.

Opportunity to obtain hydrographic observations in winter in Hudson Bay is rare, and a preliminary attempt at Fort Churchill in March was unsuccessful because water of reasonable depth could not be reached at the time. In March 1955, however, Mr. A. W. Mansfield arrived at Coral Harbour, Southampton Island, and was able to obtain temperatures and water samples from the surface to 50 m. during April, May and June. The results are given in Table IV. All the

TABLE IV. Data from winter stations in South Bay, Southampton Island, 1955.

Date	Location	Depth	Temperature	Salinity	Density
		<i>m.</i>	<i>°C.</i>	<i>‰</i>	<i>σ<sub>t</sub></i>
April 3	63°45'N. 83°02'W.	1	-2.20	32.75	26.38
		10	-1.72	33.19	26.70
		25	-1.75	33.19	26.72
		50	-1.72	33.28	26.80
April 28	63°40'N. 82°40'W.	1	-1.57	32.94	26.52
		10	-1.65	32.94	26.53
		25	-1.73	32.97	26.55
		50	-1.79	33.12	26.67
May 17	63°50'N. 83°25'W.	1	-1.62	32.94	26.52
		10	-1.62	32.94	26.52
		25	-1.77	33.12	26.67
		50	-1.79	33.49	27.05
May 27	63°43'N. 83°37'W.	1	-1.42	33.03	26.59
		10	-1.43	33.06	26.61
		25	-1.64	33.06	26.62
		40	-1.75	33.08	26.64
June 7	63°46'N. 83°30'W.	1	-1.60	32.45	26.12
		10	-1.60	32.54	26.21
		25	-1.47	32.54	26.20
		50	-1.81	33.21	26.75
June 18	63°47'N. 83°25'W.	1	-1.33	30.91	24.88
		10	-1.20	32.50	26.15
		25	-1.60	32.72	26.34
		50	-1.78	33.08	26.64



stations are in the vicinity of South Bay, immediately south of Coral Harbour. The marked similarity in temperatures, salinities and densities from the surface to 50 m., up to the middle of June, is quite plain and leaves no doubt that there is vertical exchange during the winter. Comparison of the density values at 50 m. with those at 100 and 200 m. in summer shows there is no reason to suppose that the vertical exchange fails to reach the bottom of Hudson Bay. The reduction in salinity and very slight rise in temperature at the surface on June 18 indicates that melting of the ice had begun to take effect by that time.

#### FJORDS AND INLETS

It is characteristic of the typical fjord, with its shallow threshold at the mouth and deep water inside, that the water below the level of the threshold is more or less cut off from the circulation of the water outside and therefore loses heat; the result is that the deeper water inside the fjord is considerably colder, depth for depth, than the water outside the fjord. This is the characteristic which distinguishes the so-called "Arctic" fjords of West Greenland, with thresholds, from the "Atlantic" fjords, without thresholds, in which there is free interchange between the fjord water and the main current water outside. Sometimes the deep fjord water is so far removed from contact with the coastal water, and for such long periods of time, that it becomes stagnant and devoid of aerobic life, as in certain fjords in Norway (Strøm, 1939), British Columbia (Pickard, 1953a) and one fjord in northern Foxe Basin (Grainger, personal communication).

The *Calanus* expeditions of 1949-54 worked in several inlets, some of which are of interest for this and other reasons. A typical, though small, example of the threshold fjord with cold deep water is Victoria Bay on the northeast coast of Frobisher Bay, a small inlet at the mouth of the Countess of Warwick Sound, which appears to have been Martin Frobisher's main base in the 1570's. Victoria Bay is 100 fathoms (183 m.) deep and has a threshold of about 30 fathoms (55 m.). The Countess of Warwick Sound is nowhere much deeper than 55 m. and has a shallower region along its line of contact with Frobisher Bay itself, so that the effective depth of the threshold into Victoria Bay is less than this, probably (according to sounding runs made from the open water) about 20 fathoms (37 m.). Owing to the peculiar bathymetry of Frobisher Bay, depths similar to that of Victoria Bay do not occur within several miles of the mouth of the Countess of Warwick Sound; the closest are towards Station 324 to the west and 315 to the south. Temperatures and salinities for these two stations are given here in Table V, compared with those from Victoria Bay (Station 329).

The differences between the fjord water and the outside water are of course not so striking as in an area such as Ameralik Fjord in West Greenland (Dunbar, 1951), where the outside water is a great deal warmer than it is in Frobisher Bay. Nevertheless, the situation is the same in all important aspects. The temperatures in the upper layers down to the 50-m. level are higher than at the stations in Frobisher Bay, which is probably the result of vertical circulation set up by westerly winds blowing into the inlet; below this layer, from 100 m. down, the water is colder than outside, which is the normal fjord effect described above.

TABLE V

Station:	315		324		329	
Date:	Aug. 8		Aug. 13		Aug. 21	
Depth	Temp.	Salinity	Temp.	Salinity	Temp.	Salinity
m.	°C.	‰	°C.	‰	°C.	‰
0	1.40	31.44	3.40	31.23	2.40	31.52
10	-0.10	32.31	1.84	31.76	1.33	32.20
25	-0.84	32.52	-0.13	31.85	1.15	32.16
50	-1.06	32.90	-0.96	32.16	0.52	32.27
100	-1.16	32.47	-1.16	32.49	-1.66	33.31
160	...	...	...	...	-1.74	33.52
200	-0.94	33.32	-1.38	32.69	...	...
300	...	...	-1.39	33.04	...	...

The bathythermograph slide (not published here) for Station 329 shows that the thermocline is deep, between 50 and 65 m. The high salinities of the 100- and 160-m. water are also an indication of the degree to which the sub-threshold water in Victoria Bay is cut off from the circulation of the deeper water outside.

In two other inlets visited, at depths shallower than 100 m., water temperatures at all levels are warmer than those outside the fjord, not colder as in the case of the upper 50 m. of Victoria Bay. These are Sugluk Inlet (Station 617, Fig. 31) and Adlorilik (Fig. 35). Sugluk is on the Quebec shore of Hudson Strait;

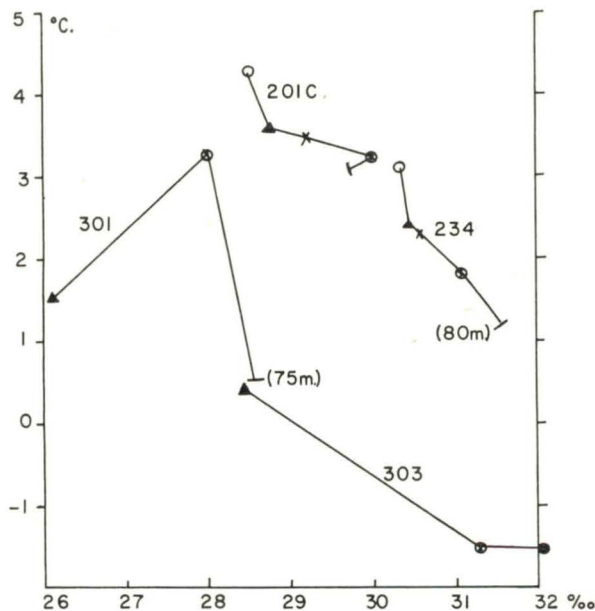


FIG. 35. Temperature-salinity correlation for stations in Adlorilik fjord (201C, August 29, 1950; 301, July 3, 1951) and outside the fjord in Ungava Bay (234, August 31, 1950; 303, July 4, 1951). Depth symbols as in Fig. 28.



Adlorilik is situated on the east side of Ungava Bay,  $59^{\circ}30'N$ ,  $65^{\circ}26'W$ . It is called on the charts and topographic sheets "Abloviak", "Ablluik" and other variants, none of which approaches the Eskimo pronunciation of the name. (See station list map, Dunbar and Grainger, 1952.)

The effect is more emphasized in the Adlorilik case than at Sugluk. Stations 201C (inside the fjord) and 234 (outside) were occupied on August 29 and 31, 1950; Stations 301 (inside) and 303 (outside) on July 3 and 4, 1951. In both pairs of stations the temperatures inside the fjord are quite considerably higher, and the salinities lower, than outside the fjord, depth for depth. The 1951 observations were made within two weeks, at the most, of the break-up of the ice in the fjord, so that the high temperatures at Station 301 at 50 and 75 m. must be the result of the retention of heat within the fjord throughout the winter. The 50-m. temperature in fact was the same on July 3, 1951, as on August 29 of the previous summer.

The sill depth at the mouth of Adlorilik is only about 22 to 25 m., so that the degree of isolation of the fjord water is considerable. A "hole" just inside the sill was sounded at 95 fathoms (174 m.); this appeared to be a deep pocket within an otherwise much shallower inlet, and no station was made in it. With this exception, the fjord is less than 100 m. deep.

The high temperatures and remarkably low salinities in Adlorilik, as compared with stations immediately outside the fjord, would suggest that down to 80 m. the only water in the fjord is water from the upper few metres of Ungava Bay, and that there is a constant or intermittent "flushing out" of the water, at least down to the depths measured; a phenomenon which must for the present remain unexplained. The prevailing northwesterly winds, the tidal current in a fjord of the long, narrow shape of Adlorilik, and the influx of water from the river at its head probably all play a part in the mechanism. The low salinity, which even at 80 m. is less than the surface salinity in late August in the body of Ungava Bay, is no doubt due to the freshwater influx. The derivation of the water of the fjord, or the great part of it, from the surface water of the bay outside, is further indicated by the nature of the plankton in the fjord, which will be dealt with in a later paper. There is a marked scarcity of Calanoid copepods and of copepods in general, and an abundance of Medusae at greater than normal depth.

The last inlet to be discussed here is a somewhat special case. Lake Ogac, meaning "Cod Lake", lies at the head of Ney Harbour, an inlet on the southwest shore of Frobisher Bay (Stations 312 and 312A, Grainger, 1954). At spring high tides there is some influx of salt water into the lake, in amounts at present unknown; for the rest of the time there is a current of overlying fresh water running into Ney Harbour, the outflowing stream being about 240 feet long. This outflow is of considerable volume, the stream being fast-flowing, about 90 feet wide on the average, and some 2 to 3 feet deep. The lake itself is quite small, in the shape of an "L" in which the longer arm is about a mile long and the shorter about  $\frac{3}{4}$  mile. There are three small basins in the lake, separated by shallower water, of which the central one is a little over 60 m. deep. The inner basin was

not sounded but is probably shallower, and the outer basin is about 20 m. deep. In the central basin there are three quite distinct layers of water: an overlying, very shallow fresh water layer derived from the inflowing drainage at the head of the lake, a layer of salt water of fairly low salinity, and a bottom layer of stagnant water rich in hydrogen sulphide and devoid of dissolved oxygen. The transition between the two lower layers appears to be gradual. There is no stagnant layer in the outer basin, which is small. Table VI gives temperatures, salinities and dissolved oxygen concentrations for two stations in the lake (312 in the central basin, 312A in the outer basin), and one station (313) in Ney Harbour.

TABLE VI. Ogac Lake and Ney Harbour; temperature, salinity and dissolved oxygen concentration.

Station: Date:	312 August 4, 1951			312A August 4, 1951			313 August 5, 1951		
	Temp.	Salinity	Oxygen	Temp.	Salinity	Oxygen	Temp.	Salinity	Oxygen
Depth									
m.	°C.	‰	cc./l.	°C.	‰	cc./l.	°C.	‰	cc./l.
0	7.40	0.00	7.35	7.70	0.00	8.30	4.40	28.00	8.64
10	7.31	22.32	7.54	6.40	26.99	7.09	1.21	31.83	8.17
18				3.88	27.47	4.11			
25	8.12	26.10	2.01				0.03	32.35	6.89
50	4.50	26.95	0.00				-0.39	32.56	7.55
100							-0.93	32.62	6.33
160							-1.25	32.94	5.07

Lake Ogac can be considered as the extreme case of the fjord condition, with threshold so high that salt water can enter only in small quantity and intermittently, and with the "fjord" itself so small that there is very limited mixing between the overlying land-drainage water and the salt water below. The anaerobic layer at the bottom is also an extreme fjord characteristic. The salt water is heated by solar radiation to temperatures quite extraordinarily high for the geographical area, and it is insulated against heat loss by ice and snow in winter. The lake contains an unusual animal population including an isolated group of Atlantic cod (*Gadus callarias*). A thorough study of the lake is in progress in the field.

#### CONCLUSION

No lengthy discussion of the results, presented here somewhat tersely, is necessary. Emphasis should, however, be laid on one point, namely that much of the hydrodynamic pattern in the region under study is dominated and determined by the tides, and that the basic studies from which understanding of the tides would come have not yet been made. The behaviour of water under extreme tidal forces in these narrow seas can only be guessed at. The undulating profiles found in Ungava Bay, the behaviour of the currents in Frobisher Bay, the setting up of negative stabilities (presumably for quite limited periods), the fate of Atlantic water entering Frobisher Bay, and certain of the special conditions found in small fjords—all these appear to be determined, to a greater or lesser extent, by tidal forces. Since these phenomena are of great practical interest both in



the physical and biological sciences, it is fitting to close this paper with a plea for intensive study of the tides of this eastern Arctic area in particular, and of tidal behaviour in contained waters in general.

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# STUDIES ON MYTILUS EDULIS L. OF THE "CALANUS" EXPEDITIONS TO HUDSON BAY AND UNGAVA BAY

"CALANUS" SERIES No. 16<sup>1</sup>

I. LUBINSKY

## Abstract

The "Calanus" expeditions of the Fisheries Research Board of Canada give the first detailed data on the distribution of *Mytilus edulis* L. in Ungava Bay, Hudson Strait, and the northern part of the Hudson Bay. Types of shells of this mollusc and their growth in the above regions are described. The comparison of the growth of *M. edulis* from Canadian Eastern Arctic, west Greenland, and the northwestern shores of the Atlantic Ocean shows that northward from the Canadian Maritime Provinces the growth of *M. edulis* slows down. In the region investigated by "Calanus", growth diminishes from Ungava Bay to Hudson Bay. The dependence of the distribution of *M. edulis* on the types of water masses and its relation to the northern limits of the subarctic zone in the Canadian Eastern Arctic is discussed.

Our knowledge of the distribution of *Mytilus edulis* L.—the edible mussel—in the Canadian Eastern Arctic has hitherto been very limited. This species has previously been recorded from only two localities in Ungava Bay, namely the mouth of Koksoak River (13) and Cape Hopes Advance (59). It has also been reported from an unspecified locality in Hudson Bay (66), from Fullerton, Roes Wellcome (15), Southampton Island (4), and Chesterfield Inlet (39). It was found in Ashe Inlet in the Upper Savage Island in Hudson Strait (66).

The "Calanus" expeditions of the Fisheries Research Board of Canada, 1947–1953, have shown that this mollusc is widely distributed in the region from Port Burwell on the northeastern shore of Ungava Bay to Churchill on the western shore of Hudson Bay. Specimens of *M. edulis* were taken in Ungava Bay, stations 212, 208, 8, 5, 31, 107, 224, 66, 67, and 215; in Wakeham Bay at station 217; in Hudson Bay at stations 525, 528, 504, 555, 513, and 519. The description of the above stations and their location is given by Dunbar and Grainger (22), Grainger (31), and Grainger and Dunbar (32).

*Mytilus* was collected exclusively in the intertidal zone. Samples contained 5–15 specimens, with the exception of those from Burwell, where 38 specimens were collected. Numerous empty shells of this mollusc were often found scattered on the shores. Sometimes it was difficult to decide whether they originated from contemporary nearby beds or were washed out from raised ancient beaches, which contain numerous shells of this mollusc (39, 49, 52, 63). It is hard to say whether at present *Mytilus* is as abundant as it has been previously. The "Calanus" expeditions have shown it to be abundant only in a few localities: near Port Burwell, along southwestern shores of Ungava Bay, and in Harbour of Nuvuk.

This paper is based on a limited material and has to be regarded as a preliminary report.

<sup>1</sup>Manuscript received April 18, 1958.

Based on material collected by the "Calanus" expeditions of the Fisheries Research Board of Canada.



TABLE I  
DIMENSIONS (IN MM) AND AGE OF SHELLS OF *Mytilus edulis* L. IN  
HUDSON BAY AND UNGAVA BAY

	Age	L	H	W	H/L	W/L	W/H
Hudson Bay							
Port Churchill	14	47	25	10	0.53	0.44	0.76
Station 555 L <sup>1</sup>	9	37	18	13	0.48	0.35	0.72
	11	40	18	13	0.45	0.32	0.72
	9	38	18	14	0.47	0.37	0.78
	4	27	14	12	0.51	0.37	0.71
	2	21	11	7	0.50	0.33	0.70
Nuvuk Harbour	12	53	29	25	0.54	0.47	0.89
Station 528 L <sup>6</sup>	11	48	25	21	0.52	0.43	0.89
Station 525 L <sup>5</sup>	8	43	22	20	0.51	0.44	0.98
	10	59	81	25	0.52	0.42	0.80
	10	51	24	20	0.47	0.39	0.85
	5	33	17	15	0.51	0.45	0.88
	0	49	25	22	0.51	0.45	0.88
	4	32	19	14	0.50	0.43	0.79
	4	31	18	15	0.58	0.46	0.83
	3	20	11	10	0.54	0.41	0.90
	3	21	12	9	0.57	0.42	0.75
Wakeham Bay	11	68	35	27	0.57	0.39	0.77
Station 217 L <sup>11</sup>	10	62	29	27	0.46	0.39	0.93
	10	60	25	26	0.41	0.43	1.04
	7	56	27	24	0.47	0.44	0.93
	8	55	31	23	0.56	0.43	0.76
	7	55	29	22	0.53	0.40	0.76
	7	50	24	23	0.48	0.46	0.95
	8	51	26	25	0.50	0.49	0.56
	5	49	24	21	0.50	0.74	0.80
Ungava Bay							
Southern shores	11	81	38	36	0.47	0.44	0.94
Station 8 L <sup>11</sup>	8	76	37	32	0.49	0.42	0.86
Station 31 L <sup>14</sup>	10	74	34	31	0.46	0.40	0.31
Station 5 L <sup>8</sup>	8	64	31	30	0.49	0.46	0.36
	7	67	33	28	0.49	0.41	0.96
Port Burwell	12	72	36	29	0.50	0.40	0.80
Station 67 L <sup>4</sup>	10	59	32	24	0.54	0.40	0.79
Station 224 L <sup>15</sup>	10	62	31	24	0.50	0.40	0.80
Station 66 L <sup>3</sup>	11	65	39	25	0.60	0.40	0.76
	8	57	31	22	0.54	0.40	0.70
	9	56	30	23	0.53	0.43	0.78
	8	55	26	21	0.50	0.40	0.78
	4	45	23	19	0.51	0.41	0.83
	6	43	22	20	0.51	0.46	0.90
	5	38	19	18	0.50	0.77	0.50
	4	32	16	14	0.50	0.43	0.87
Cape Hopes Advance	7	50	27	22	0.54	0.44	0.82
Station 212 L <sup>8</sup>	7	36	18	18	0.50	0.50	1.07
Station 208 L <sup>7</sup>	3	29	15	12	0.51	0.71	0.80
	5	33	15	14	0.57	0.50	0.74
	6	48	23	23	0.49	0.49	1.00
	7	32	18	13	0.56	0.40	0.89
	3	29	16	14	0.55	0.48	0.88
	5	23	18	11	0.56	0.48	0.84
	6	55	28	22	0.50	0.40	0.79
	5	49	24	18	0.50	0.39	0.73
	4	44	27	22	0.57	0.47	0.81
	5	46	26	20	0.56	0.43	0.80
	4	42	18	17	0.55	0.40	0.80



### Shell Types of *Mytilus edulis*

*Mytilus* in our material varies in size, shape, and color from station to station and to some degree within the same station (Table I). Despite this they form three natural groups: *Mytilus* from the southwestern shores of Ungava Bay, those from Hudson Strait, and those from Hudson Bay. The difference in the length of shells in these groups is considerable (Fig. 1). The individuals of the first group are the largest and those of the third group the smallest. The second group is intermediate and the shells comprising this group vary in size but slightly. *Mytilus* from Burwell can be regarded as representative of this group.

Table II summarizes the data on the length of 5-year-old specimens of these groups. The relations of differences of means to the corresponding errors show that the differences in length in these three groups are significant. Specimens of above groups differ also in the shape of their shells. This shape can be characterized by the ratio of height to length (H/L), width to length (W/L), and width to height (W/H). The mean values of indices of shells of the three groups are shown in Table III. The shells of the first group are low and wide (W/H=0.89), those of the third group narrow and high.

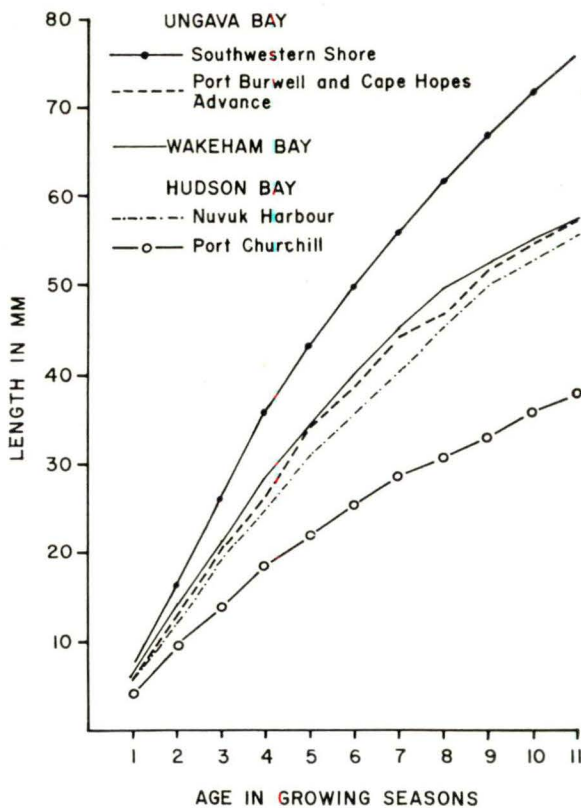


FIG. 1. Growth in length of *Mytilus edulis* L.

The difference of mean values of indices  $W/H$  between the second and the third group is insignificant, probably because of the small number of shells from the latter locality. But the difference of mean values of this index of the first group ( $0.89 \pm 0.02$ ;  $\sigma = \pm 0.05$ ) and of the third group ( $0.75 \pm 0.02$ ;  $\sigma = \pm 0.05$ ) is probably significant:  $(M_1 - M_2)/\sqrt{\sigma_{M_1}^2 + \sigma_{M_2}^2} = 3.5$ . To be significant, for  $n = 11$ , this relation has to be  $\geq 3 + 6/(n - 4)$ , thus  $\geq 3.86$ .

TABLE II  
MEAN LENGTH (IN MM) OF 5-YEAR *Mytilus* FROM DIFFERENT LOCALITIES

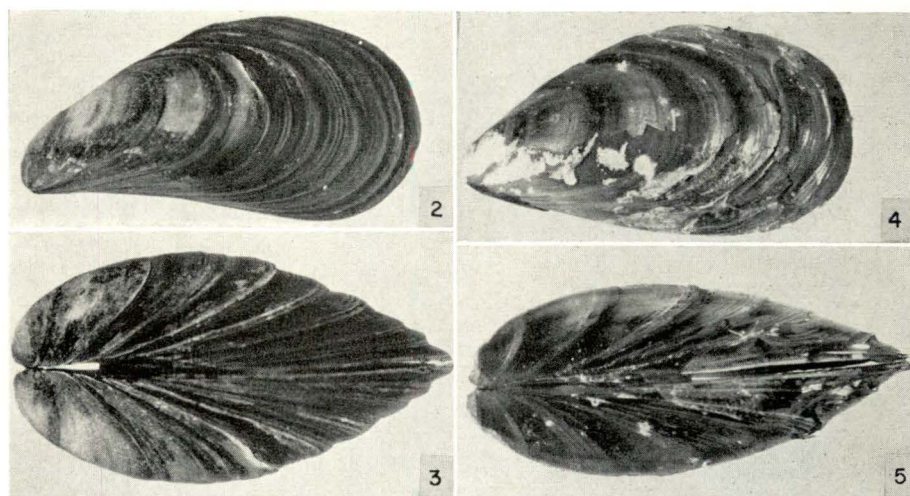
Groups	Number of shells	$M \pm \sigma_M$	$\sigma$	$(M_1 - M_2)/\sqrt{\sigma_{M_1}^2 + \sigma_{M_2}^2}$
1. Southwestern shores of Ungava Bay	5	$41.6 \pm 1.23$	$\pm 2.70$	1-2 gr: 6.1 ( $\geq 3.26$ )
2. Burwell	22	$32.9 \pm 0.72$	$\pm 3.03$	2-3 gr: 12.9 ( $\geq 3.26$ )
3. Churchill	5	$22.2 \pm 0.53$	$\pm 1.18$	1-3 gr: 21.8 ( $\geq 4.0$ )

TABLE III  
MEAN VALUES OF INDICES  $H/L$ ,  $W/L$ ,  $W/H$ , OF *M. edulis* FROM DIFFERENT LOCALITIES

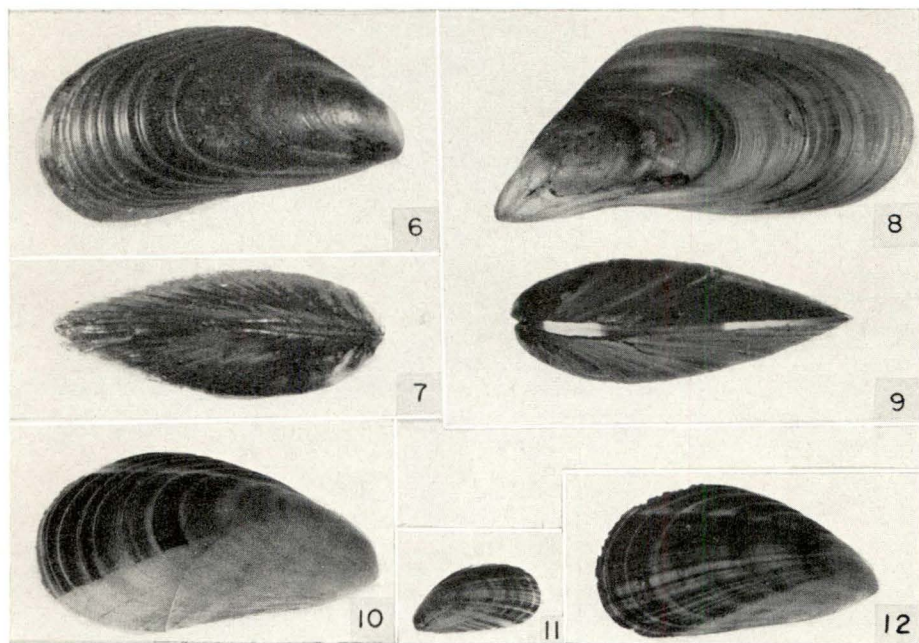
Groups	Mean values of indices			Number of shells
	$H/L$	$W/L$	$W/H$	
1. Southwestern Ungava	0.48	0.43	0.89	5
2. Wakeham Bay	0.49	0.43	0.88	9
Cape Hopes Advance	0.53	0.44	0.83	14
Burwell	0.52	0.43	0.83	22
Nuvuk	0.52	0.44	0.85	11
3. Churchill	0.49	0.37	0.75	6

Beside size and proportions, *Mytilus* of these groups differ also in their habitus. Shells from Ungava Bay are heavy, of blue-brown color, their outer surface rough and often damaged. They are flattened dorsoventrally, with very broad base. The anterodorsal ridge and the upper angle are smooth (Figs. 2, 3). The anterior part of the shell is often bent downward. The largest specimen is 89 mm long and 11 years old. The shells of the second group are also heavy, the periostracum dark brown to light gray brown, often lustrous. The marks of arrested growth are clearly visible as dark lines (Figs. 4, 5). The shape of shells is variable. The largest specimen is 72 mm long and 12 years old. *Mytilus* from Churchill are small, black, lustrous. The marks of arrested growth are visible as step-like sculpture on the surface of the shell (Figs. 6, 7). The shells are narrow and their base in transverse section is V-shaped.

PLATE I



FIGS. 2-5 *Mytilus edulis* L. Figs. 2, 3. From southern shores of Ungava Bay, length 8 cm. Figs. 4, 5. From Burwell, length 7 cm.



FIGS. 6-9. *Mytilus edulis* L. Figs. 6, 7. From Churchill, Hudson Bay, length 4.2 cm. Figs. 8, 9. From Liverpool Bay, mouth of Mackenzie River, length 7 cm. Figs. 10-12. *Mytilus pellucidus* Penn. Fig. 10. From Mansel Island, Hudson Bay, length 6 cm. Fig. 11. From Churchill, length 2 cm. Fig. 12. From Diana Bay, Hudson Strait, length 5 cm.



The peculiarity of the shells of the first and partially of the second group is their diverging beaks. These protrude as two tapering tubercles and may reach a length of 3 mm with a distance between the apices of up to 4 mm. The divergence of beaks is more pronounced in dorsoventrally flattened shells with broad base.

*Mytilus* with diverging beaks were described over a century ago by Lamarck (38(7), p. 46) as *Mytilus borealis*. This *Mytilus* "habite l'ocean boréale de l'Amérique, côté de New York. Aspect de la moule commune ou comestible, mais beaucoup plus grande. Elle en diffère par ses crochets . . . (diverging beaks-Auct.)." Lamarck's specimen was larger than *Mytilus* from Ungava Bay. Similar shells were later described by Reeve (51) in the legend to the "species 20", depicted in his Plate 6: "*Mytilus borealis*—the northern *Mytilus*. A light ovale, swollen shell of a dark shining olive-black colour, tinged with violet at the umbones, which are somewhat removed from each other. Hab. Newfoundland". Shells from Ungava Bay are in many respects similar to those described by Lamarck and Reeve.

According to these authors this peculiar form of *Mytilus* is a separate species. However, in our material it is connected by intermediate forms to the usual form with beaks in close contact. Its peculiar shape can be interpreted as an adaptation to habitats exposed to the mechanical action of ice and currents. Flattening of the shell lessens its lateral surfaces, whereas the widening of its base secures a better attachment. The beaks diverge as a result of extreme widening and bending of the shell. This form is found in the Ungava Bay, where the tidal currents are very strong. The high environmental plasticity of *Mytilus* is well known. It is interesting that some forms of *M. galloprovincialis* Lam. from the Gulf of Naples (2) are similar to those in Ungava Bay.

The second form of *Mytilus* in the "Calanus" collections is *M. pellucidus* Pennant, 1777, with a beautiful pattern of dark purple rays on the shell (Figs. 10, 11, 12). The rays are clearly visible in thinner shells and in those deprived of periostracum. In some of them the pattern expands over the whole surface but usually is represented by a single narrow ray, visible in transmitted light.

Dodge (17) points out some characters peculiar to *M. pellucidus*, which are so constant that he is "strongly inclined to consider it a good species." The presence of rays, however, in shells from our material is not correlated with morphological characters mentioned by Dodge; for example in our shells the upper angle is smooth and situated far from the beaks. The shells are usually dark colored; the light-colored shells from Wakeham Bay and Port Burwell do not exhibit rays. The scarcity of material does not allow us to make conclusions on the range of variability of *Mytilus* in Hudson Bay and in Ungava Bay. Further research is needed to understand the reactions of this species to the Arctic environments and to "find the correlation between the morphological differences and conditions of habitat" (57).

### Growth of *Mytilus edulis*

Observations on the growth of this mollusc in Hudson Bay and in Ungava Bay are based on 67 specimens. The length of shells in successive growing seasons was measured on the basis of lines of arrested winter growth. The method used was that discussed by Mossop (44, pp. 3, 4). The results of measurements are represented in Fig. 1, where the shell length is plotted against the time in growing seasons. The curves of growth are S-shaped (Figs. 1, 13). The differences in the rate of growth in different localities are obvious from the shape of the curves and from their relative positions. *Mytilus* from southern shores of Ungava Bay show the highest growth rate; those from Churchill, the lowest. In other localities growth rates vary but slightly and fall between these two extremes (Fig. 1). The difference in size between the fast-and slow-growing shells (from southwestern Ungava and from Churchill) is about 4 mm at the end of the first growing season; it increases to 23 mm by the 6th season, and is about 35 mm in the 11th growing season.

The relative sizes of the shells in different localities remains, however, almost constant throughout the life of the mollusc. The length of shells from Churchill is about half that of shells from the western Ungava Bay in the 1st as well as in the 11th growing season. The length of shells from Burwell is 0.79 that of shells from the southwestern Ungava in the first growing season, and 0.85 in the 11th season. As a result of differences in the growth rates,

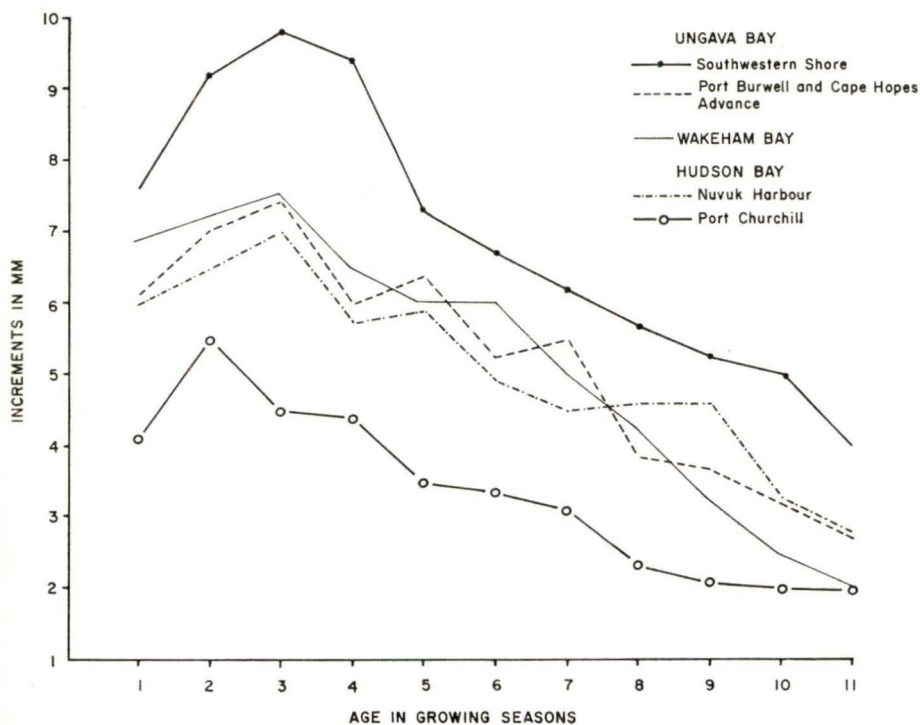


FIG. 13. Annual increments in length of *Mytilus edulis* L.

*Mytilus* from the southwestern shores of Ungava attain the length of 35 mm in the 4th, from Burwell and Nuvuk Harbour in the 6th, and Churchill in the 10th growing season.

Annual increments as a function of age are represented in Fig 13. The pattern of growth of shells from different localities is almost identical: after a rapid increase in the course of the first three growing seasons with the maximum in the third season, the growth rate gradually decreases. In fast-growing shells the period of rapid growth is prolonged, whereas in slow-growing shells it is limited to the first two growing seasons.

The average annual rate of growth is high in the first two to three growing seasons and decreases with age. In the second five years of life of *Mytilus* it is approximately half of that of the first five years (Tables IV and V).

TABLE IV  
THE AVERAGE ANNUAL RATE OF GROWTH OF *M. edulis*

Districts	Age		
	3	5	10
	Average annual rate of growth (in mm)		
Southwestern shores of			
Ungava Bay	8.8	8.6	7.2
Port Burwell	6.8	6.3	5.5
Churchill	4.6	4.4	3.6

TABLE V  
THE AVERAGE ANNUAL INCREMENT DURING THE FIRST AND SECOND 5-YEAR PERIOD  
OF THE LIFE OF *M. edulis*

Districts	Average annual increment (in mm)	
	First 5 years	Second 5 years
Southwestern Ungava Bay	8.6	4.7
Port Burwell	6.6	3.3
Churchill	4.4	2.4

### Discussion

Data on growth of *M. edulis* in the western Atlantic are scarce, and confined mostly to observations on the increment in young mussels (43, 12, 45, 63). In Woods Hole, Mass. (25, 54), this mollusc grows to about 75 mm in 5–6 years, in Nova Scotia to the length of 60–80 mm in 4–6 years (43). The shells from Ungava Bay attain this size in about 8–10 years, and in some localities they seldom if ever attain such dimensions (Fig. 1).

The first data on the size of *Mytilus* in consecutive growing seasons were published by Mossop (44). In the first growing season the shells attained the



length of 16 mm in St. Andrews, N.B., and 25 mm in Digby, N.S. Thus they were larger than any shells in our material, which at that age averaged 7–10 mm. The average annual increment of shells in Nova Scotia and New Brunswick varied from 10.8 mm to 16.8 mm, thus was higher than in shells of same age from Ungava Bay (8.6 mm). There is only one note in the literature, that of Mossop (44), on the growth of *Mytilus* in Hudson Bay. According to her the average annual increment of four shells from James Bay, which "appear to be dead when collected", was 8.4 mm, close to that of shells from Ungava Bay.

The distribution and growth of *M. edulis* in the Canadian Arctic is little known. We had the opportunity to examine six specimens of this species collected in the Liverpool Bay near the mouth of the Mackenzie River, now in the collection of the Fisheries Research Board of Canada, Arctic Unit (Table VI). These specimens resemble "species 33a" depicted by Reeve (51). The shells are elongated and narrow, with lustrous yellowish-brown periostracum. Valves light, translucent. When deprived of periostracum they are of light blue color with no traces of any pattern. The anterior part of the shell is long, narrow, beaks in close contact. Ridge and angle on the upper margin of the shell are well expressed (Figs. 8, 9). Their growth is fast (Fig. 14). The period of rapid growth extends into the fourth growing season and therefore, from this period on, they are larger than shells of the same age from Ungava Bay. The average annual increment in 6-year-old *Mytilus* from Liverpool Bay is 9 mm, the highest observed in northern latitudes.

TABLE VI  
DIMENSIONS (IN MM) OF *M. edulis* FROM LIVERPOOL BAY

L	H	W	H/L	W/L
69.2	28.8	23.5	0.41	0.35
59.0	27.0	19.0	0.46	0.32
58.2	28.5	20.1	0.49	0.34
54.2	25.0	17.5	0.46	0.32
54.2	24.6	21.0	0.45	0.37
53.0	24.0	19.0	0.45	0.36
53.5	25.7	18.8	0.48	0.35
37.8	18.5	13.0	0.49	0.34

On the shores of western Greenland *Mytilus* attains considerable size: the largest specimen collected in Godhavn was 78 mm long; in Upernavik, 72 mm (37). In the Thule district the largest specimen measured 93 mm and was probably over 15 years old (62). Other specimens from the same district were: 4 years old and 44 mm long; 5 years old and 29 mm long. The length of 7-year-old specimens varied from 38 to 59 mm. The annual rate of growth calculated on the basis of these data was 5.4–5.8 mm. and attained a maximum of 8.5 mm. It was thus comparable with the rate of growth of *Mytilus* from Ungava Bay and Hudson Bay.



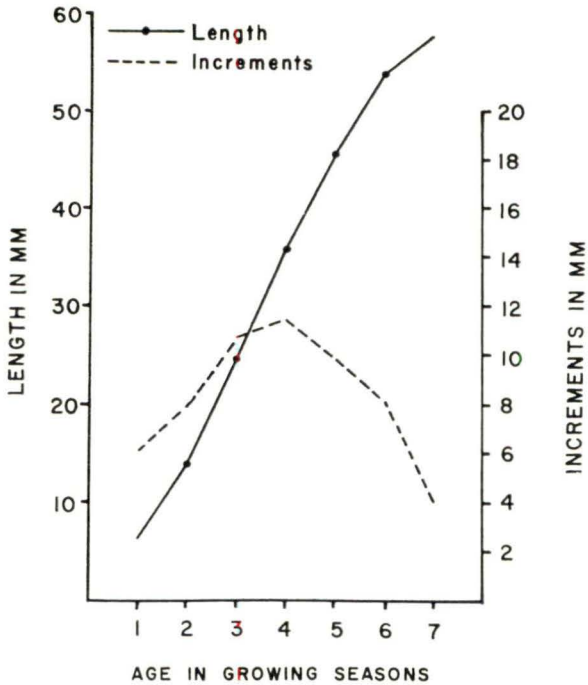


FIG. 14. Growth in length of *Mytilus edulis* L. from Liverpool Bay.

The above data show that north of the Canadian Maritime Provinces the growth of *M. edulis* slows down. This reduction of growth rate in colder waters is a general phenomenon in pelecypods. Thorson (61) pointed out that the growth of arctic species of lamellibranchs is exceedingly slow. The growth of *Mya arenaria* (1, 45, 61), *Mytilus californianus* (10), *M. diegensis*, *Tivela stultorum* (9), *Siliqua patula* (64, 65), as well as of fresh-water bivalves (7), depends on the temperature and on the heat budget of their habitats. It is obvious, moreover, that factors other than temperature influence their growth, e.g. abundance of food, timing of sexual maturity, etc. (48, 61, 8, 9, and many others). Recent observations on the influence of temperature on the activity of poikilotherms show that many species may be relatively independent of this factor. The observations of this type on pelecypods were reported by Spärk (58), Thorson (61), Orton (48), Bruce (5), Fox (26, 28), Rao (50), and their data summarized by Bullock (6). The growth rate, however, does depend on the temperature. "Thus at present there is an apparent contradiction between activity and growth rates" (16, p. 118). As regards gastropods, it has been shown that *Thais emarginata*, *Lacuna carinata*, and *Crepidula nummaria*, while in the egg capsules, grow more rapidly in Alaska than in California (16). Some Cypræidae and Patellidae are larger in higher latitudes. Other gastropods are larger near the center of their area of distribution, and decrease in size toward the periphery, e.g.

*Buccinum undatum*, which is often over 100 mm in length near Ireland but attains only half that size in the Barents Sea, near Iceland, and in west Greenland (56).

Weymouth, McMillan and Rich (65) and Weymouth (64) have shown that the northern clams grow more slowly, but live longer and become larger, than the southern ones. The life span of *M. edulis* is not known. The maximum age of specimens in the "Calanus" collections was 14 years; half of the specimens were 10 or more years old. The largest specimen was 8.2 mm long and 11 years old.

Many factors restrict the distribution and inhibit the growth of *Mytilus* in the Arctic: the period of plant and animal growth is short and depends on variable snow and ice conditions (23). Salinity varies considerably and its decrease often affects the growth of *Mytilus*. The inhibition of growth of this mollusc in brackish waters was observed in the Gulf of Bothnia (42), in Kaiser Wilhelm Kanal (3), and in the Baltic Sea (56). In the southern Hudson Bay where the surface salinities are less than 23‰ and mixing of water is poor, *Mytilus* remains small, despite comparatively high temperature. Shells of larger size are found at the mouth of Hudson Bay where salinity attains 32‰, and there is an influx of waters from Foxe Channel and Hudson Strait. In the Ungava Bay, high tides, sweeping across the bay, maintain the circulation, salinity is high and there is an admixture of Atlantic waters (19).

The northern boundaries of the distribution of *M. edulis* in the Eastern Canadian Arctic and in Greenland coincide in general with those of the subarctic zone, as delimited by Madsen (40, 41), and by Dunbar (18, 20, 21). *M. edulis* occurs as far north as Angmagssalik in east Greenland, and Thule in west Greenland. In the Eastern Canadian Arctic it was found, however, near Ponds Inlet (39, 24), thus farther north than the Padloping Island—the northern limit of the subarctic zone in this region (18, Fig. 1). In Hudson Strait it was taken off Southampton Island, and, on the northern shores of Canadian mainland, in the Coronation Gulf. In these last localities the exact position of the boundary of the subarctic zone is not yet known.

Discussing the distribution and growth of *M. edulis* it is necessary to take into consideration the character of water masses in the area. Waters of Canadian Arctic are predominantly of polar character with low salinity and of low temperature. The waters of Hudson Strait, of Ungava Bay, and of west Greenland are of mixed type. The penetration of Atlantic waters can be traced into Ungava Bay, Hudson Strait, and along the shores of west Greenland as far as Thule district (18, 19, 20, 21). As can be inferred from the distribution and growth of *Mytilus*, the best conditions for this mollusc are in the Atlantic waters and to some extent in waters of mixed type. This may explain its better growth in Ungava Bay as compared with Hudson Bay, as well as the penetration of *Mytilus* far northwards along the shores of west Greenland. Its intensive growth in Liverpool Bay may depend on the penetration of Pacific waters, and possibly on the proximity of the estuary of Mackenzie River.



The hydrographic conditions of the Canadian Arctic are complicated, and the latitudinal retardation of the growth of *Mytilus* may be obscured by the peculiarities of its various habitats.

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The Annual Oceanographic Cycle at Igloolik in the Canadian Arctic  
II. The Phytoplankton<sup>1</sup>

"CALANUS" SERIES, No. 17

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ABSTRACT

Phytoplankton populations near Igloolik, northern Foxe Basin, began to increase in late April, and reached their climax in mid-August. The rapid late-August decline of the phytoplankton populations coincided with diminishing light. Diatoms were the main biomass producers in Igloolik and the principal food for the marine fauna. The succession of spring Pennatae and summer Centriceae apparently was caused by light and ice conditions. Taxonomic composition of the Igloolik phytoplankton was influenced by the fast ice and by the shallowness and hydrographic uniformity of the adjacent areas. Descriptions are given of two new species of dinoflagellates, *Gyrodinium arcticum* and *Gymnodinium intercalaris*, and the new coccolithine flagellate *Pontosphaera ditrematolitha*.

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## INTRODUCTION

IGLOOLIK ISLAND has been visited only on rare occasions by arctic expeditions. The *Calanus* expedition occupied a collection station near Igloolik from September 1955 to September 1956 (Fig. 1). The continuity of the hydrographic observa-

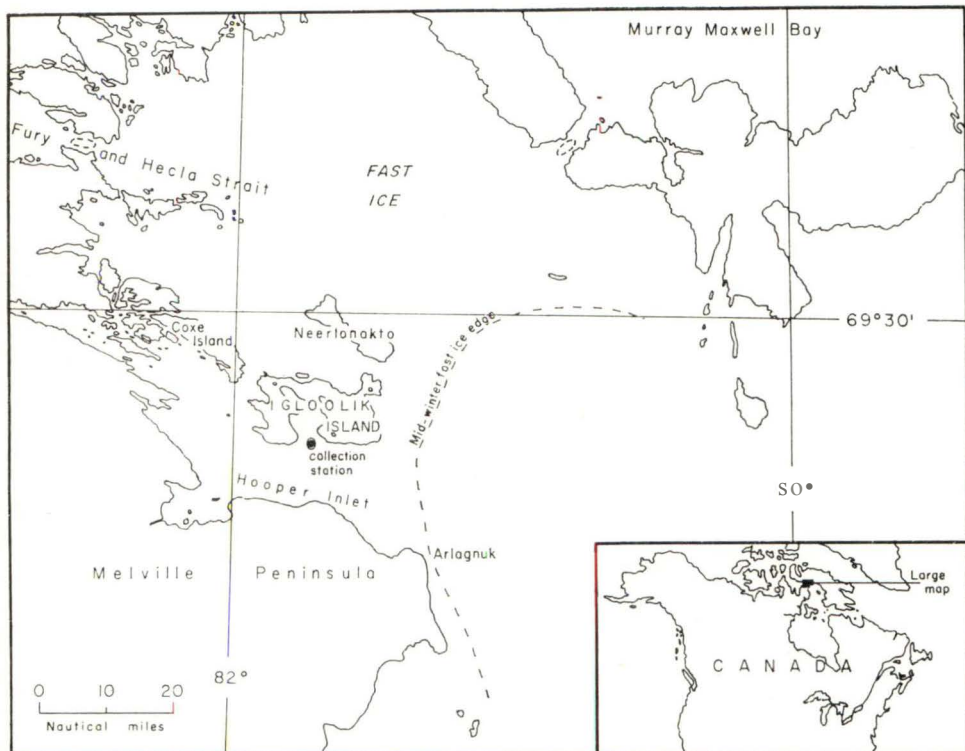


FIG. 1. Northwestern Foxe Basin and the eastern end of Fury and Hecla Strait. The area represented on the large map is shown in the inset.

tions and plankton collections, taken about twice a month, makes this material especially valuable from the oceanographic point of view. Details of sampling procedure have already been described in part I of this series which deals with the zooplankton and physical and chemical data (Grainger, 1959).

## METHODS

Quantitative phytoplankton samples collected with a Nansen water-bottle were stored in 170-ml glass bottles with plastic tops, and were later examined with the Utermöhl inverted microscope. Quantitative phytoplankton estimates were made on 25-, 10-, and 5-ml samples after sedimentation in cylinders. Rare organisms, and those difficult to identify, were transferred with a pipette to the



objective glass, then studied under the required magnification with a compound microscope with front phase illumination. It was sometimes convenient, however, to move the dinoflagellates into more suitable positions for identification. This was done by tapping a pencil against the top of the sedimentation cylinder after the quantitative examination of the sample was completed. Both quantitative and vertical net hauls, taken with a net of No. 20 silk, were preserved with neutralized 5% formalin. The efficiency of the taxonomic examination of the vertical net hauls was increased by examination of 1 or 2 cc of net plankton observed later with the inverted microscope. This method seems to be advantageous for studying rare organisms that are often missed when a small number of preparations are studied with the compound microscope. Lugol solutions and methylene blue were used for staining membranes and starch. Javel water was applied for examination of the membrane plates in dinoflagellates. The numerical estimations of plankton were made with objectives 10 $\times$ , 25 $\times$ , and 40 $\times$ . Oculars of 6 $\times$ , 8 $\times$ , and 12 $\times$  were used according to the size of the organisms under examination.

#### GENERAL HYDROGRAPHICAL AND ECOLOGICAL FEATURES OF IGLOOLIK

All data on ice, light, temperature, oxygen and phosphates discussed here were obtained from Grainger (1959). Emphasis here will be placed on the biological aspects of the phytoplankton and the relation of the phytoplankton to hydrographical conditions.

##### LIGHT

Light is a limiting factor for photosynthesis of plankton in arctic, ice-bound regions. Submarine light measurements were not made at Igloolik; however, the duration of the screening effect of ice upon light penetration of the water, lasting from late November until mid-January, is shown in Fig. 2. During this period direct light was completely absent. Direct light lasting 24 hours per day extended from mid-May until the end of July, with nearly equal periods of direct light and darkness occurring in early October and in early March.

##### TEMPERATURE

Temperature and salinity in northern seas are never limiting factors for plankton as a whole, only for some species (Steemann-Nielsen, 1935). According to Steemann-Nielsen and Hansen (1959), "in the arctic the influence of the low temperature on the rate of photosynthesis is counteracted by a higher concentration of enzymes". The temperature extremes at Igloolik were very narrow (Fig. 2b), between +1.72°C and -1.80°C. The maximum water temperature occurred at the beginning of September, at a time of decline of phytoplankton. The 7-month period of subzero temperature (November-May) was a stagnant one for plants, but one of significant reproductive activity for part of the zooplankton. The first slight increase of phytoplankton populations took place



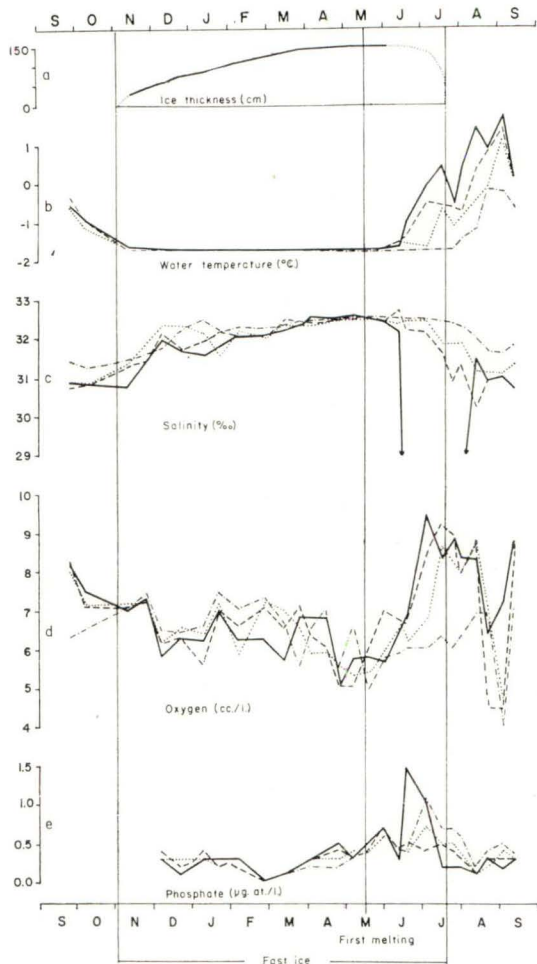


FIG. 2. The annual cycles of (a) ice thickness, (b) water temperature, (c) salinity, (d) dissolved oxygen, and (e) dissolved inorganic phosphate, from September 1955 until September 1956.

Depths are indicated as follows: *surface*, full line; *10m*, broken line; *25m*, dotted line; *50m*, dots and dashes.

after winter when a small rise of temperature ( $0.5^{\circ}\text{C}$ ) in May was noticed. According to Braarud (1945) small temperature changes in *Chaetoceros* induce microspore formation. Supposedly a similar effect is induced during temperature changes in plankton.

## ICE

In the Igloolik area ice thickness increased from November until early May, when it reached 152 cm. Melting began in early May, and continued until mid-July (Fig. 2a).

Ice affects salinity, temperature, light penetration and plankton present in arctic waters. Gran (1904, 1908) found 84 diatom species in the arctic ice previously originated in various ecological niches. The true planktonic forms were more common than freshwater and brackish species. The surface of the arctic ice, melting ponds on the ice, and the under surface of the ice are inhabited by diatoms and flagellates. The flora of these ecological niches varies according to the origin of the ice and its locality. It includes benthic, planktonic, estuarine and freshwater organisms frozen during ice formation.

Regularly stratified ice structure, as observed by the author, was common around Baffin Island in 1956. It developed supposedly in inshore waters, in non-turbulent areas where phytoplankton is abundant. The amorphous, old ice contained benthic organisms when freezing of turbulent water areas took place. As observed by the author during the expedition of the *Labrador* to Foxe Basin in 1956, brown-green layers alternating with colourless ice were formed by trapped plankton diatoms. A piece of ice taken in Lancaster Sound (1956) was melted by the author. Many diatoms became motile again but a great many were plasmolized or dead. Since enormous populations of diatoms are trapped in the arctic ice, ice melting favours their return to the plankton, mostly in June and July. The markedly stratified structure of ice supposedly develops when diatom populations accumulate under the ice surface when freezing takes place. The wider green layers of ice may form when diatoms are numerous and water is calm in late August and September when freezing starts.

A diatom film, collected by the Atlantic Oceanographic Group on March 27, 1957 in the Gulf of St. Lawrence and examined by the author contained 32 species, mostly of planktonic origin. Since they were taken in March and represented large populations it is thought that they had begun to grow early in winter darkness (unpublished data).

The dirty yellow ice of Foxe Basin, typical for this area, shows no special structure, according to Campbell and Collin (1958). It is usually old pack ice which has lost its structure while freezing and refreezing. Four to 8 million tons of ice sediment are formed annually in Foxe Basin, as estimated by Campbell and Collin (1958). During the ice-melting period all nutrients contained in the ice enter the water, stimulating plankton metabolism. Observations by Dr A.W. Mansfield (personal communication) indicate that a prevalent north wind

accelerates the speed of the ice floes carried out from Fury and Hecla Strait. It largely clears the ice from northwest Foxe Basin, as happened in 1956. As a result of southeast winds huge ice fields covered the northern part of Foxe Basin in 1957. Since persistent ice delays the maximum of phytoplankton (Braarud and Hope, 1952), the annual production of diatoms in Foxe Basin is evidently affected.

According to Hutchinson (1957) there is only a small effect of ice-melt water upon growth. The influence of the ice-melt waters under arctic conditions is of particular significance from the biological point of view. Recent research on the phytoplankton productivity in Hudson Bay and in northern Foxe Basin (author's unpublished data), show that low salinities during the ice melting period are associated with poor phytoplankton populations, which increase with higher salinities found in the deeper water layers. In Igloolik the immediate surface layer harboured initial populations of diatoms at a time when no melting had occurred; with a decrease of salinity, plankton populations simultaneously decreased from late May until mid-June, by which time diatom populations were markedly reduced. The gradual increase of the surface populations coincided with rising salinities (Fig. 3) observed between July and September. If occasionally larger diatom populations were found at the surface with low salinity they were presumably brought up from the lower depth where production of phytoplankton was always higher.

#### SALINITY

Salinity as an ecological factor in the marine phytoplankton was studied by Braarud (1951), who reported variation in the rate of reproduction with varying salinities in Coccolithineae, Cryptomonadineae and Dinoflagellatae. Though specialized salinity requirements were shown for various arctic diatoms (Grøntved and Seidenfaden, 1938), the ecological characterization of species is still far from being settled. The surface phytoplankton is exposed to greater salinity changes than deeper water layers. Microstratigraphy of the surface salinities at Rowley Island (Foxe Basin) made during the *Calanus* expedition of 1957 shows that great salinity changes take place only within 0-2 metres of the surface.

At Igloolik, salinity values varied between 30.70‰ and 31.50‰ at all depths from September 25 until November 10 (Fig. 2c). In early December they rose at all depths, to 32.03‰ at the surface, to 32.12‰ at 10 m and to 32.36‰ at 25 m, and to 32.48‰ at 50 m in early January. Drops in salinity at all depths began in early February and lasted until early May, when they were everywhere between 32.48‰ and 32.59‰. Salinity changes in the deeper layers were slow and presumably did not affect phytoplankton metabolism. Coincident with the first indication of spring melting, the salinity at the surface fell slowly from May 5 until June 13, then rapidly to 27.01‰ on June 19, to 1.68‰ on July 2, and to less than 1.68‰ on July 15. It rose again to 10.41‰ on July 25, to 19.94‰ on August 1, and to 31.56‰ on August 11.



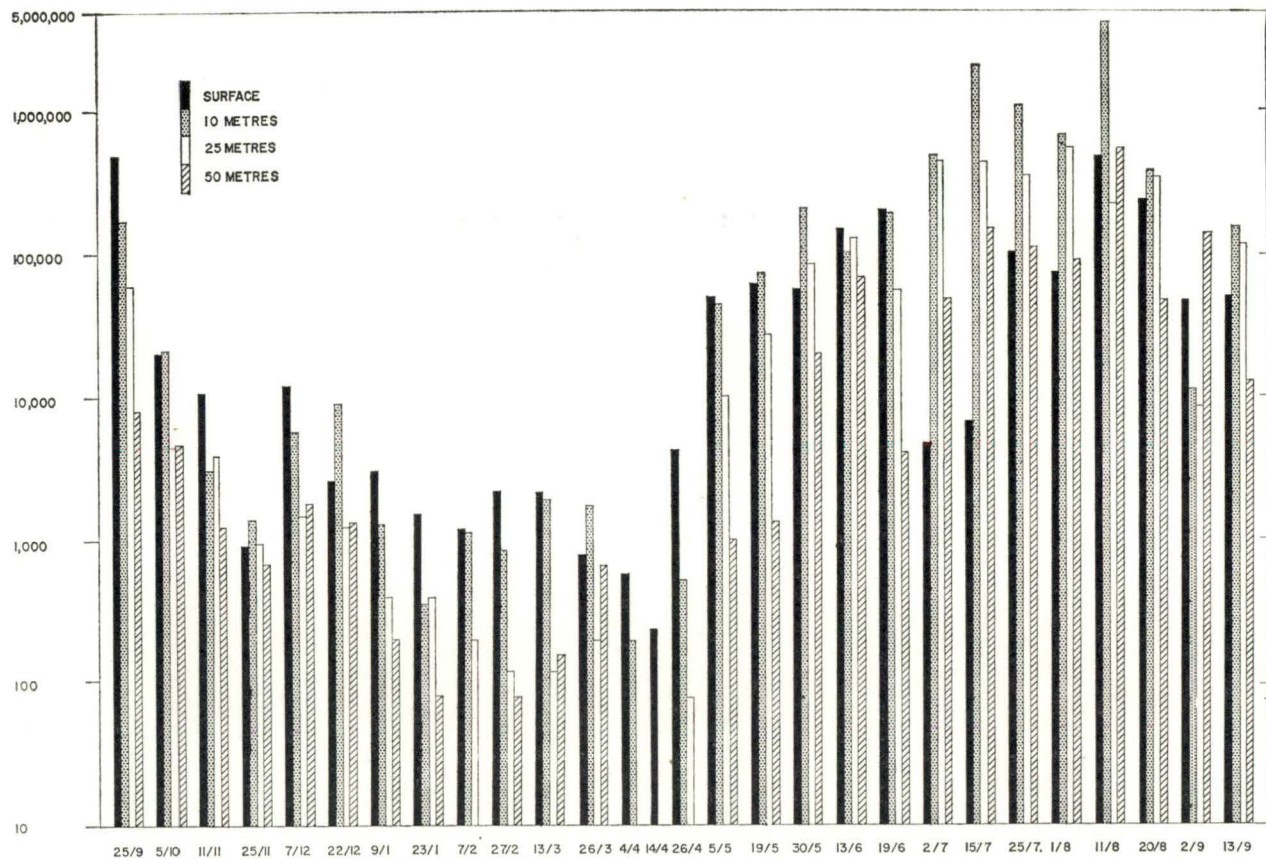


FIG. 3. Histogram showing quantitative features of phytoplankton populations of Igloolik during the entire year at four depths. Counts are given as cells per litre on the logarithmic scale on the left.



## OXYGEN

Oxygen distribution at Igloolik is illustrated by Fig. 2d. Oxygen saturation values increased from relatively low values on January 9 to 81.55% at the surface, 82.5% at 10 m, 83.6% at 25 m and 86.5% at 50 m on January 23. This increase could probably be related to introduction of new water masses from the open water area newly illuminated by the sun at that time. Decrease of oxygen took place again on February 7. Increase on February 27 was found not at the surface but at 10 and 50 m. Minor oxygen fluctuations occurred from this time until the end of May, although the size of the diatom population appeared to be sufficient to produce higher oxygen content if light conditions had been more favourable. Dim light under the ice continued until June 19, when a low oxygen level was found in spite of large populations of diatoms. The situation changed on July 2 when supersaturation occurred at 10 m and oxygen saturation percentage reached 102.3%. This could be related to the great phytoplankton populations counted at that depth. The very poor populations at the surface and the relatively high oxygen content of 91.0% were presumably caused by vertical mixing. Further vertical extension of the supersaturated oxygen layer was noticed on July 15, when oxygen reached its highest supersaturation value, 110.3% at the surface and 103.7% at 25 m. Although further increase of phytoplankton populations took place on July 25, there was a slight decline in the oxygen content. This was a time when pennate diatoms were still common but were forming cysts. A rise in saturation values took place from the surface to 25 m on August 11, when the climax of the annual production was reached, with the occurrence of the intensively metabolizing *Centriceae*. Rapid decline in oxygen production on August 20, in spite of large diatom populations, is basically explained by the approaching end of the season and the mass production of resting spores. This decline occurred particularly in the water layer from 10 to 50 m, where the oxygen content was reduced from 55.9 to 49.4%. Some changes occurred on September 13, associated with the replacement of water masses richer in phytoplankton than those observed on September 2, and these may be responsible for the rise in oxygen values to supersaturation at the surface and 10 m, and for the subsaturation at 50 m. Probably new water masses containing still greater diatom populations and higher oxygen content entered the collection station.

Since the general form of the oxygen curve is in fact built up from the oxygen cycles of many plankton organisms, the succession of species and physiological activity in this period of the season could be of value for oxygen interpretation. Since I have observed that great diatom populations are often associated with low oxygen values because of reduced photosynthesis during resting spore formation, a list of species is given, showing: (a) a group of species producing resting spores and auxospores; and (b) species in which formation of the resting spores are not observed. (Tables I and II).

TABLE I. Species of diatoms in which formation of resting spores was observed.

<i>Melosira arctica</i>	<i>Chaetoceros laciniosus</i>
<i>M. islandica</i>	<i>Ch. wighamii</i>
<i>Melosira</i> sp.	<i>Ch. curvisetus</i>
<i>Thalassiosira nordenskjoeldi</i>	<i>Ch. debilis</i>
<i>Th. gravida</i>	<i>Ch. socialis</i>
<i>Th. rotula</i>	<i>Ch. gracilis</i>
<i>Coscinodiscus grani</i>	<i>Chaetoceros</i> sp.
<i>Coscinodiscus</i> sp.	<i>Biddulphia aurita</i>
<i>Coscinodiscus oculis iridis</i>	<i>Fragillaria cylindrus</i>
<i>Rhizosolenia styliformis</i>	<i>Navicula grani</i>
<i>Rh. alata</i>	<i>N. septentrionalis</i>
<i>Chaetoceros teres</i>	<i>Achnantes taeniata</i>
<i>Ch. lorenzianus</i>	<i>Lauderia glacialis</i>
<i>Ch. compressus</i>	<i>Denotula confervacea</i>
<i>Ch. constrictus</i>	<i>Synedra</i> sp.
<i>Ch. affinis</i>	<i>Amphiprora hyperborea</i>

TABLE II. Species of diatoms in which resting spores were not observed.

<i>Coscosira polychorda</i>	<i>Bacteriosira fragilis</i>
<i>Thalassiosira aestivalis</i>	<i>Navicula</i> sp.
<i>Th. decipiens</i>	<i>Gyrosigma spenceri</i>
<i>Th. subtilis</i>	<i>Pleurosigma</i> sp.
<i>Chaetoceros atlanticus</i>	<i>Nitzschia closterium</i>
<i>Ch. eibeni</i>	<i>N. longissima</i>
<i>Ch. concavicornis</i>	<i>N. seriata</i>
<i>Ch. decipiens</i>	<i>N. pungens</i>
<i>Ch. perpusillus</i>	<i>Navicula pelagica</i>
<i>Eucampia zodiacus</i>	<i>Thalassiothrix longissima</i>
<i>Streptotheca thamensis</i>	

It is useful, for general orientation, to compare oxygen data from other arctic and subarctic regions. Oxygen content around the Faeroes and Iceland (Steemann-Nielsen, 1935) rarely shows supersaturation, as at Igloolik. In Denmark Strait higher oxygen values and frequent supersaturation were observed by Braarud (1935). In Allen Bay conditions similar to Igloolik were found (Apollonio, MS, 1956). Oxygen data in Hudson Bay show variable features at many stations. High oxygen content in Hudson Strait (Campbell and Collin, 1958) suggests that conditions for growth of phytoplankton in that area are more advantageous than at Igloolik.

Formation of auxospores was encountered in only 6 planktonic diatoms and was rarely observed. No noticeable effect would be made by such a small population on the total oxygen content. The production of the resting spores found in 34 common diatoms and in three dinoflagellates is obviously more significant and may affect total oxygen content of phytoplankton during resting spore formation (Table I). The resting spores appeared first at the beginning of

spring, increased in mid-season, and reached their peak in August. Factors inducing encystment are different; some dinoflagellates form cysts soon after ingestion of other organisms (Schiller, 1933). Germination of cysts takes place in *Chaetoceros* immediately if conditions are favourable (Braarud, 1945). Encystment in *Goniaulax* species in plankton and in *Gyrodinium californicum* in culture has to be related to salinity-temperature changes (author's unpublished data).

#### PHOSPHATES

Both light and nutrient supply control metabolic activities of phytoplankton (Brandt, 1899). When nutrients are exhausted phytoplankton growth becomes inhibited in northern waters (Braarud, 1935, Kreps and Verjbinskaya, 1930). Decrease of phytoplankton populations in the antarctic took place before any depletion of nutrients (Hart, 1934). Riley (1946, 1953) shows close correlation between the amount of phytoplankton and nutrients.

The values for inorganic phosphate at Igloolik (Fig. 2e) ranged from 0.1 to 0.4  $\mu\text{g-at/l}$  during December, January and February. The lowest values, close to zero, were found in late February. The maximum occurred in mid-June and values declined in mid-July, and were related to increased populations of diatoms. The highest values of phosphates were noticed when salinity dropped during the ice-melting period.

#### STABILITY

The effect of vertical mixing caused by turbulence may be of considerable importance for phytoplankton dynamics (Braarud, 1935; Gran and Braarud, 1935; Riley and Bumpus, 1946). A stable water column generally permits greater phytoplankton growth (Braarud *et al.*, 1953).

At Igloolik, because the maximum depth is only about 50 m, stability seems to have had very little effect, at least upon photosynthesis, since all populations inevitably were suspended within the eutrophic layer. While slight inhibition of photosynthesis may have occurred at the bottom because of slightly reduced light, the entire 50-metre column may for all practical purposes be considered as being within the depth of active photosynthesis.

Horizontal stratification began in May and became gradually more evident during the summer. This had the effect of creating vertical discontinuity in the phytoplankton distribution, resulting in decreased numbers of individuals in the upper layers during the ice-melting period (when the upper layers underwent drastic salinity reductions). Maximum phytoplankton occurrence was between less than 10 and more than 25 m during most of the spring and summer period. Physical changes occurring on September 2, reducing vertical stability, were accompanied by changes in the vertical distribution of the phytoplankton, many of which evidently ceased photosynthetic activity, formed cysts, and sank to the bottom.



## SHORT DESCRIPTION OF THE PHYTOPLANKTON CYCLE

The quantitative assessment made with the inverted microscope showed a steady increase of phytoplankton populations starting from late April. After that time the number of species and their populations increased markedly at various depths. The first diatom maximum occurred in mid-July, after which time a considerable decrease was observed. The second peak, associated with the appearance of more species, began in August. The later rapid increase of populations was associated with formation of resting spores in the majority of diatoms. Large populations of diatoms still occurred in September of both 1955 and 1956. The rapid quantitative decline started in October, and the typical winter minimum with its small populations was observed from November until mid-April (Fig. 3).

## SEASONAL CHANGES IN PHYTOPLANKTON IN 1955-1956

SEPTEMBER 25<sup>2</sup>

Phytoplankton populations on September 25, 1955 were still numerous as far as total number of species was concerned. There were 23 diatom, 9 dinoflagellate, 4 coccolithophorid and 5 ciliate species recorded. The upper waters showed oxygen close to saturation, 96.8% at the surface, 97.2% at 10 m. Maximum production was found at the surface represented by 491,040 cells per litre. At 10 m there were 168,860 cells per litre, at 25 m 57,520 cells, and at 50 m 6,575 cells. The day before this collection was made weather was calm with the temperature near freezing. The quantitative decline of phytoplankton in September is not only an effect of grazing by zooplankton, probably mainly copepods as shown by Grainger (1959), but also is a result of grazing by ciliates which have their climax after the phytoplankton maximum (Fig. 3). Great oxygen reduction took place during the time of zooplankton maximum. The limited light supply at the surface finally stopped photosynthesis and the majority of species produced resting spores.

## OCTOBER 5

Phytoplankton populations in October showed equal numbers of cells at the surface and at 10 m. They still represented a sufficient bulk of food for zooplankton in the entire column of water, although the total number of cells was nearly 20 times smaller in October than in September. *Chaetoceros* species were still represented. *Ch. affinis*, *Ch. curvisetus*, *Ch. wighamii*, and *E. zodiacus* exhibited their late maxima of 2,800 cells per litre at the surface, 1,620 at 10 m, and 860 at 25 m. *Fragillaria cylindrus* showed continuous vertical distribution starting from 7,880 cells per litre at the surface, gradually decreasing to 3,260 at 50 m. The smaller number of ciliates showed that both plants and herbivorous forms had reached their final low limit before winter rest.

## NOVEMBER 11, 25; DECEMBER 7, 22

The autotrophic plankters were reduced strongly after October 5. The water surface froze and ice reached 33 cm thickness in early November. Five species of *Chaetoceros* formed small populations of a few hundred cells per litre, except for *Ch. compressus*, represented by 1,360 cells per litre at 25 m. Tiny holozoic flagellates were found at all depths in populations varying from 5,600 to 560 per litre. A relatively large number of ciliates (4,260 per litre) and copepods at the surface presumably reduced the phytoplankton to its observed minimum. It is thought that when diatom populations become so reduced that they are insufficient as food, the zooplankton is able to change its diet by devouring various ciliates which are still quite numerous at that time. A further drop in plankton populations took place November 25; 12 species observed under the inverted microscope on that date were represented by only a single or a few individuals. Collections

<sup>2</sup>Copies of tables showing the quantitative occurrence of phytoplankton species on this and the following dates discussed in this section may be obtained from the author.

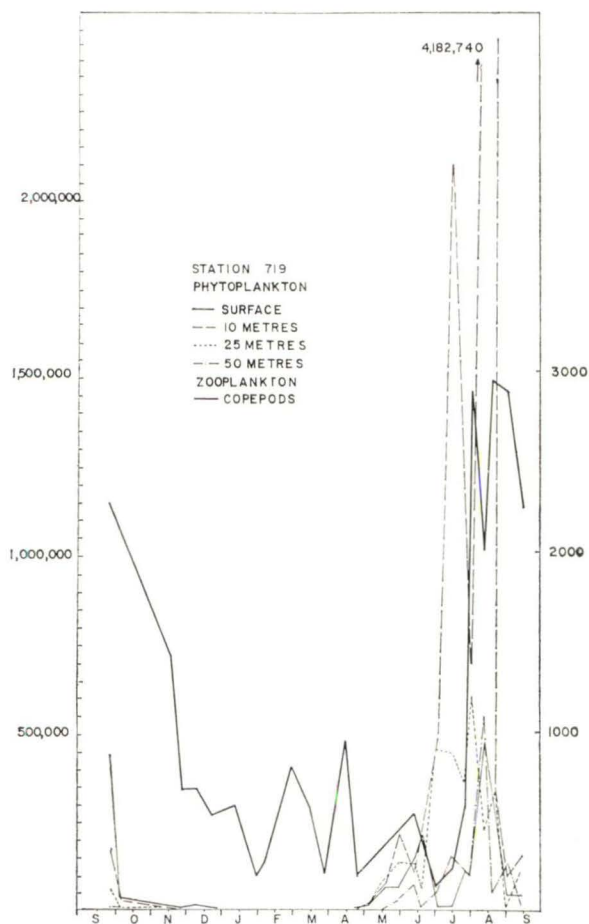


FIG. 4. Phytoplankton populations expressed as number of cells per litre for the four sampled depths, and copepods given as number of individuals per haul.

on December 7 and 22 showed a noticeable increase in diatoms, mainly *Ch. constrictus*, not previously recorded. Presumably this is due to invasion of some allochthonous populations that shifted towards Igloolik. These new populations could be distinguished from the local previously-observed populations by the increased number of *Gymnodinium* sp. and *Warnovia* sp. Observations in December showed further reduction of phytoplankton, especially at the surface and at 10 m. At 25 m there were 17,400 cells per litre of diatoms and flagellated forms. Since the multiplication rate of phytoplankton probably had declined, it is likely that this population was brought in from another area.

JANUARY 9, 23; FEBRUARY 7, 27; MARCH 13, 26

This period showed the typical features of arctic winter. The limiting effects of the ice cover and reduced light supply, associated with low oxygen, drastically reduced the autotrophic plankton to a few individuals per litre. Although poor populations occurred in the sedimentation cylinders (4 diatom species), 14 diatom species and 2 flagellates were found in the net. The lowest point in winter production was reached on April 4 and 14, when only 2 specimens of *Nitzschia closterium* and some holozoic flagellates were recorded. The fluctuation of the total phytoplankton population is shown by the following numbers: January 9, 4,000; January 23, 1,720; February 7, 1,360; February 27, 2,680; March 13, 4,340; March 26, 2,340.

APRIL 4, 14 AND 26

The first increase of diatoms was recorded on April 26, close to the surface under the ice. Arctic diatoms characteristic of melting ice, *Achnantes taeniata* and *Fragillaria cylindrus*, were represented by 1,200 and 1,720 cells per litre. Both populations are considered as initial, after winter minimum. There had been little change in temperature and salinity since April 14. It is supposed that decrease in oxygen percentage from April 14 (79.7% at the surface) to April 26 (59.2% at the surface) is related to the under-ice movement of water. Digby (1953) observed the first diatoms under the ice on April 29 in Scoresby Sound, East Greenland. He concluded that these diatoms could have been brought in by water movements from distant open water areas. My opinion is that the diatoms at Igloolik could have originated as an under-ice film, but could be brought from open water areas as well.

Complete absence of phytoplankton occurred only on April 14.

MAY 5, 19 AND 30

Populations of *Achnantes taeniata* and *Fragillaria cylindrus* increased more than 3 times between April 26 and May 5, providing evidence that spring growth of diatoms proceeded in spite of poor light conditions under the ice. Both diatoms occurred as gradually increasing populations and descended into deeper layers. Small populations of *Chaetoceros compressus* and *Ch. curvisetus* appeared. Small unidentified flagellates occurred between the surface and 25 m in numbers close to the number of diatoms. May 19 showed a still more accentuated phase of increasing autotrophic plants, with the dominant *Ach. taeniata* rapidly developing into populations of 47,960 at the surface, 33,800 at 10 m, 22,400 at 25 m and 1,020 at 50 m. During this period the ice began to melt (Fig. 2). This is also reflected in the salinities of May 5: 32.59‰ at the surface, 32.48‰ at 10 m and 32.50‰ at 25 m. Similar features were found on May 19. After May 5 new species appeared: *Denotula confervacea*, an arctic-neritic form with a population of 21,540 cells per litre at 10 m, and the less abundant *Thalassiosira nordenskiöldi* and *Chaetoceros wighami*. The total number of species included 14 diatoms, 2 dinoflagellates and other minor forms. After mid-May the sun remained above the horizon 24 hours of the day. The rapid increase of the diatom population followed progressive heating of the surface and ice-melting. Though salinity at the surface was only slightly different (32.45‰) from that at 10 m (32.41‰), the surface showed 4 times greater production than deeper layers (Fig. 3). Oxygen at the surface had the relatively low value of 66.3%, despite the fairly large populations of diatoms. It increased to 82.4% at 10 m, then decreased at 25 m where larger populations were found. This presumably indicates more stable waters, which favour phytoplankton metabolism. The maximum May production was reached by *Achnantes taeniata* at 10 m with a population of 174,440 cells per litre, and 66,220 at 25 m.



## JUNE 13 AND 19

There was a slight decrease in oxygen at 10 m from May 30 to June 13, and a decrease in surface salinity from 32.45‰ to 32.18‰. More intensive melting began in June and areas of rotting ice appeared over the entire fast ice surface. Plankton production was in an advanced phase, as reflected in the great size of populations and the number of species: 16 diatoms were observed in the inverted microscope and 5 additional ones in the net hauls. Among the flagellated species, some *Pontosphaera*, *Scyphosphaera* and *Lohmannosphaera* were found for the first time in the eastern Canadian arctic.

Observations on June 19 show a further drop in salinity to 27.01‰ at the surface, and relatively smaller populations. This probably occurred because of ice-floes covering wide areas for considerable periods of time. Conditions on June 19 at Igloolik show many similarities to observations made by Braarud (1935) in the pack-ice areas of Denmark Strait in respect to phytoplankton composition and water characteristics. However, this similarity is partly accidental, since environmental conditions in the two areas differ considerably. Braarud's (1935) observations are as follows: when the ice was near by, no large volume of plant production was found, oxygen content was low, the concentration of nutrients was almost the same at the surface as at the lower levels, and salinity was nearly the same at all levels. In all four instances given by Braarud the surface had a smaller phytoplankton crop than the 10-metre layer, where the maximum was found. Though no direct quantitative evaluation of ice influence could be made at Igloolik, it is obvious that ice affects greatly both photosynthetic metabolism and growth. Results of Apollonio (1956) at Allen Bay, Cornwallis Island, show some similarity to those found at Igloolik. Further discussion has to be postponed until more data are available.

## JULY 2

There was striking decrease in the size of the population at the surface, as compared with June 19, associated with a drop in salinity to 1.68‰. The fast ice had cleared away from Igloolik Island, and by the middle of July the edge had moved into Hooper Inlet, about half way between southeastern Igloolik Island and Turton Bay. Seventeen diatom species were found with the inverted microscope, including the previously absent *Coscinosira polychorda* and *Navicula vanhoeffeni* which exhibited their initial phase of growth. *Thalassiosira rotula* and *Streptotheca thamensis* were also observed for the first time. *Chaetoceros decipiens*, *Ch. furcellatus*, *Ch. wighami* and *Fragillaria nana* were found in the net hauls. The surface population became reduced to a few individuals per litre. The great populations of *Achnantes taeniata* (267,000), *Fragillaria cylindrus* and *Fr. islandica* (69,000), *Navicula grani* (53,000), *Thalassiosira nordenskjöldi* (34,000) and other less numerous species indicate that the 10-metre depth showed optimal conditions for diatom growth. However, the dominant *Ach. taeniata* had its maximum at 25 m (403,600 cells per litre) and was still represented by 48,280 cells at 50 m. It was the first time that supersaturation of oxygen at 10 m was reached (102.3%). Although very poor populations were recorded at the surface, oxygen was 91.0% of saturation. Oxygen was thought to be produced by metabolically active diatoms before they sank to the lower depths, where plankton populations were much larger than at the surface. In spite of the fairly large number of diatoms, a decrease of oxygen to 79.8% saturation was observed at 25 m, and furthermore it was 71.1% at 50 m. This was a period of intensive increase of pennate diatoms and the appearance of important biomass producers, among which the genus *Thalassiosira* became more important as the season advanced.

## JULY 15 AND 25

This was the period of maximum production of the pennate diatoms, of which *Achnantes taeniata* showed 1,440,000 cells per litre at 10 m. Meanwhile *Chaetoceros wighami* and *Ch. socialis* increased at 10 m to great populations of 146,000 and 72,000 cells per litre. Sixteen species of diatoms were found with the inverted microscope, while in the net samples still more occurred, though in small quantities, including *Chaetoceros karianus*, *Ch. septentrionalis*, *Nitzschia pungens*, *N. frigida*, *Fragillaria nana* and *Lauderia glacialis*. Marked increase of species of *Nitzschia* and *Navicula* and *Melosira islandica* indicates that these forms become a potentially strong component of the phytoplankton. This was still more marked in *Thalassiosira nordenskjöldi* and *Th. rotula*,

represented by 153,400 and 135,000 cells per litre found at 10 m. There was further increase in oxygen percentage at 10 m to 110.3%. At 25 m oxygen still showed supersaturation (103.7%), associated with numerically smaller populations and weaker light conditions. On July 23 the ice edge moved almost to Turton Bay, at whose entrance the collection station was situated (Fig. 1), and by the end of July it was inside the bay. The surface water at that time presumably contained much newly melted ice, and its salinity was low (10.41‰). The brackish forms *Chaetoceros socialis*, *Ch. wighami* and *Nitzschia pungens* became more abundant at that time, being better adapted to the low salinities. The general composition of phytoplankton on July 25 showed gradual decline of pennate diatoms, represented by *Achnantes taeniata* and *Fragillaria cylindrus*. Some Centriceae, such as *Chaetoceros wighami* showed their maxima at 10 m, reaching 461,000 cells per litre. The numerical increase in populations of *Denotula confervacea*, *Nitzschia pungens*, *Melosira islandica* and especially of *Thalassiosira* species, also of flagellated organisms, became more noticeable.

#### AUGUST 1, 11 AND 20

In early August and September 1956 only small patches of fast ice, along with offshore grounded floes, remained around Igloolik. Only occasional ice floes drifted into Hooper Inlet and Turton Bay. On August 1 the total amount of phytoplankton had decreased only insignificantly at all depths, since the previous observation. The taxonomic composition of the diatoms however was changed by the appearance of new species and decrease in the spring forms. The inverted microscope showed 33 species of flagellated groups and ciliates. The net samples showed another 21 species. This was a period of phytoplankton abundance (Fig. 3). In spite of the large autotrophic populations, oxygen values are below saturation. These probably could be interpreted as a result of cloudy weather conditions. Surface diatom production shows only a slight quantitative increase in spite of a considerable salinity increase. This was probably a result of surface water drift, which can not yet be estimated from our observations. Though the largest diatom populations were found at 10 m, those at 25 m were not much smaller. This indicated continuous vertical distribution of phytoplankton. The 10-metre depth showed fairly large maxima of *Chaetoceros furcellatus* of 122,000 cells per litre, 248,000 *Ch. socialis*, 61,000 *N. seriata* and 56,000 *Th. rotula*. This was a period during which the most important diatoms produced resting spores and ceased their metabolic activities, disappearing from the surface.

The climax of the annual production occurred on August 11. Centriceae predominated over the receding pennate forms. The genus *Chaetoceros* was represented by 7 species among which *Ch. socialis* was most numerous and reached its climax of 3,770,000 cells per litre at 10 m. *Ch. wighami* showed a population of 147,000 cells per litre, and *N. pungens* of 124,800 cells per litre. The increase of surface salinity from 19.94‰ on August 1 to 31.56‰ on August 11 is associated with the increase of *Ch. socialis* to 112,000 cells per litre. Similar increases concerned *Nitzschia pungens*, *Ch. furcellatus* and *Ch. wighami*. Dinoflagellates reached their climax and were represented by 9 species, among which the holozoic *Gymnodinium rubrum* exhibited a maximum of 45,000 cells per litre (Fig. 5, 6). It often ingests various diatoms, dinoflagellates and ciliates, and it is thought to constitute an effective grazing element at the time of its maximum. Various Cocolithineae, previously rare or unnoticed, appeared to be abundant (Fig. 8, 9a-n). The supersaturation extending from the surface to 25 m indicated active photosynthesis, decreasing at 50 m on account of reduced light at that level.

Observations made on August 20 showed an evident decline in the number of species and the number of organisms, resulting from decreased light supply, although the number of species was still relatively high. Physiological rest of autotrophs is suggested by lower oxygen values at the surface and within the lower levels.

Observations made on August 26 show a continuing decline of phytoplankton, which could be effectively grazed by the relatively large populations of ciliates and plankton crustaceans and other animals near their annual maximum, as reported by Grainger (1959). The flagellated organisms were mainly represented by *Pontosphaera huxleyi*, with some other species of Cocolithineae found at all depths (Fig. 8).

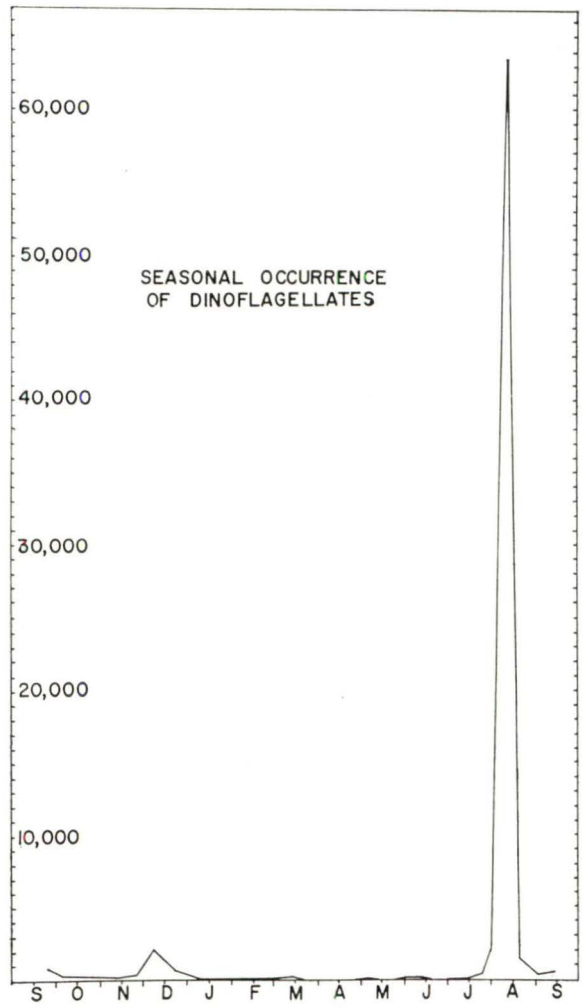


FIG. 5. Seasonal occurrence of dinoflagellates at Igloolik.



## DINOFLAGELLATES, FLAGELLATES AND CILIATES - SEASONAL DISTRIBUTION AND MAXIMA

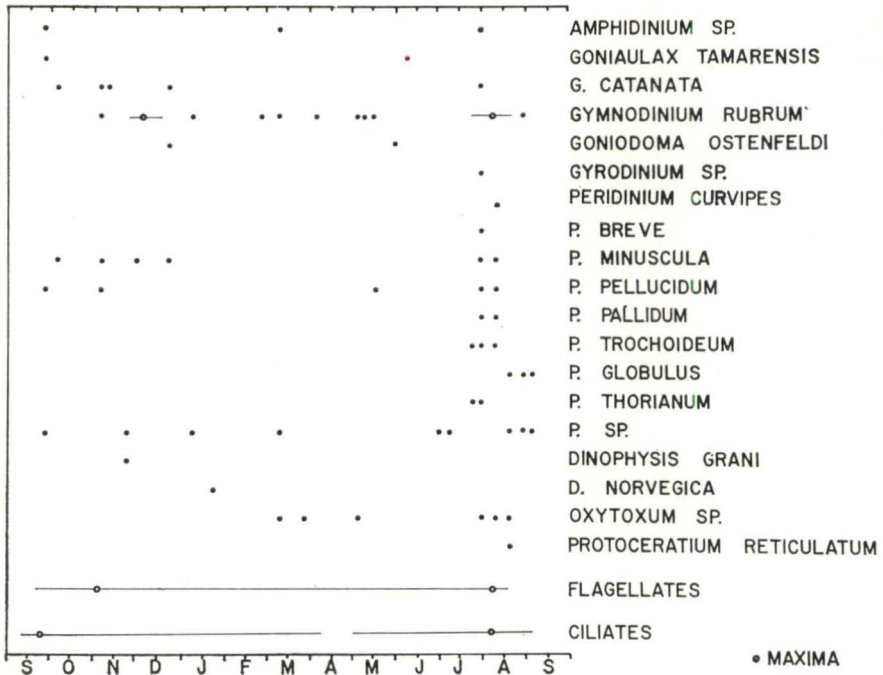


FIG. 6. Seasonal distribution and maxima of dinoflagellates, flagellates and ciliates.

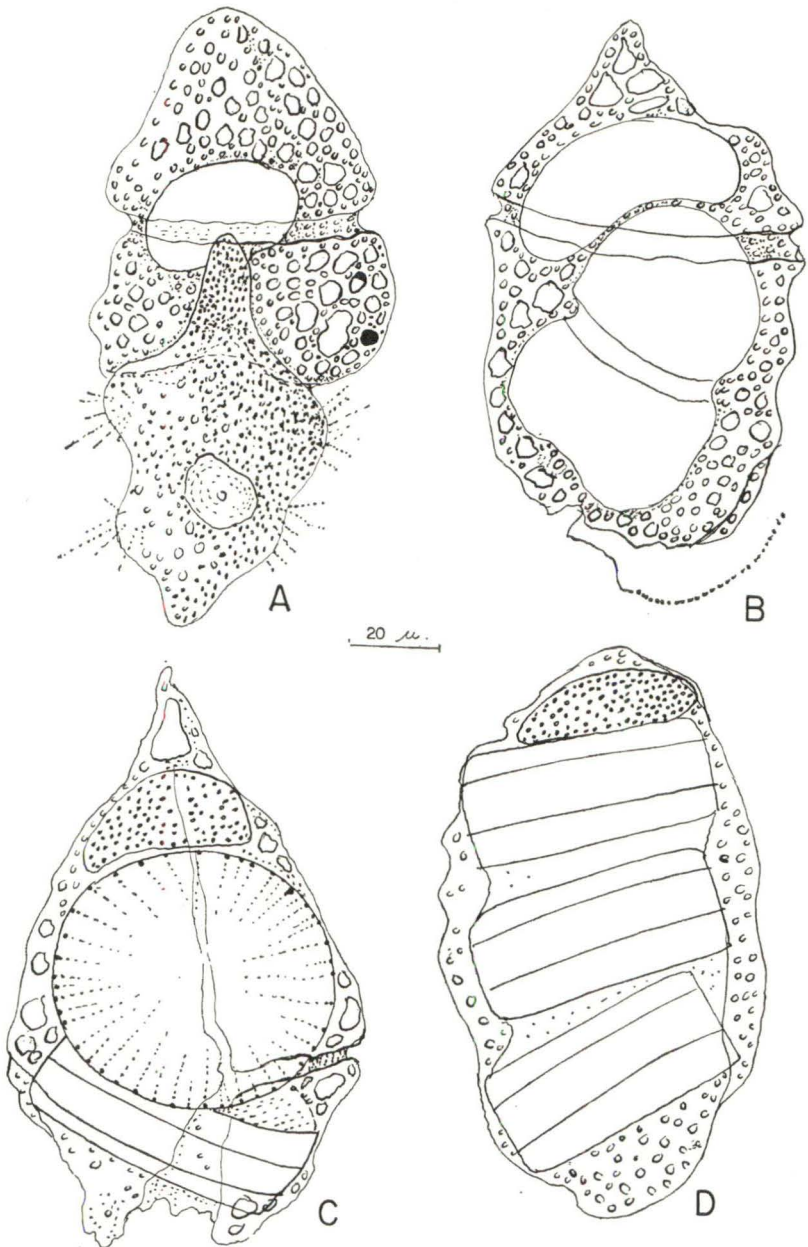


FIG. 7. *Gymnodinium rubrum*. (a) ingesting a ciliate *Strombidium*; (b) containing *Gymnodinium* cell; (c) containing *Thalassiosira rotula*; (d) utterly deformed, containing three cells of *Coscinosira polychorda*, showing nucleus at the apex.

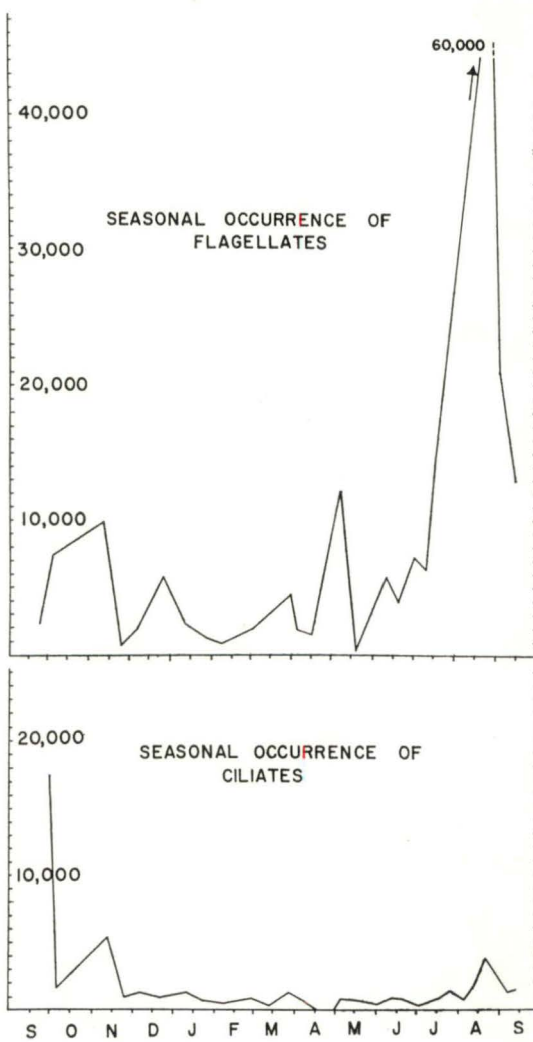


FIG. 8. Seasonal occurrence of flagellates (top), and of ciliates (bottom).



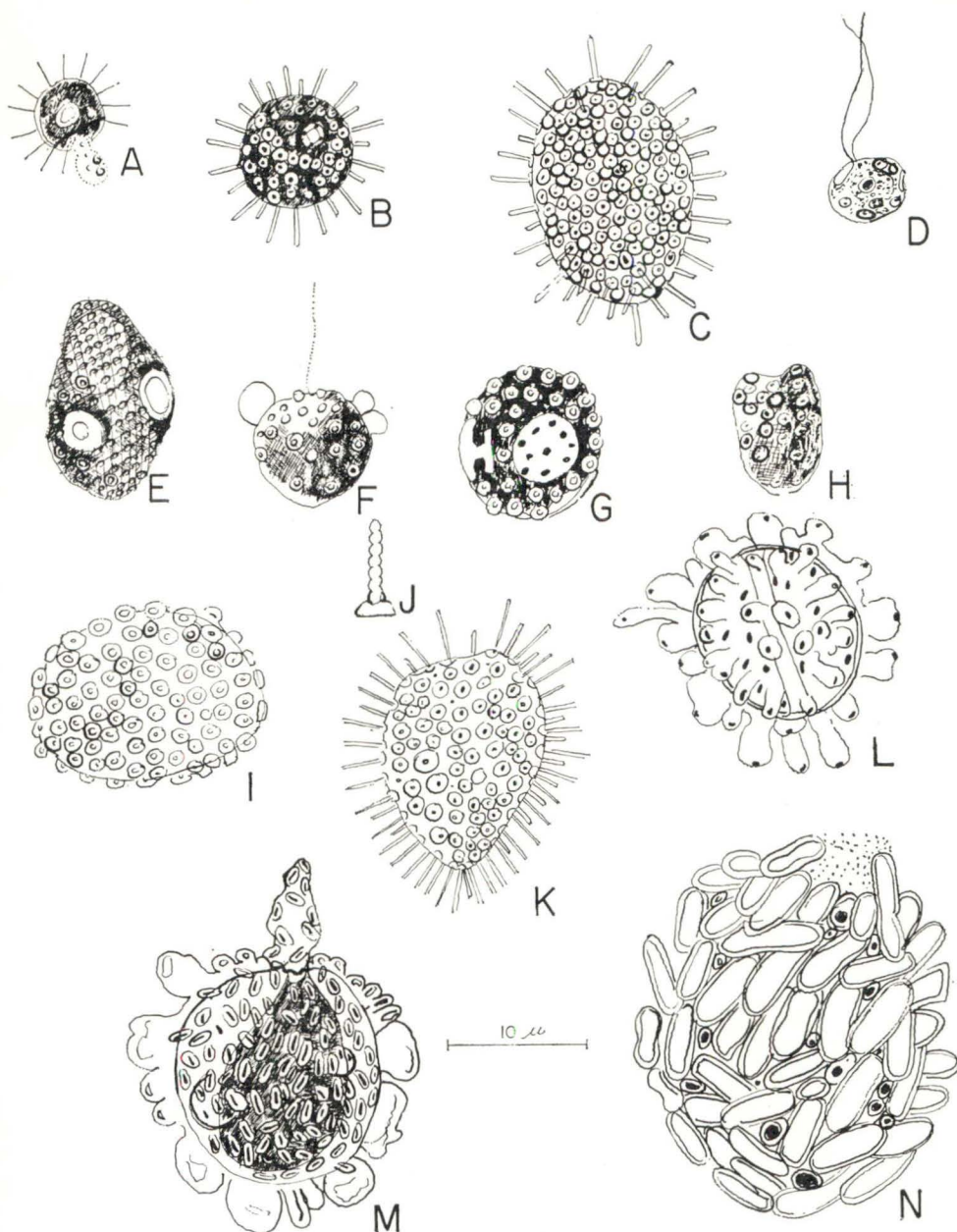


FIG. 9. *Pontosphaera nigra* (a-c), *Pontosphaera huxleyi* (d), *Pontosphaera ditrematolitha* (e-g), *Syracosphaera* sp. (h), *Pontosphaera* sp. (i), *Scyphosphaera* sp. (k), a single coccolith (j), *Lohmannosphaera* sp. (l, m), *Coccolithus pelagicus* (n).

SEPTEMBER 2 AND 13

Autotrophic organisms were represented by 18 species, a great reduction since the late August observation. There seemed to be a definite cessation in metabolic activities except for formation of resting spores, which was quite commonly observed. Vertical oxygen distribution shows subsaturation; the highest value was 93.3%, at the surface, decreasing rapidly to 55.9% at 10 m and 58.3% at 25 m. The water layer at 50 m showed a still lower oxygen content, 49.4% though a relatively large population of over half a million diatoms was found in it.

Observations on September 13 showed an increase of oxygen saturation to 105.2% at the surface and 102.7% at 10 m, while at 25 and 50 m 96.2% and 83.8% were recorded. Presumably new water masses with larger phytoplankton populations replaced the local phytoplankton of September 2. It is not possible, however, to explain this irregularity with certainty, because no data from adjacent areas were taken simultaneously.

#### VERTICAL DISTRIBUTION OF PHYTOPLANKTON

The vertical distribution of phytoplankton has to be related to various factors such as shape of cells, presence of bristles, and oil or gaseous vacuoles (Gran, 1912; Allen, 1932). Oily discharges from *Coscinodiscus* occurred at the surface of the North Sea (Grøntved, 1952). Experiments were made by the author on preserved *Coscinodiscus* plankton samples. These diatoms which contained large drops of oil gathered in large numbers at the surface of the sedimentation cylinders, while those in which oil was not yet developed covered the bottom of the cylinder. There was also a number of cells suspended in the middle of the cylinder. The floating capacity of diatoms appears to be associated also with the frequency of cell division (Gross and Zeuthen, 1948). Small phytoplankters are better adapted for flotation than are the larger forms (Munk and Riley, 1952). Sinking of phytoplankton in the sea does not necessarily occur in sheltered or calm waters (Grøntved and Steemann-Nielsen, 1957). Igloolik observations indicate that the sinking of diatoms took place when the largest standing crop of plankters was observed to contain resting spores, with membranes of greater specific weight than protoplasm.

Total estimates of the annual mean standing crop at the four depths show striking differences in size of populations (Table III).

TABLE III. Mean annual standing crop of phytoplankton at Igloolik, in number of cells per litre.

Surface	71,038
10 m	357,464
25 m	101,453
50 m	45,043

The surface water, in spite of the high solar illumination, harbours small populations which are exposed to drastic salinity fluctuations. These reach their

lowest values during the ice melting period. The Fisheries Research Board of Canada's *Calanus* expedition in 1957 at Rowley Island showed that brackish water of the lowest salinities formed a layer 2 m deep (unpublished data). Such conditions create a real osmotic barrier for euryhaline plankters from higher salinities below. The maximum phytoplankton production was confined to the 10-metre depth. It was 5 times greater than the production at the remaining depths. The high oxygen values found at 10 m and below in Hebron Fjord in Labrador (Nutt and Coachman, 1956) and those of Igloodik allow one to conclude that the largest autotrophic populations of diatoms generally are found between approximately 5 and 19 m. The mean annual standing crop in Igloodik at 25 m is nearly equal to that at the surface. The mean annual standing crop at 50 m, in spite of the low amount of solar energy, is not much less than the surface crop. This depth in arctic latitudes is usually considered as non-productive, and plankton populations found in it probably do not originate *in situ* but have sunk down from the surface layers.

#### QUANTITATIVE RELATIONSHIPS

##### MAIN TAXONOMIC GROUPS

Quantitative relationships among the main taxonomic groups: diatoms, dinoflagellates and ciliates, are shown in Fig. 10. The totals for each group were obtained by adding all plankters of the surface, 10-, 25- and 50-metre samples taken at Igloodik during the 28 station occupations. The largest block of phytoplankton organisms is represented by diatoms, for which the average density was 150,000 cells per litre in the 112 litres of water sampled during the entire season of observation. The main block of the column is divided into a left section representing Centricae, which produced twice as large an "annual crop" as Pennatae, shown on the right side. The extreme quantitative disproportion is apparent when the total of all flagellates, averaging 2,200 cells per litre, is compared with the large number of diatoms. Although dinoflagellates were represented by 32 species, their total "annual crop" was relatively small, averaging 660 individuals per litre. Because the majority of dinoflagellates found in Igloodik were holozoic and only a small fraction were autotrophic most of them may represent grazers, while a small number only are real autotrophic producers of biomass. The smallest block of ciliates, with an average population of 240 individuals per litre, represents real grazers which are of unknown significance in the food chain of plankton. The reader may evaluate briefly the total participation of each group concerned by comparing their "annual standing crops" (Fig. 10).



QUANTITATIVE RELATIONSHIP OF DIATOM SPECIES,  
FLAGELLATES, DINOFAGELLATES AND CILIATES

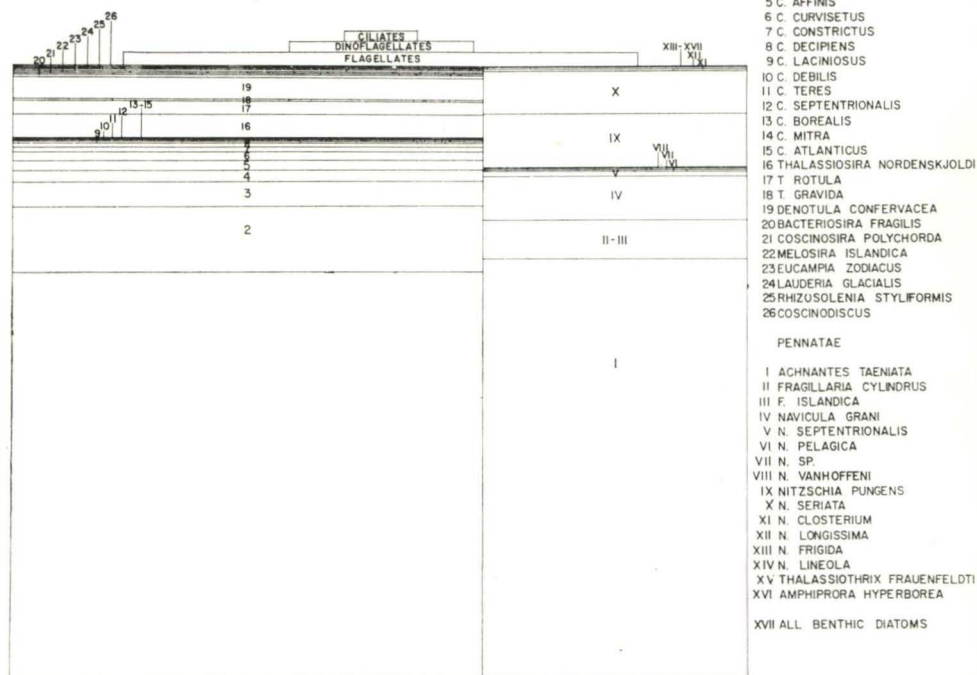


FIG. 10. Quantitative relationship of diatoms, flagellates, dinoflagellates and ciliates.  
Explanation in text.

#### ABUNDANCE OF THE VARIOUS SPECIES

The total number of individuals of each species was arranged into 3 groups called major, intermediate and minor, according to frequency of occurrence in the collections. The major group consists of 16 species which are the main biomass producers (Table IVa). The typical arctic diatom element was mainly represented in this group.

The intermediate group consists of 16 species of mixed ecological origin, mostly cosmopolitan and arctic (Table IVb).

The minor group has been divided into those found in the inverted microscope (Table IVc) and those which occurred only in the net hauls (Table IVd). This is in fact the group with the greatest number of species, including 39 diatoms, 30 dinoflagellates, 4 flagellates and 6 Coccolithineae. This group is considered a potential seeding stock, and under favourable conditions may increase in size, thus becoming significant food for zooplankton.

TABLE IV. Major, intermediate and minor groups of phytoplankton species, with their average numbers in cells per litre.

Species	Number	Species	Number
A. MAJOR GROUP			
<i>Chaetoceros socialis</i>	62,685	<i>Nitzschia pungens</i>	4,611
<i>Ch. wighami</i>	10,269	<i>N. seriata</i>	3,640
<i>Ch. furcellatus</i>	3,778	<i>Navicula grani</i>	3,758
<i>Ch. compressus</i>	1,749	<i>Fragillaria islandica</i>	
<i>Ch. subsecundus</i>	1,563	and <i>cylindrus</i>	3,313
<i>Ch. affinis</i>	1,514	<i>Thalassiosira nordenskjöldi</i>	3,514
<i>Ch. decipiens</i>	667	<i>Th. rotula</i>	2,092
<i>Achnantes taeniata</i>	36,432	<i>Denotula confervacea</i>	3,316
B. INTERMEDIATE GROUP			
<i>Chaetoceros laciniosus</i>	394	<i>N. septentrionalis</i>	395
<i>Ch. debilis</i>	162	<i>Navicula</i> sp.	78
<i>Ch. teres</i>	154	<i>Lauderia glacialis</i>	192
<i>Ch. septentrionalis</i>	153	<i>Coscinosira polychorda</i>	286
<i>Bacteriosira fragilis</i>	303	<i>Eucampia zodiacus</i>	264
<i>Melosira islandica</i>	285	<i>Nitzschia closterium</i>	193
<i>Navicula pelagica</i>	209	<i>N. longissima</i>	190
<i>N. vanhoeffeni</i>	0.36	<i>Rhizosolenia styliformis</i>	96
C. MINOR GROUP, FOUND IN THE INVERTED MICROSCOPE			
<i>Chaetoceros borealis</i>	36	<i>Coscinodiscus</i> sp.	11
<i>Chaetoceros atlanticus</i>		<i>Amphiprora hyperborea</i>	4
and <i>Ch. mitra</i>	6	All benthic diatoms	29
<i>Nitzschia frigida</i>	28	<i>Thalassiothrix frauenfeldi</i>	8
<i>N. lineola</i>	23		
D. MINOR GROUP, FOUND ONLY IN THE NET SAMPLES			
<i>Chaetoceros eibeni</i> , <i>Ch. gracilis</i> , <i>Ch. perpusillus</i> , <i>Ch. karianus</i> , <i>Melosira arenaria</i> , <i>M. borrieri</i> , <i>Synedra</i> sp., <i>Coscinodiscus excentricus</i> , <i>Coscinodiscus</i> sp., <i>Fragillaria</i> sp., <i>Pleurosigma</i> sp., <i>Pinnularia</i> sp., <i>Navicula</i> sp., <i>Gyrosigma spenceri</i> , <i>Gyrosigma</i> sp., <i>Nitzschia bilobata</i> , <i>Streptotheca thamensis</i> , <i>Thalassiosira subtilis</i> , <i>Th. condensata</i> , <i>Thalassiosira</i> sp., <i>Cocconeis placentula</i> , <i>Cocconeis</i> sp.			

## SOME DYNAMIC FEATURES OF MORE COMMON DIATOM POPULATIONS

Thirteen diatom species were chosen in order to show quantitative fluctuations of their populations in the plankton (Fig. 11–13). Some diatoms, like *Thalassiosira gravida*, *Th. nordenskjöldi*, *Melosira islandica* and *Chaetoceros furcellatus* develop only a single maximum during a vegetative season, this cycle being called unimodal. Species like *Chaetoceros wighami*, *Ch. constrictus* and *Thalassiosira rotula* are called bimodal, since two separate maxima are formed by their populations. The polymodal species show three or more even or uneven maxima.

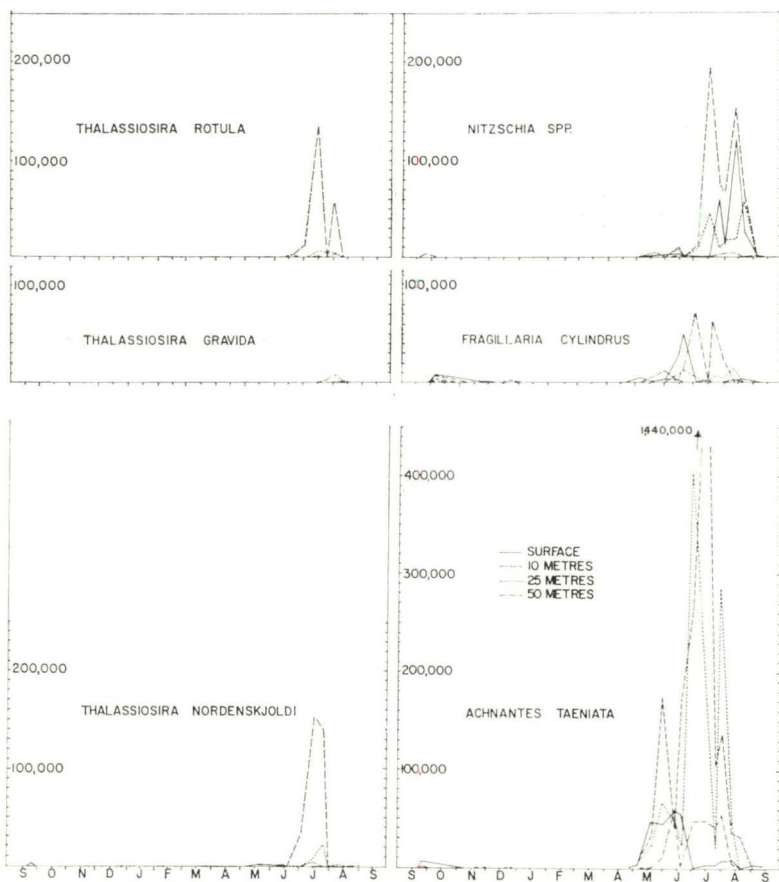


FIG. 11. Quantitative dynamics of the more common diatoms and their annual cycles.



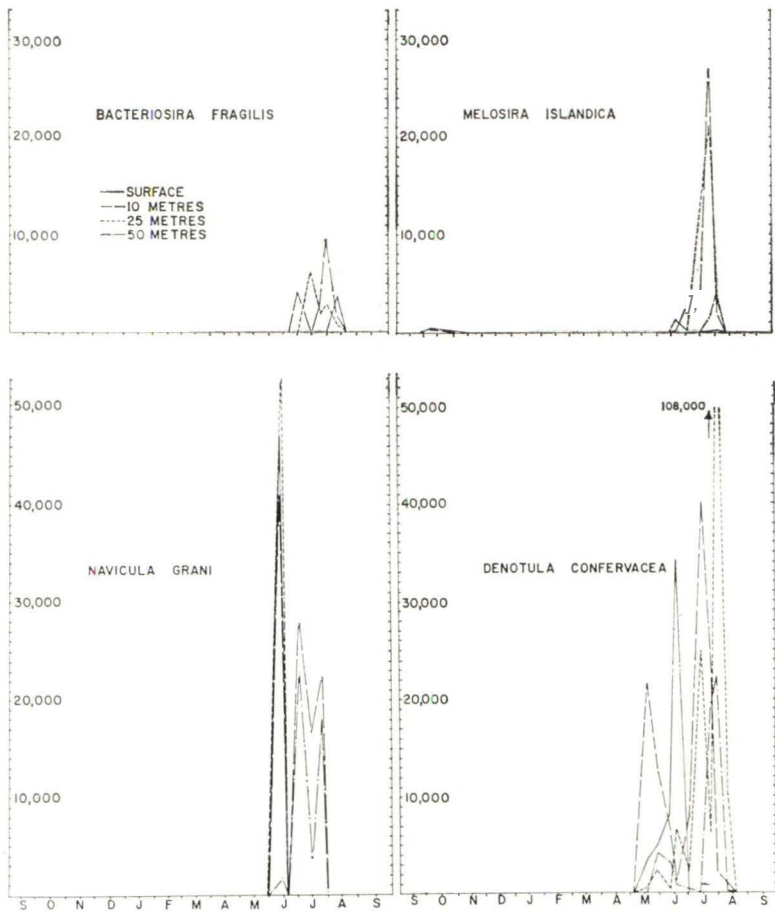


FIG. 12. Quantitative dynamics of the more common diatoms and their annual cycles.

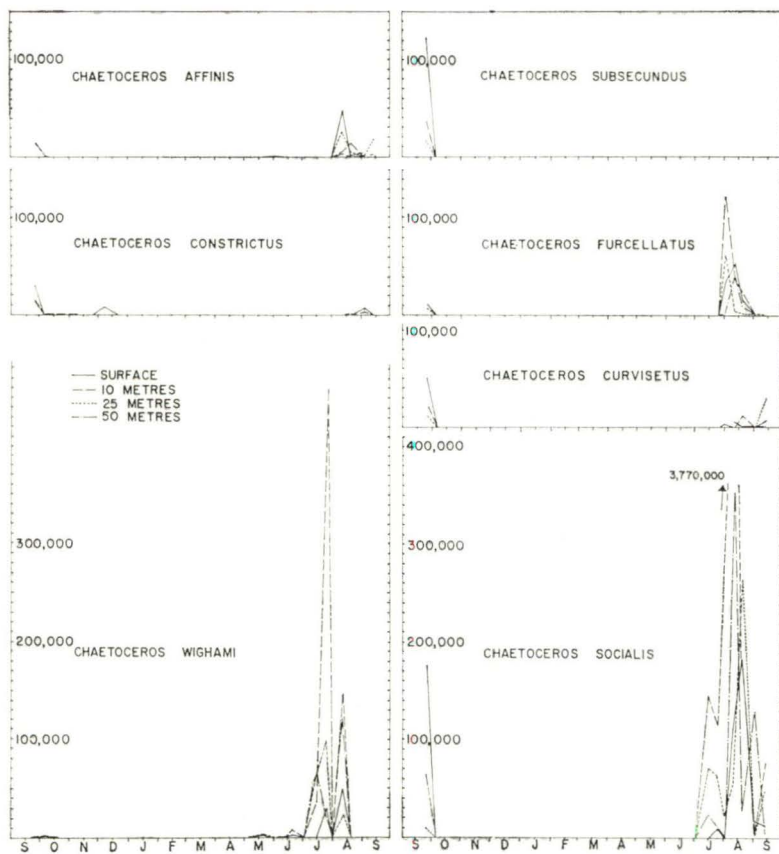


FIG. 13. Quantitative dynamics of the more common diatoms and their annual cycles.

In this group belong *Bacteriosira fragilis*, *Navicula grani*, *Denotula confervacea*, *Fragillaria cylindrus* and *Achnantes taeniata*. Taxonomic identification of diatoms was made using the monographs of Hustedt (1930) and Cupp (1943).

The nature of the quantitative fluctuations in plankton is unexplained. It is supposed that the unimodal type of cycle develops in species where populations are physiologically uniform and show similar features in growth and reproduction. Species exhibiting polymodal curves may consist of physiologically heterogeneous populations, probably differentiated into various physiological groups, which alternate in the sea in sequence with the seasons.

#### DINOFLAGELLATES

Thirty-two species of dinoflagellates found in Igloolik samples were common only in August and September. The occurrence of most of them in the net hauls was usually restricted to single individuals only, or they were absent from the inverted microscope chambers. To increase the chance of finding rare forms of dinoflagellates, 1 or 2 ml of the plankton sediment were taken with a calibrated pipette and examined with the inverted microscope after filling the sedimentation chambers with water. Such a procedure increases the possibility of finding rare organisms by about 150 to 300 times over the use of single ordinary compound microscope preparations. The time-consuming identifications usually make it possible to examine only a few preparations, so the chance of finding rare species with the inverted microscope are very much better than with the ordinary compound microscope. Works by Schiller (1933, 1937), Paulsen (1908, 1949), and Wood (1954) were used for identification of dinoflagellates.

The thecate forms of dinoflagellates were represented by 19 species, forming small populations seldom exceeding 300 cells per litre. Although the athecate forms were represented by 6 species only, the yearly total of cells collected averaged more than 450 cells per litre. The total number of dinoflagellates taken at Igloolik averaged 665 individuals per litre. The largest populations were 45,000 cells per litre at the surface and 17,670 at 10 m, observed on 11 August, consisting mainly of *Gymnodinium rubrum*.

Some Igloolik dinoflagellates were efficient grazers. Among them *G. rubrum* was able to ingest diatoms (*Thalassiosira*, *Coscinosira*), dinoflagellates and protozoans larger than itself (Fig. 7, a-d). Holozoic nutrition was observed on a few occasions in *Peridinium globulus* (Fig. 14). The cosmopolitan group was dominant, while typical arctic species were less abundant. *Peridinium grani*, *P. quarnerense*, *P. pallidum*, *P. pellucidum*, and *P. minuscula* were more common than *P. roseum*, *P. groenlandicum*, *P. thorianum*, *P. breve*, *P. curvipes*, *Dinophysis grani*, *D. norvegica*, *Goniodoma* sp., *Goniaulax tamarensis* and *G. catenata*.

The preponderance of holozoic over autotrophic dinoflagellates in the Igloolik area is interpreted as a common phenomenon in the arctic biotope, where a natural selection is imposed by the long period of darkness and low temperature. Holozoic



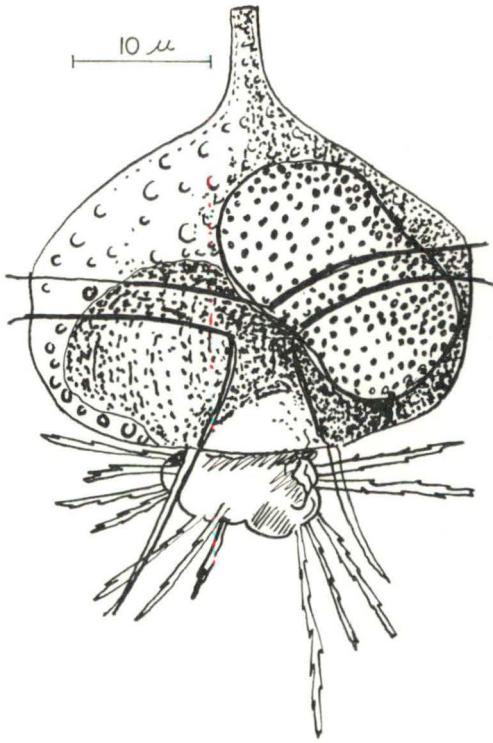


FIG. 14. *Peridinium globulus* ingesting an unidentified flagellate.

plankters appear to be less affected by both these factors, obtaining their energy requirements by phagocytosis, heterotrophy or osmotrophy. Obligatory autotrophs, requiring a light supply as a source of energy, suffer during the long winter.

Intrusion of pelagic *Ceratium arcticum* and *C. longipes*, recorded in the adjacent waters of Foxe Basin evidently did not occur in Igloolik. However, both species are considered as arctic and oceanic (Grøntved and Seidenfaden, 1935), and in the Newfoundland area they are described as essentially cold-water organisms (Frost, 1938). The absence of the large *Peridinium depressum*, found in both cold and warm waters of coastal and pelagic areas, might be explained to some extent in the same way as the absence of *Ceratium* in Igloolik. Probably it is mainly temperature and not salinity which primarily affects the geographical distribution of dinoflagellates, particularly *Ceratium* species (Graham, 1941). This is indicated also by the increase in population density and number of species of dinoflagellates from Igloolik southward towards Hudson Bay. Because dinoflagellates are transported by currents at different times and conditions, they are useful as indicators of the movement of water masses (Wood, 1954). Such

application cannot be practiced without new collection methods however, for dinoflagellates are rare in the arctic. The occurrence of new species, *Gyrodinium arcticum*, *Gymnodinium intercalaris*, *Cenchridium globosum* and *C. spherula* show that the taxonomy of arctic species should be more extensively studied before other problems can be solved.

#### TAXONOMIC DESCRIPTIONS OF DINOFLAGELLATES

##### GENUS *Cenchridium* (EHRENBERG)

This genus comprises 4 species incorporated into the family Prorocentraceae (Schiller, 1933). Ehrenberg suggested affinities with Foraminifera. Bütschli considered *Cenchridium* as being associated with warm seas (from Schiller, 1933). The systematic position of the genus is not yet established because the organisms are rare and thus not readily available for study. Both species of *Cenchridium* found at Igloodik appear to be benthic forms occasionally brought into the plankton. The dorso-ventral organization of distinct ventral and dorsal valves occurs only in *C. globosum* (Fig. 15c, d). No intervalvar suture is found in *C. spherula* (Fig. 15b). Both flagellar pores are located at the front of the tube (Fig. 15a, c). The typical membrane pores, as in other Prorocentridae, are found in *C. globosum* (Fig. 15c), while in *C. spherula* parallel warts cover the membrane (Fig. 15c). This form is more elongated than those figured by Ehrenberg. Dimensions of *C. spherula* are  $37 \times 27 \mu$ , of *C. globosum*  $38 \times 20 \mu$ . Both species are not previously reported from the arctic. They have been found in the South Pacific (Schiller, 1933).

##### ***Gyrodinium arcticum*** N. SP. (Fig. 16a, b, c)

Body subspherical, asymmetrical and circular in cross section. Sulcus slightly sigmoidal, with a small cavity within the intercingular area, starting on the dorsal surface. Girdle ends prominently displaced. The left end of the girdle usually narrower, laterally oblique, dorsally straight. Sulcus deeply incised, with marked edges. Left lobe of hypocone ending with an acute, subcentrally descending notch and a noticeable margin within the epicone. Fine parallel and horizontal sutures forming distinct square or rectangular plates. Anterior flagellum emerging from the flagellar pore situated at the edge of the upper margin of the girdle. Sulcus deeply incised with marked edges ending as an acute notch where hypocone starts. Membrane surface covered with fine lines running both antapically and horizontally, the latter being less well defined, forming small plates of rectangular and square form. Regularly situated spherical inclusions within the membrane sutures. These inclusions absent within more densely distributed lines in the sulcus. Anterior flagellum starting at the upper edge of the girdle ridge as a flagellar pore. Posterior flagellum emerging at the level where the hypocone notch ends. A hyaline flap of the right hypocone lobe in some specimens covering the flagellar pore. Protoplasm dense, containing small

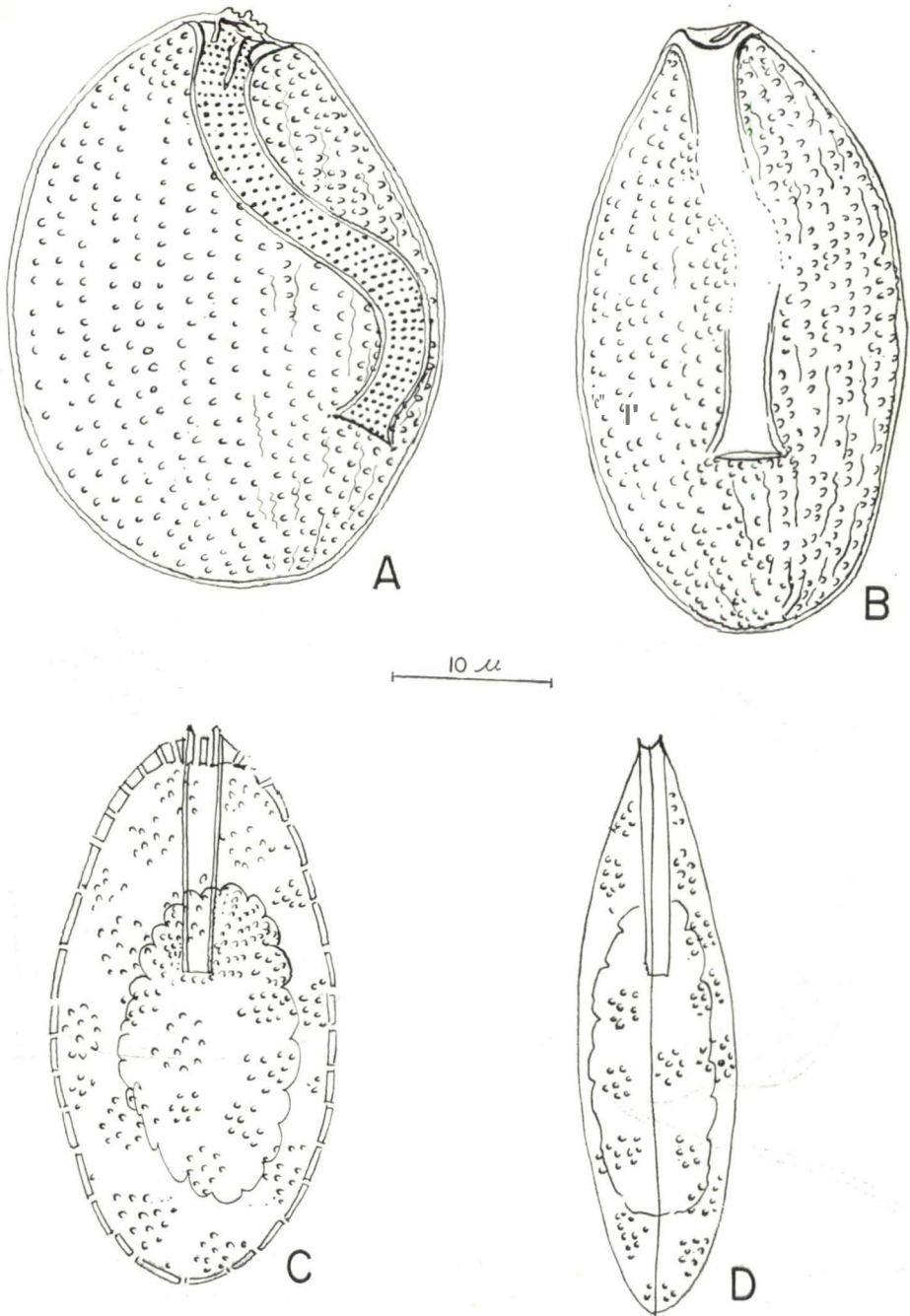


FIG. 15. *Cenchradius spherula*. (a) lateral view; (b) sagittal view. *Cenchradius globosum*. (c) lateral view; (d) sagittal view.



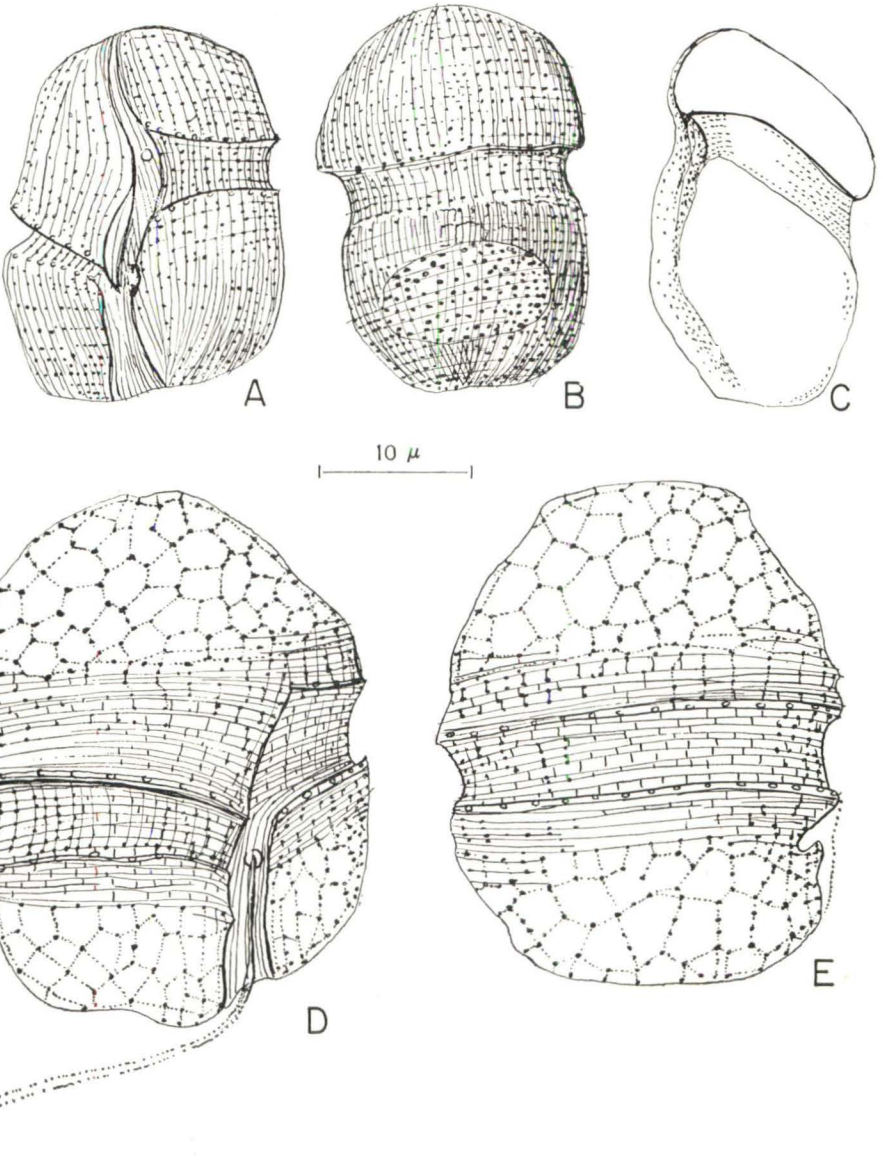


FIG. 16. *Gyrodinium arcticum* n. sp. (a) ventral view; (b) dorsal view; (c) ventro-lateral view.  
*Gymnodinium intercalaris* n. sp. (d) ventral view; (e) dorsal view.

globular inclusions. Nucleus subspherical with distinguishable chromosomes situated within the hypocone.

Dimensions: length 26–30  $\mu$ , breadth 20–28  $\mu$ .

Affinities: *Gyrodinium arcticum* appears to be distinct from a group of small and similar species such as *G. hamulus* Kofoed and Swezy, *G. grammaticum* Kofoed and Swezy, *G. incertum* Herdmann and many others insufficiently studied using only low microscope power. All aspects of the morphodynamics of this entire group have to be re-examined in order to establish a proper basis for taxonomic affinities of its members.

Occurrence: Igloolik, August 1956. Net and Utermöhl microscope samples.

***Gymnodinium intercalaris* N. SP. (Fig. 16d, e)**

Body broadly rounded in most cells, subhexagonal in some. Subspherical in cross section with deeply impressed girdle and sulcus. Both ends of the girdle even or slightly displaced. Right section of the girdle three times broader than the left. Sulcus deep but short, ending within a deep edge of the girdle and not appearing within the epicone. Left lobe of epicone larger than the right. Left hypocone lobe twice as large as the right lobe. Epicone ending as an acute, strongly marked edge, clearly separated from the girdle, and protruding over the intercingular area. A small cavity beneath the left edge of the sulcus, visible in dorso-ventral position (Fig. 16e). Posterior flagellum emerging at the level of the left end of the girdle (Fig. 16d). Anterior flagellum not observed. Well marked equatorially located membrane sutures forming a wide belt of "circuli" in which vertical sutures also occur. These structures extending up and down from both sides of the girdle edges. Parallel lines in the sulcus, without horizontal sutures. Both surfaces of epicone and hypocone covered with large polygonal reticulum, containing spherical inclusions. Many suboval chromatophores observed in some cells while others appeared to be holozoic. Small inclusions found in protoplasm. Nucleus not observed.

Dimensions: 34–45 $\mu$ .

Affinities: *G. intercalaris* may be easily identified by its "circuli", not observed in other forms. There is some similarity with *G. grammaticum*, but this form is distinct from it and other small *Gymnodinium* already described by Biecheler (1952), Hulburt (1957), and Schiller (1933, 1937).

Occurrence: Igloolik, September, 1956.

COCCOLITHINEAE AND OTHER FLAGELLATES

Great progress in our knowledge of Coccolithineae has been made since the introduction of the electron microscope. The taxonomic nomenclature of some groups has been changed (Braarud and Nordli, 1952; Halldal, 1953; Halldal and Markali, 1954; Braarud, 1955, 1955a; Braarud *et al.*, 1955). The light microscope permits only preliminary observations of the general features of Cocco-

lithineae. The final determination of coccoliths, including taxonomic identification, has to be completed with the electron microscope. In view of this the new taxonomic descriptions of Coccolithineae found in the Igloolik samples are given in a preliminary way only. It is thought that observations made here may be confirmed in the future by the electron microscope, as has happened with diagnoses by Schiller (1930), Lecal-Schlauder (1951), Chatton (1952), Deflandre (1952), and other others.

Coccolithineae are of less importance in the food chain economy of the arctic seas than in the warm seas where they are very abundant (Schiller 1930; Kofoid and Swezy, 1921). The maximum of Coccolithineae in Igloolik was represented by only 60,000 cells per litre, which is in great contrast to the populations of half a million cells per litre found in Hudson Bay (*Calanus* expeditions, 1953-54). There are probably more advantageous temperature conditions in Hudson Bay which particularly favour the development of larger populations of this flagellate.

*Pontosphaera huxleyi* LOHMANN (Fig. 9d)

*Pontosphaera huxleyi* was always a dominant component among other species of Coccolithineae. The low degree of calcification of coccoliths found in Igloolik seems to be associated with the low temperature, because such organisms from warmer waters appear to possess well calcified coccoliths.

*P. huxleyi* was a dominant species among the Coccolithineae. Its maximum appeared late in August, reaching 60,000 cells per litre. Owing to its small size it was identified with difficulty with the inverted microscope. It was more common than any other form of its group at Igloolik and in Hudson Bay. It seems to be common in northern seas (Braarud, 1935; Steemann-Nielsen, 1935).

*Pontosphaera nigra* SCHILLER (Fig. 9a-c)

Polymorphic form: Populations of this form consisted of spherical and subspherical specimens (Fig. 9a, b). Its spherical coccoliths were usually arranged irregularly, in some individuals densely and in others loosely. Each coccolith was built up of a spherical plate of 0.1 to 1.5 $\mu$  diameter from which a fine stalk emerged. The length of the stalks varied from 1.5 to 3.5 $\mu$ . The colour of the shell varied from dark brown to dark brown-yellow. The length varied between 3.5 and 24 $\mu$ .

Occurrence: July to September, Igloolik.

*Pontosphaera ditrematolitha* N. SP. (Fig. 9e, g)

Spherical and subspherical cells easily distinguished by their large trematoliths, found mostly as 2 in each cell. Apart from large trematoliths, very small coccoliths also found. These arranged spirally (Fig. 9e) except in the apical area, where absent. The trematoliths of some cells with a large unperforated margin (Fig. 9e), while in some individuals, from 3 to 10 perforations observed. Such trematoliths in side view (Fig. 9g) deeply incised, and both their top and



bottom surfaces joined with a columella. Nucleus apical. Large lateral chromatophore. Single flagellum emerging from the apex.

Dimensions: spherical forms from 9 to 16 $\mu$ , subspherical forms from 6 to 12 $\mu$ .

Occurrence: August, Igloolik.

*Syracosphaera* sp. (Fig. 9h)

Some specimens of *Syracosphaera* sp. were observed with the inverted microscope and were also studied with the standard compound microscope. It was not possible to establish more detailed features, since it was not common enough in the collections. Single minute perforated coccoliths in some specimens covered almost the entire surface of the cell, or else were rare and dispersed. Two flagella of uneven size were seen in some specimens. A single chromatophore and a posterior nucleus occurred.

Dimensions: length from 6.5 to 11 $\mu$ , breadth from 5 to 9 $\mu$ .

Most of the cells were badly deformed and not suitable for identification purposes. It was rare in net plankton from August to September.

*Pontosphaera* sp. (Fig. 9i)

Mostly subspherical, seldom spherical, individuals of this organism were not observed in the motile stage. They were covered with tiny spherical coccoliths irregularly placed. Larger specimens of this form measured between 15 and 22 $\mu$ . This organism seems to be closely related to *Coccolithophora pelagica*, described also from the English Channel by Lebour (1923). Single individuals occurred rarely in the net plankton in August.

*Scyphosphaera* sp. (Fig. 9k)

This was distinguished from *Pontosphaera nigra* by its pointed antapex and broad apex. Its coccoliths were of uneven length and heteromorphic, perforated and varying in size. Single coccoliths consisted of a discoid stalk and a stalk with distinct segments. Its calcareous shell was very fragile. Diameter from 10 to 15 $\mu$ . Its taxonomical position is uncertain. It occurred in August.

*Lohmannosphaera* sp. (Fig. 9l, m)

These are subspherical cells, easy to distinguish by their apical appendages at the apex of which a usually dark dash-formed perforation is found. A thin fragile membrane of some cells contained two parietal chromatophores (Fig. 9l). In some individuals the cell membrane was colourless, in others, yellow-brown. The length of appendages was greater in larger forms, in which a large apical protuberance usually was formed (Fig. 9m), upon the surface of which dark perforations occurred. *Lohmannosphaera* sp., after treatment with 0.1% HCl, changed its colour to pale yellow and showed small bubbles associated with solution of the calcareous structure.

Dimensions: length of 9 measured specimens was between 15 and 28...

Occurrence: Igloolik, September.

*Coccolithus pelagicus* (WALLISCH) SCHILLER (Fig. 9n)

Shells were spherical or subspherical with wide apical openings. Coccoliths were large and elongated, sometimes with a distinct septum in the centre, and a narrow margin. In some specimens smaller coccoliths were found close to the apex, while the larger coccoliths were within the antapex. Some were constricted in the middle. Coccoliths were usually placed irregularly on top of each other. Igloolik specimens were similar to those found by Schiller (1930). Halldal (1953) reported it from the Norwegian Sea with a maximum of 16,500 cells per litre; Gaarder (1954) from the Atlantic. Holmes (1956) described it as not abundant from the Labrador Sea.

Dimensions: 32 $\mu$ .

Occurrence: Rare in net plankton in August.

## CHOANOFLLAGELLATES

*Salpingoeca natans* Grøntved (Fig. 17a-h)

Two species of choanoflagellates, *Salpingoeca natans* and *Monosiga* sp., were occasionally found in the inverted microscope chambers and net hauls. Both organisms were most common on September 13, 1956, and occurred in small populations of 200 and 500 cells per litre. Thanks to Dr Jul. Grøntved, who kindly sent the author his original sample (No. 6583), taken at 20 m from the southern North Sea, it was possible to compare the Igloolik choanoflagellates with the original specimens. *S. natans* was reported from the Limfjord, Denmark, and from West Greenland. *S. natans* from Igloolik samples appears to be identical with those described from other localities by Dr Grøntved (1952, 1956). However some of the Igloolik individuals were larger. The main difficulty in identifying the Igloolik species was the absence of the outer collar in the majority of flagellates. Only a single collar, showing great morphological variability, was found (Fig. 17a-h). *S. natans* was finally determined when typical individuals with both collars were found (Fig. 17h). The organism is a highly variable one, as far as form and shape of collars is concerned. No stalk appeared in some individuals, which excrete mucus at their antapex, which serves for attachment upon a solid substrate (Fig. 17d). A fine square reticulum of lorica was observed without staining, but was accentuated with methylene blue, which also intensified tiny inclusions in intersections of the sutures. Some protomonades were attached by a small stalk to the inner side of the lorica (Fig. 17h). It was possible to distinguish a cell body from the lorica. A rectangular structure at the base of the outer collar seems to be associated with movements of the collar (Fig. 17h).

A single flagellum slightly longer than the entire length of the lorica with the stalk, emerged from the apex of the protomonade. A well distinguished nucleus was located centrally or subcentrally, containing a large nucleolus.

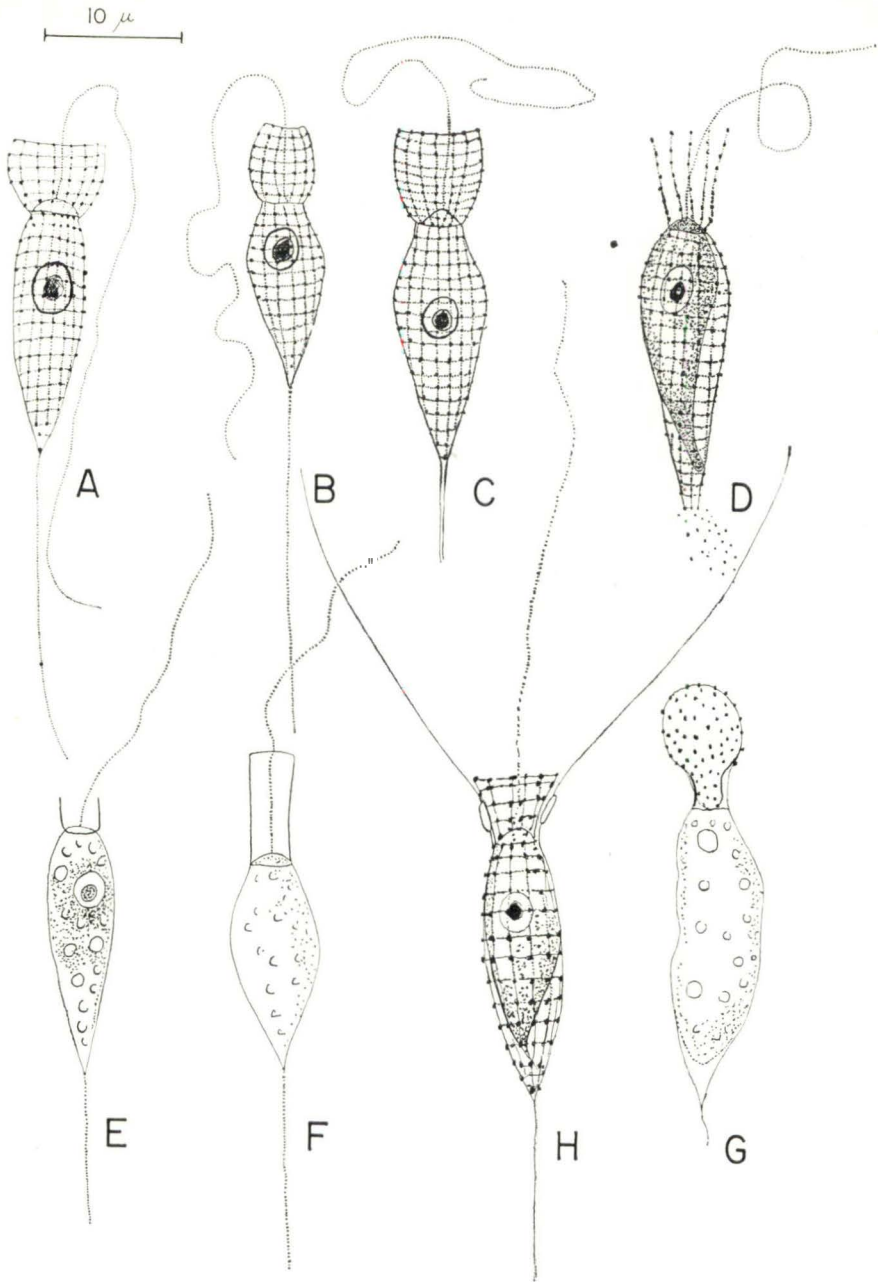


FIG. 17. *Salpingoeca natans*. (a, b) individuals with the long stalks showing fine reticulate structure of the lorica, flagellum and nucleus; (c) individual with short stalk; (d) individual without stalk, the protomonade attached to the wall of the lorica, with some mucus discharged at the antapex; (e, f) individuals with single collar; (h) individual with both outer and inner collar; (g) resting spore formation.



Spherical inclusions in the protoplasm represented reserve materials but were absent in some individuals. Finely diffused brown-green pigment was found in some cells and was most concentrated around the nucleus. It was also observed by the author in some choanoflagellates studied alive (unpublished data). Few individuals were found with the spherical structures attached to the apex, which appears to be a cyst formation. This requires more observations *in vivo*. *S. natans* was associated with a large number of bacteria which, as suggested, it may ingest as food, as observed in other forms.

Occurrence: In August and September more common than in other months.

*Monosiga* sp. (Fig. 18a-e)

A solitary elongated protomonade was attached to the antapical part of the lorica by a short stalk, and contained a nucleus with a nucleolus. The lorica consisted of three segments partitioned perpendicularly by 10 sutures. Its widely opened collar contained spherical inclusions, stained with methylene blue, within the intersection of the membrane sutures and within the edge of the outer collar. The flagellum was of varying length, usually shorter than the length of the body.

Dimensions: length  $26\mu$ , width  $19\mu$  (expanded collar).

Occurrence: Rare, mostly found in August.

This species is similar to *Corbicula socialis* (Braarud, 1935), which is colonial, while this form is solitary. Its antapical sutures were well distinguished with front phase illumination. Three segments of the lorica were clearly cut out by the horizontal sutures. Ten antapical sutures divided the lorica into 30 distinct membrane areas, containing fine inclusions, wider within the apex and narrower within the antapex. *Monosiga* sp. appears however to be a distinct species since it shows different morphodynamic features which seem to be absent in the other known species. Final determination was not done because more information is required and its morphological variability should be investigated. It is possible that in some circumstances two collars could be formed in this *Monosiga* as was found in *S. natans*. The possibility of two collars has to be taken into account, since *Diplosiga* sp. (Grøntved, 1956) has two collars and this form seems to be quite similar to the Igloodik organism.

Some details of cell division were observed, showing that both daughter loricas are joined by the edges of their umbrellas, while both protomonades are still joined by a single flagellum (Fig. 18d). The triangular and barrel-like shapes of the loricas in dividing specimens indicated that these are not rigid structures but are able to perform some movement. Some of the protomonades were found separated from the antapical part of the lorica and were freely floating in the plankton (Fig. 18b). *Monosiga* sp. appears to be a non-obligatory plankton organism which can also float freely in plankton or be attached to the surface of diatoms (Fig. 18a).

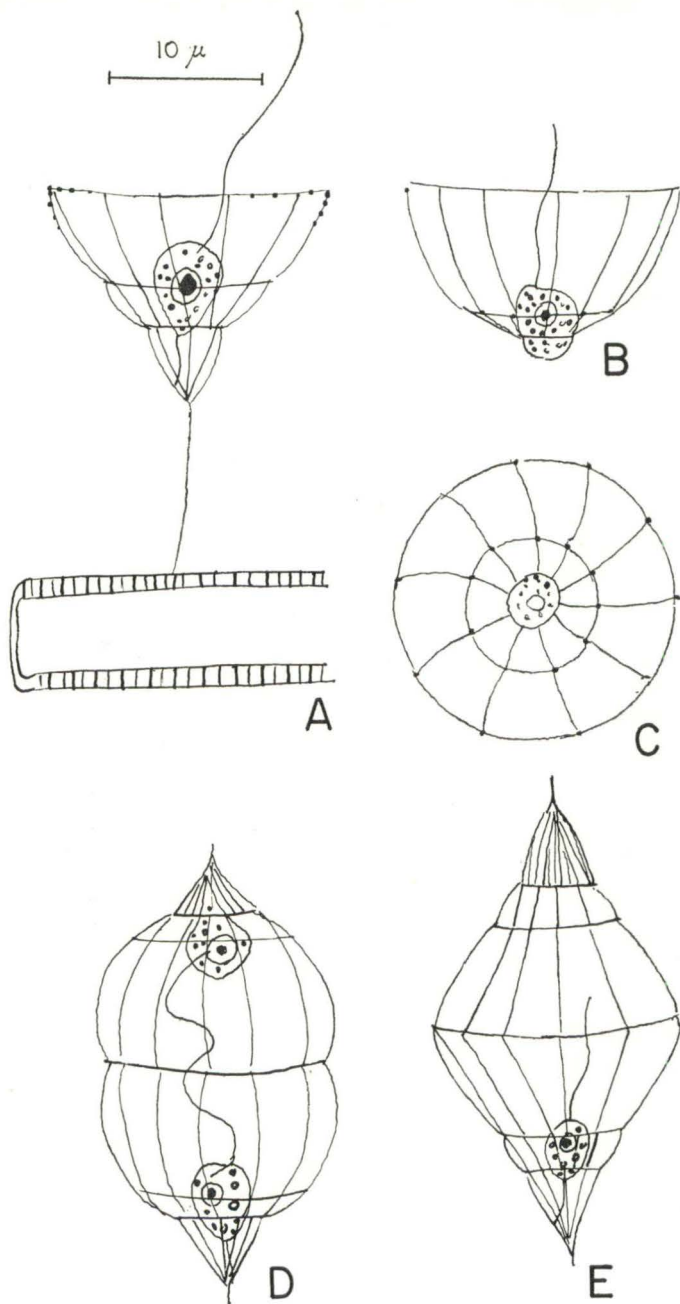


FIG. 18. *Monosiga* sp. (a) an epiphytic individual upon diatom surface; (b) motile individual consisting of the protomonade and upper parts of lorica; (c) observed in front view; (d) two daughter-individuals with a single unseparated flagellum; (e) two daughter-loricas after completed division, of different shape than (d); containing only a single protomonade.

## OTHER FLAGELLATES

Some other flagellates found in the Igloolik samples were not abundant enough to be studied in all details. They were identified as *Bodo* sp. and as *Lepocinclis* sp., epiphytic on *Achnantes*. Since *Lepocinclis* Lemmermann (1908) belongs to a freshwater group, it must here be specially adapted physiologically to the marine environment. It was observed in March, when only very poor plankton was observed (Fig. 19).

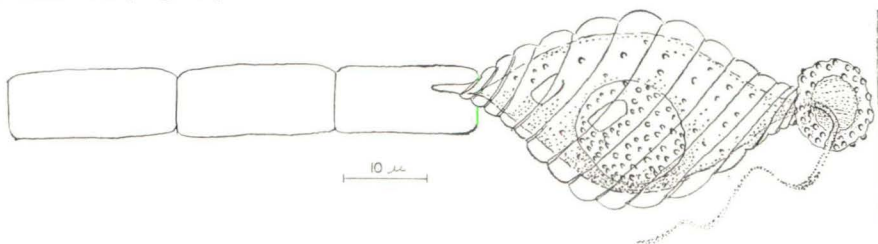


FIG. 19. *Lepocinclis* sp. An epiphytic individual on the membrane of the diatom *Achnantes taeniata*.

## CILIATES

Among eleven species of ciliates (identified from Leegaard, 1915) found at Igloolik, *Mesodinium rubrum*, *Lohmanniella oviformis*, and *Laboea conica* were more common than Tintinnidae. Populations of ciliates seldom exceeded a few hundred individuals per litre. The scarcity of species and their small populations seems to be caused by the long period of low temperatures and hydrographic uniformity of the Igloolik shelf. In Hudson Bay (unpublished data) where 27 species were found and greater populations of ciliates occurred, biological conditions appear to be more advantageous. The number of ciliates (28) found in Denmark Strait (Braarud, 1935) is very close to that found in Hudson Bay, while the number (34 species) in Greenland waters collected by Seidenfaden is somewhat higher. It is however not the number of species but the higher total crop per litre which is typical of the higher productivity standard of other geographical areas quoted here. The mean number of ciliates collected at the four depths was 671 individuals per litre. The mean for the surface samples was 135 per litre; there were 148 at 10 m, 268 at 25 m (the maximum), and 120 at 50 m. The seasonal occurrence of ciliates (Fig. 8) shows a late maximum in October and a lower peak in August. When crops of ciliates at Igloolik are compared with populations of single samples from the Norwegian Sea, where 14,200 were found per litre (Halldal, 1953) or with a Labrador Sea sample of 17,200 *Laboea conica* per litre (Holmes, 1956), the low productive level at Igloolik is obvious. Ciliates appear to be effective grazers. Little is known of their individual grazing capacity. They ingest flagellates, diatoms and copepod eggs.



## GRAZING

Grazing by herbivorous zooplankton upon phytoplankton is recognized as a significant factor in reducing the size of populations (Steemann-Nielsen, 1935; Braarud, 1935; Fleming, 1939; Riley, 1946, 1953; Riley and Bumpus, 1946; Cushing, 1955). Comparisons of the phytoplankton and zooplankton cycles at Igloolik and Scoresby Sound, Greenland, show that similar general features occur in both areas. It is difficult to make closer estimates since different methods were used in both areas. Data from Igloolik show that the spring increase in phytoplankton and zooplankton occurred almost simultaneously. The increase in phytoplankton and in the number of copepod nauplii (the major herbivores) in April is evident. The commonly described gap between phytoplankton and zooplankton summer maxima does not appear in the Igloolik cycle where the interval, if real at all, does not exceed more than a few days.

The rapid decline of diatoms at Igloolik in the autumn is related to the end of the summer season and increased grazing of great populations of zooplankton. The simplified scheme of grazing in seas usually shows phytoplankton as the main biomass producers and all herbivorous animals as feeders. It is true, but we find that the ciliates and the holozoic flagellates must be also of importance as grazers, and they are not included as a grazing link. The holozoic Gymnodinioideae, which are able to ingest diatoms, Coccolithineae or ciliates (Fig. 7, 14), are significant grazers since they can appear in larger populations per litre than zooplankters. The complexity of grazing has many aspects (Cushing, 1955) which preferably should be studied in the field. In the arctic it is of particular interest to estimate the under-ice film of diatoms found in spring and summer, and probably in winter.

Preliminary investigations were made by the author in order to estimate the intensity of grazing during various seasons as shown by the number of fecal pellets produced by different plankton animals from preserved and unpreserved samples. For such purpose a larger volume of sea water than was used here has to be examined. As the largest number of pellets occurred in August and September, this is the season of most intensive grazing in the arctic. Some of the pellets contained single *Chaetoceros socialis* frustules, while others consisted of empty thecas of *Peridinium* and *Goniaulax*. Both were apparently selectively grazed. The unknown animal whose pellets contained dinoflagellates which were absent in net and quantitative samples, shows great efficiency as a grazer in finding such rare food. The fecal pellets of the omnivorous grazers contained frustules of many diatom species. The number of feeders and size of standing crop of phytoplankton fluctuates according to the seasons, hydrographic conditions, and biodynamics of herbivores. Estimates from Scoresby Sound (Digby, 1953), compared with Igloolik data (Grainger, 1959), show that the size of populations of zooplankton in both areas was similar. The quantitative estimates of the phytoplankton crop show that a hungry season for herbivorous animals began in mid-September and ended in mid-May. This was a period of 8 months, during which fats previously deposited in animal tissues were utilized. It seems possible, however, that many animals may feed on microflora and microfauna of the benthos or turn to cannibalism.

## MAIN FEATURES OF THE IGLOOLIK PHYTOPLANKTON

The character of the phytoplankton and its hydrographical background in the Igloolik area cannot be dealt with in isolation, since similar features probably exist within a wide region of coastal Foxe Basin as well as in higher arctic latitudes. The main limiting factor for the marine life at Igloolik is the long duration of fast-ice, which by freezing and melting affects salinity, light penetration and temperature. Shallowness and fast-ice conditions appear to increase the arctic oligotrophy within the wide area where the hydrographical uniformity is caused by a limited water mass exchange with other localities. The phytoplankton populations of the Igloolik station appear to be largely autochthonous because the area concerned is away from the main course of the Fury and Hecla current and mixing is limited. The inflow of this current is directed by the Bouverie Islands towards the southwest side of northernmost Foxe Basin, while its smaller ramification goes through Richards Bay which is very shallow and is covered in some places by grounded ice. This factor minimizes intrusion of Fury and Hecla waters and foreign phytoplankton populations. Allochthonous phytoplankton populations may probably enter within the wide area between Igloolik Island and the Melville Peninsula coast during tidal changes and southeasterly wind activity. The pelagic element is particularly rare, and represented by *Chaetoceros atlanticus*, *Ch. decipiens*, *Ch. lorenzianus* and *Ch. subsecundus*. It seems not to be native to Igloolik, having presumably drifted into the area from the south. The scarcity of warm-water forms like Coccolithineae and dinoflagellates, and the preponderance of arctic and cosmopolitan diatoms, represented by 74 species, indicates ecological features which can be found elsewhere in northern waters. Benthic diatoms were rare, represented by 8 cosmopolitan species, which were noticed more frequently and in larger populations in the Hudson Bay phytoplankton than at Igloolik. The mud-covered bottom of Igloolik does not favour the development of microflora and algae, since only a single rhodophycean, *Phyllophora brodiei*, was taken with the Van Veen bottom sampler. Adjacent Turton Bay appears to be richer and more favourable for both zoobenthos and phytobenthos.

## DURATION AND SUCCESSION OF PLANKTON SPECIES

The length of time during which some plankton organisms remain in the floating planktonic phase depends upon the completion of their life cycle. Because the optimum conditions for growth in the arctic are restricted to a few months, the majority of planktonic forms have to complete their cycles in a short period of time. The arctic diatoms soon disappear from the plankton after cyst formation (Gran, 1904). This was observed also at Igloolik, but it was applicable mainly to the brackish neritic diatoms, including melting-ice species.



The pelagic forms like *Chaetoceros atlanticus*, *Ch. borealis* and *Ch. teres* persisted for a much longer period of time in the plankton than those which formed resting spores. The frequency of occurrence of pelagic forms was lower in the sedimentation chambers than in the net samples, in which they appeared continuously even in winter when vertical dispersal affected the number of species in net and sedimentation chambers.

Plankton elements are placed in groups according to the length of time which they spend in suspension in the water (Fig. 6, 20). Those which remained in plankton the entire vegetative season include: *Achnantes taeniata*, *Fragillaria cylindrus*, *Nitzschia seriata* and *Thalassiosira nordenskjöldi*. The others showed a gradually shorter duration in plankton, and include: *Nitzschia closterium*, *Denotula confervacea*, *Nitzschia* sp., *N. grani*, *Chaetoceros decipiens*, *Nitzschia pungens*, *Melosira islandica*, *Lauderia glacialis*, *Eucampia zodiacus*, *Thalassiosira rotula*, *Th. gravida*, *Chaetoceros compressus*, *Ch. affinis*, *Ch. constrictus* and *Navicula pelagica*. The group of shortest duration is represented by *Chaetoceros septentrionalis*, *Ch. debilis* and *Bacteriosira fragilis* (Fig. 21). Diatoms,

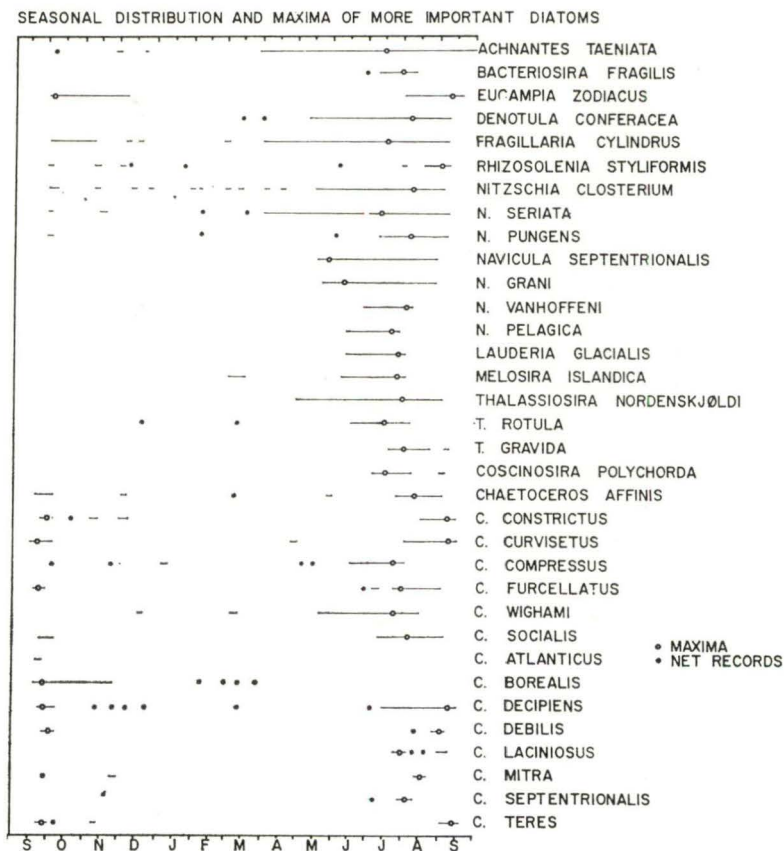


FIG. 20. Seasonal distribution and maxima of the more important diatoms.



as compared with dinoflagellates, flagellates and ciliates, show a distinct dominance.

Seasonal succession in plankton has probably many causes; noticeable in spring are diatoms, and in summer, dinoflagellates. Early spring diatoms were determined as arctic and the latter as boreal. The trend of succession depends upon composition of the initial stock at any time, and it may vary from year to year (Braarud *et al.*, 1953). Apart from the environmental factors, some phytoplankton species can inhibit or stimulate growth of other species by diffusion of metabolites into the water (Rice, 1954). It is thought that diffusion of metabolites may affect not only the size but also the succession of some species. How such biochemical warfare is carried out among different species in the seas is completely obscure. Conover (1956) studied successions of Long Island Sound.

Margalef's (1957) data from Rio Vigo (Mediterranean) show 3 or 4 complete successions of regular pattern, hardly distorted by local irregularities. Winds and tides have hardly any effect upon a pattern of succession. The author is convinced that an arctic type of succession is repeated from year to year, but it could be distorted by turbulence or other factors, as particularly observed at Point Barrow, Alaska (author's unpublished data). The idea of biogeographical regionization and the use of succession for the ecological analysis of plankton and productivity of the arctic (Bogorov, 1958) appears to be useful in its application.

Observations made in different arctic latitudes (Braarud, 1935; Steemann-Nielsen, 1935; Shirshov, 1938; Bogorov, 1938, 1958, 1958a), when contrasted with the Igloolik data, indicate many differences concerning quantitative features of primary production, taxonomic composition and species successions. Davidson's (1931) observations in Hudson Bay on early development of phytoplankton are not sufficient to show annual successions.

Phytoplankton succession in Denmark Strait, begun with flagellates, was continued by *Achnantes-Fragillaria* and *Thalassiosira-Chaetoceros* vegetation, poor populations of *Denotula*, and dinoflagellates (Braarud, 1935). The pennate diatoms appeared in early summer while *Chaetoceros* with dinoflagellates occurred later in the season in the East Greenland current (Steemann-Nielsen, 1935). A succession of *Thalassiosira gravida*, *Fragillaria oceanica*, *Achnantes taeniata* and *Denotula confervacea*, observed by Shirshov (1937; after Bogorov, 1958a) in the arctic seas, was classed as a group of spring species, which were followed by the late-spring species *Chaetoceros furcellatus* and the summer species *Ch. debilis*, *Ch. compressus*, *Ch. diadema*, *Ch. mitra* and *Ch. teres*. Dinoflagellates increased in number as the season advanced. An early spring succession in East Greenland (Digby, 1953) began with *Nitzschia frigida*, *Amphiprora hyperborea*, *Navicula septentrionalis*, *N. grani*, *N. pelagica*, *Fragillaria oceanica*, *Thalassiosira norden-skjöldi* and *Th. gravida*. Because different methods were applied by investigators, the above considerable differences in results have to be expected. Except for flagellates, similarities in the successions were observed between Denmark Strait and Igloolik. All other references indicate in general similar sequences of spring Pennatae, summer Centriceae and dinoflagellates. In the main outlines, succession of the taxonomic groups appears to be repeated within a similar general

pattern established by ecological niches and dynamics of individual species of phytoplankton.

In September 1955 and 1956, Centriceae were represented by 13 species, which obviously dominated the Pennatae. A similar situation occurred in October. The unbalance between Centriceae and Pennatae began in November and continued throughout the winter until the end of April. Initial spring populations under the ice were observed in the late days of April and they started with *Achnantes-Fragillaria* increasing in numbers, associated with initial populations of *Denotula*, *Navicula*, *Nitzschia* and a small number of *Thalassiosira*. Though *Achnantes-Fragillaria* still dominated in early June, the secondary *Denotula-Navicula* grouping became more significant. The decline of "shade" Pennatae took place after July 15, and marked the climax of *Achnantes*. The Centriceae rapidly increased in number of species and size of population. *Chaetoceros* species became most significant until the climax of the Centriceae was reached on August 20. The ribbon-shaped Pennatae constituted a main spring succession, extending into early summer, and became gradually replaced by the summer phase of diatoms, represented by the dominant Centriceae, and late summer dinoflagellates. The comparisons point to the phytoplankton of the waters west of Greenland showing close similarities to Igloolik phytoplankton in the seasonal succession of species (Grøntved and Seidenfaden, 1938). When the ice breaks at Igloolik, a rich plankton, chiefly of *Fragillaria*, is developed. It is replaced later by *Thalassiosira*, and later still by a number of *Chaetoceros* species and the Peridineae. The central Labrador Sea, which is characterized by oceanic species, has a succession distinct from that of Disko Bay, Greenland.

The annual phytoplankton cycle at Igloolik is of the "bimodal" type (Fig. 3). The spring "shade" pennate diatoms exhibited their climax sooner than the summer Centriceae. There was a gap of 28 days which separated the climaxes of Pennatae and Centriceae (Fig. 3). It is sufficient however to classify the annual cycle at Igloolik as the "bimodal" type, in contrast to the "unimodal" type described as typical for the high arctic by Bogorov (1958). Since the net crop, which is recognized as insufficient by the majority of authors, was mainly used for establishing the high arctic type of phytoplankton cycle, the determination of successions of the arctic phytoplankton still remains an open problem in different latitudes. The final solution could be achieved by the use of sedimentation methods and nets allowing quantitative analysis of common and rare species.

#### BIOLOGICAL SEASONS IN PHYTOPLANKTON OF ARCTIC SEAS

The determination of the biological seasons in the sea has to be based upon principles other than those applied to the higher plants rooted in soil. The seasonal variation in qualitative composition and abundance of organisms permits us to distinguish biological seasons (Bogorov, 1938). Arctic biological winter is characterized by a minimum number of organisms, especially phytoplankton species. Biological spring starts with a slow increase of phytoplankton beneath



the ice. The short biological summer is characterized by an abrupt decrease of autotrophic populations at the end of the season.

Halldal (1953) distinguishes in the Norwegian Sea: winter, from December to March; spring, lasting until June; summer, lasting until September; autumn, from September until October or the beginning of November.

The scheme of biological seasons in the far north made by Bogorov (1958) has been supplemented by the introduction of data from Scoresby Sound, East Greenland (from Digby, 1953) and recent observations from Igloolik (Fig. 21).

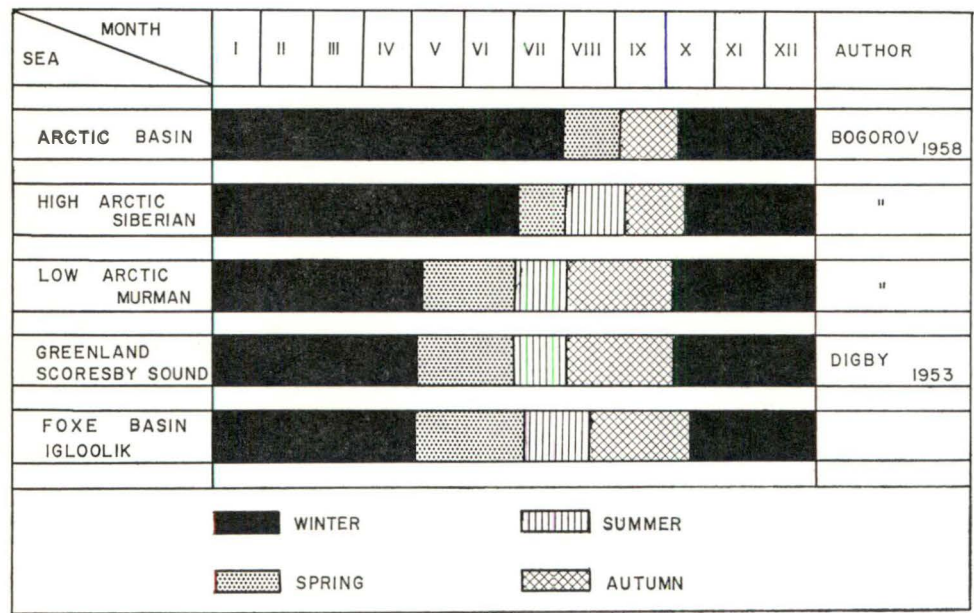


FIG. 21. Duration of the arctic phytoplankton seasons.

The high arctic seas (polar basin and Siberian polar seas) are characterized by a single maximum of phytoplankton. This biological spring corresponds to the calendar months of July and August. In the polar basin the maximum of phytoplankton occurs in August, and in the Siberian Seas in the latter half of July (Shirshov, 1938; after Bogorov, 1958a). The western Barents Sea has two maxima; the biological spring corresponds to the month of May, the biological autumn to August. The more severe winter extends up to 10 months in the arctic basin. Biological spring in the Murman area starts approximately at the same time as in Scoresby Sound or at Igloolik. The duration of biological seasons in the arctic seas (Fig. 21) shows little difference among the regions considered. The beginning of phytoplankton revival after winter has to be related to local ice conditions which vary greatly from year to year from area to area.



Sverdrup (1954; from Marshall, 1958) suggests that phytoplankton production starts in April on the Bear Island Bank and in June in the deeper Atlantic water, and second that as the ice recedes to the northeast over the Central Bank, an outburst of phytoplankton takes place in its wake. In the shallow waters of Igloolik and in Scoresby Sound, Greenland, the spring increase of phytoplankton starts at approximately the same time. It was Ross (1954) who observed that arctic diatoms start to grow even earlier, in March. The under-ice film of pennate diatoms taken in March 1957 in the Gulf of St. Lawrence, by the Atlantic Oceanographic Group, consisted of 32 species that are considered as arctic shade plankters (unpublished data). It is obvious that the plankters had started to grow earlier in the winter darkness. The spring outburst takes place at different times in open and in protected coastal areas (Grøntved and Steemann-Nielsen, 1957). Although the biodynamics of arctic phytoplankton possess their own features, these appear not to be a function of geographical latitudes in the main, as Graham (1941) suggested, but a question of nutrient addition with newly introduced water. We can agree that the intrusion of waters rich in nutrients may invigorate growth of phytoplankton if it takes place during the light optimum required for photosynthesis.

#### SOME REMARKS ON THE CHARACTER OF THE ARCTIC PHYTOPLANKTON

The pioneer works of Gran (1904, 1908, 1912), Cleve (1873, 1896) and others have been concerned mainly with taxonomic problems of phytoplankton, and its distribution in the arctic. The new approach to the biogeographical divisions of phytoplankton has been applied by Braarud *et al.* (1953). The available data of Polunin (1934), Grøntved and Seidenfaden (1938) and Ross (1954) bring many facts to light on the geographical distribution of phytoplankton species.

The arctic biotope is best characterized by the presence of ice and its ice microflora. It is obvious that the arctic ice flora can flourish in subarctic waters, where they can persist for a rather long period of time. No distinction between the arctic and subarctic can be made, as yet, on the basis of phytoplankton distribution.

Data available (unpublished data) indicate that the biogeographical distribution of phytoplankton is not a function of temperature only, but of both temperature and light. It is obvious that a group of diatoms forming a large population under the ice may be considered as a "shade" flora, if it is absent where there is no ice, and therefore typical for the arctic environment. Steemann-Nielsen, from his results of Carbon-14 investigations, concluded that light adaptation of phytoplankton is possible, and Steemann-Nielsen and Hansen (1959) concluded that "none of the many plankton surveys from the arctic has shown any indication of the occurrence of a special 'shade' flora". Large

populations of the flagellated organisms found by Rodhe (1955) beneath the ice of a subarctic lake in Sweden in winter must be considered as a "shade" group. Obviously the ribbon-shaped Pennate diatoms found in April beneath the Igloolik ice were grown under ice impenetrable by light, and must too be classed as a "shade" flora.

It is however possible that there is a considerable light adaptability in arctic diatoms which can flourish in almost any light condition found in the arctic, if nutrients are available. The Centriceae diatoms, most abundant during the open water period, where maximum light is available, may be contrasted with the "shade" Pennatae as a "sun" flora. Possibly the succession of the spring "shade" by the summer "sun" group of diatoms has been induced by different physiological requirements in each group. Diatoms are dominant in the dark arctic environment, because they can tolerate long periods of darkness at low temperature.

The size of the phytoplankton populations and their taxonomic composition is a good ecological indicator for classification of waters in different latitudes. The total list of phytoplankters from Igloolik includes 121, in the slightly warmer Hudson Bay it is 235 (unpublished data). In the region of Point Barrow, Alaska, the number of species was still higher, 286 (unpublished data). The number of dinoflagellates reflects particularly well what is said above. They increased from 32 species found in Igloolik to 91 found in Hudson Bay (unpublished data). The increase of flagellated groups from north to south is related to the weakening grip of severe arctic conditions, to the increase in temperature and in solar radiation found towards the south. Not nutrients but temperature mainly favours developments of dinoflagellates (Gran, 1912; Graham, 1941; Wood, 1954). Preponderance of flagellates over diatoms in the southern latitudes is exemplified well by the plankton list of Rampi (1945) from San Remo, Monaco, where 350 species occurred, 245 of them dinoflagellates. I believe therefore, that the character of the ecological conditions of ocean waters could also be determined from the biological balance shown by the quantitative relationship of diatoms and flagellated organisms.

#### SUMMARY

1. A collection station was situated at  $69^{\circ} 20.5' N$ ,  $81^{\circ} 43.5' W$  on the coastal shelf of the northern part of Foxe Basin. This area was covered for about 9 months by fast ice, a limiting factor for phytoplankton life.
2. Sea water samples for phytoplankton, studied by the sedimentation method, were collected about twice a month from September 1955 to September 1956, at the surface, 10, 25 and 50 metres depth. Vertical net hauls for taxonomic examination were also taken. Interpretation of temperature, salinity, oxygen and phosphates was also made.
3. The predominance of low temperatures (within a range of  $3^{\circ}C$ ), and ice and light conditions influence the taxonomic composition of the phytoplankton



and the size of its populations. The absence of various taxonomic elements and some uniformity of general phytoplankton features seems to be related also to a small degree of communication by currents with other adjacent areas.

4. The vertical occurrence of phytoplankton at Igloolik was greatly differentiated in the course of the season. Phytoplankton populations at the surface from April 26 to May 19 were nearly equal to those found at 10 m. They became slightly higher in June, and were markedly lower in July, then increased when the effect of melting ice and low salinities had diminished.
5. Although maximum phytoplankton production was at 10 m, the trophogenic layer in the ice-melting period presumably started from about 2 metres depth and extended down to about 15 m. Below 10 m phytoplankton populations diminished with increasing depth.
6. Four biological seasons were distinguished at Igloolik. *Spring* started in April, with an *Achnantes-Fragillaria* bloom, and lasted until July. It was marked by maxima of the pennate diatoms, succeeded in early summer by the Centriceae. The climax of the Pennatae appeared on July 15, that of the Centriceae on August 11. The latter coincided with maxima of dinoflagellates and Coccolithineae. *Summer* began at approximately the end of July, with increasing populations of Centriceae. September and October represented *autumn*, marked by cessation of metabolic activities. The biological *winter* lasted from November until April.
7. Since the majority of the numerous brackish-neritic diatoms were metabolically passive because of cyst formation, they were often associated with low oxygen content of the water.
8. A taxonomic list of species is given. Three new species, *Gymnodinium intercalaris*, *Gyrodinium arcticum*, and *Pontosphaera ditrematolitha* are described. For the first time two rare and little known species, *Cenchridium spherula* and *C. globosum*, were noticed in the plankton of arctic waters. Nine Coccolithineae, two Choanoflagellates and a few little known flagellates were also studied in detail.
9. The quantitative dynamics of phytoplankton populations and their vertical occurrence were contrasted with those of other geographical latitudes.
10. The general taxonomic composition of the Igloolik phytoplankton seems to be greatly influenced by the severe ice conditions associated with poor light supply, hydrographical uniformity and shallowness of the area.
11. The holozoic dinoflagellates were dominant in the Igloolik samples, while brown autotrophic species formed only small populations. The strong-membrane Peridineae and Dinophysideae were represented also by colourless holozoic forms which produced still smaller populations, presumably resulting from light and temperature slowing down their metabolic processes.



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