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TITLE

The hydrography and zooplankton
of Ogac Lake, a landlocked fiord
on Baffin Island

AUTHORSHIP

I. A. McLaren

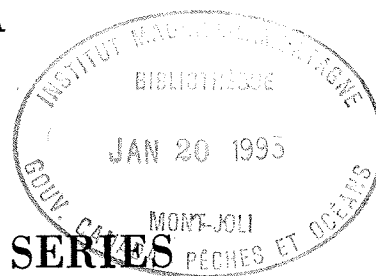
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N O T E

This is the reproduction of a thesis
submitted in May, 1961, in partial fulfilment
of the requirements for the degree of Doctor
of Philosophy in Zoology at Yale University.

ABSTRACT

Ogac Lake is the landlocked head of an inlet on Baffin Island at 62°52'N and 67°21'W, with a relict population of Atlantic cod, Gadus morhua. The lake has three morphometrically and hydrographically distinct basins separated by sills. The lake is salt and strongly meromictic. It receives predictable amounts of tidal water, varying in salinity and temperature, during highest tides in summer. These more than replenished salt lost by freshening in 1957. The lake is much warmer than the sea and its annual heat budget exceeds that of a comparable freshwater lake. Radiation is responsible for almost all heating down to about 30 m. The penetration of cold tidal water of intermediate density causes striking and stable temperature minima. Oxygen is absent below 25 m. in the lower, 30 m. in the middle and 32.5 m. in the upper basin, the differences being due to basin morphometry. Seasonal changes in oxygen are correlated with plankton cycles, and distinct minima at 10-12 m. in two basins are traced to large numbers of copepods at those depths. The holoplanktonic zooplankton consists of a depauperated selection of common marine forms, with no brackish dominants. By far the most common residents are the copepods Pseudocalanus minutus and Oithona similis, the medusa Aglantha digitale and the chaetognath Sagitta elegans. Allochthonous plankton is ill-adapted to the lake and eliminated soon after being brought in by the tides. The composition and abundance of phytoplankton differed markedly in the three basins, due to interactions of nutrients, basin morphometry and the tides. Reproduction and growth of P. minutus were dependent on the diatom Chaetoceros, and the production cycles (annual) and reproductive cycles (either annual or shorter) differed accordingly in the three basins. Two broods of some 30 eggs each were spawned by each female. Ontogenetic descent began at copepodite III and was strongly affected by temperature. Size of copepodites was governed by food in the lake. Size and egg number are known to be increased by low temperature, and it is suggested that vertical migration to cool depths may be a device for increasing fecundity. The growth and annual reproductive cycle of O. similis were unrelated to Chaetoceros; adults may have fed partly on detritus, but the young seemed dependent on nanoplanktonic diatoms. All older stages tended to live in the warm surface waters. Adult S. elegans could feed on large copepods, but their young were dependent on nauplii. The cycles therefore differed in the basins, but were essentially annual with a small second generation. Adults were half as large as arctic marine S. elegans, in apparent response to higher temperatures. Old S. elegans lived deeper in the second basin than the bulk of its prey, and this seemed to cause great overwinter mortality in middle and upper basins. Survival was virtually complete in the shallow lower basin, where S. elegans was "forced" to live amidst prey. The tiniest young of A. digitale

may have eaten phytoplankton but further growth depended on young copepods. There was an alternation of a large summer generation with a small overwintering one in middle and upper basins, but large animals seemed competitively excluded from the lower basin by S. elegans. The small size of adult A. digitale in the lake and marked vertical differences in gonad development are ecophenotypic effects of temperature. From circumstances in the lake it is argued that evolutionary opportunities may exist for the development of a specialized brackish zooplankton, but that slow growth and the compressed season of primary production, both of which seem unavoidable results of physical conditions, severely limit the number of niches in arctic seas.

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ACKNOWLEDGEMENTS

Many individuals and organizations aided in this study. The Fisheries Research Board of Canada supported the field work and my educational leave at Yale University. Among colleagues at the Arctic Unit of the Fisheries Research Board I am especially grateful to the Director, Dr. H. D. Fisher, who cared for so many of the expedition's needs when it was in the field, Dr. E. H. Grainger, whose wide knowledge of arctic marine faunas was often helpful to me, and Mr. A. S. Bursa, who gave valuable advice on the phytoplankton. The Misses B. Barry and B. Cleaver gave technical assistance.

The enthusiasm of Professor M. J. Dunbar of McGill University on discovering Ogac Lake, on my first trip north, and his continuing interest were in large measure responsible for my return in 1957.

Residents of Frobisher Bay, especially our dog-team drivers Simonee and Kalowak, extended every courtesy. Helicopter pilots of the U.S.A.F. provided a welcome link with the "outside" on several occasions during the season.

Captain Pullen, his officers and men of H.M.C.S. "Labrador", not only performed the vital functions of resupplying us in July and evacuating us in October, but did so with great efficiency and good humor.

At Yale University, my Director of Studies, Professor G. E. Hutchinson, and members of my Committee, Professors E. S. Deevey and G. A. Riley have given much knowledge and understanding. Dr. G. B. Deevey made her knowledge of the zooplankton

freely available to me.

Lastly I am most of all indebted to my wife, Bernice, who was my sole companion and assistant at Ogac Lake, and who helped make that season uniquely cherished among several in the north. Her continuing assistance has extended to the typing of this thesis.

INTRODUCTION

That large codfish existed in a lake at the head of an inlet of Frobisher Bay had long been known to Eskimos and rumoured among white residents and visitors to southern Baffin Island. There is no record of a visit until 1927, when two specimens of codfish were collected from the lake by the Rawson-MacMillan Expedition of 1927-28 and deposited in the Field Museum, Chicago (Museum Nos. 30974, 30975). The museum labels imply that the fish were taken from a lake at the head of "Griffin Bay", but no mention of them is made in any scientific report. In 1937, C. H. Ney established a geodetic bench mark on the shore of the inlet which now bears his name, Ney Harbour. Codfish were taken from a lake at the head of this inlet, and the lake appears in later maps as "Ogac Lake", ogak being the Eskimo word for codfish. The position of this lake at 62°52'N and 67°21'W is shown on Figure 1. "Griffin Bay" is applied to a different inlet on contemporary maps, and it appears certain that Ogac Lake with its codfish is unique along this coast.

In 1951 M/V "Calanus" of the Fisheries Research Board of Canada carried out much of its work in the Frobisher Bay area, under the leadership of M. J. Dunbar. On August 4 a party from the "Calanus" took the ship's dinghy over the threshold into the lake and spent a few hours studying what turned out to be a most unusual ecological situation. A brief account of that short survey has been published (Canada, 1952). The lake was found to be fresh at the surface, but quite saline (up to 27‰) at depth. It was much warmer than the

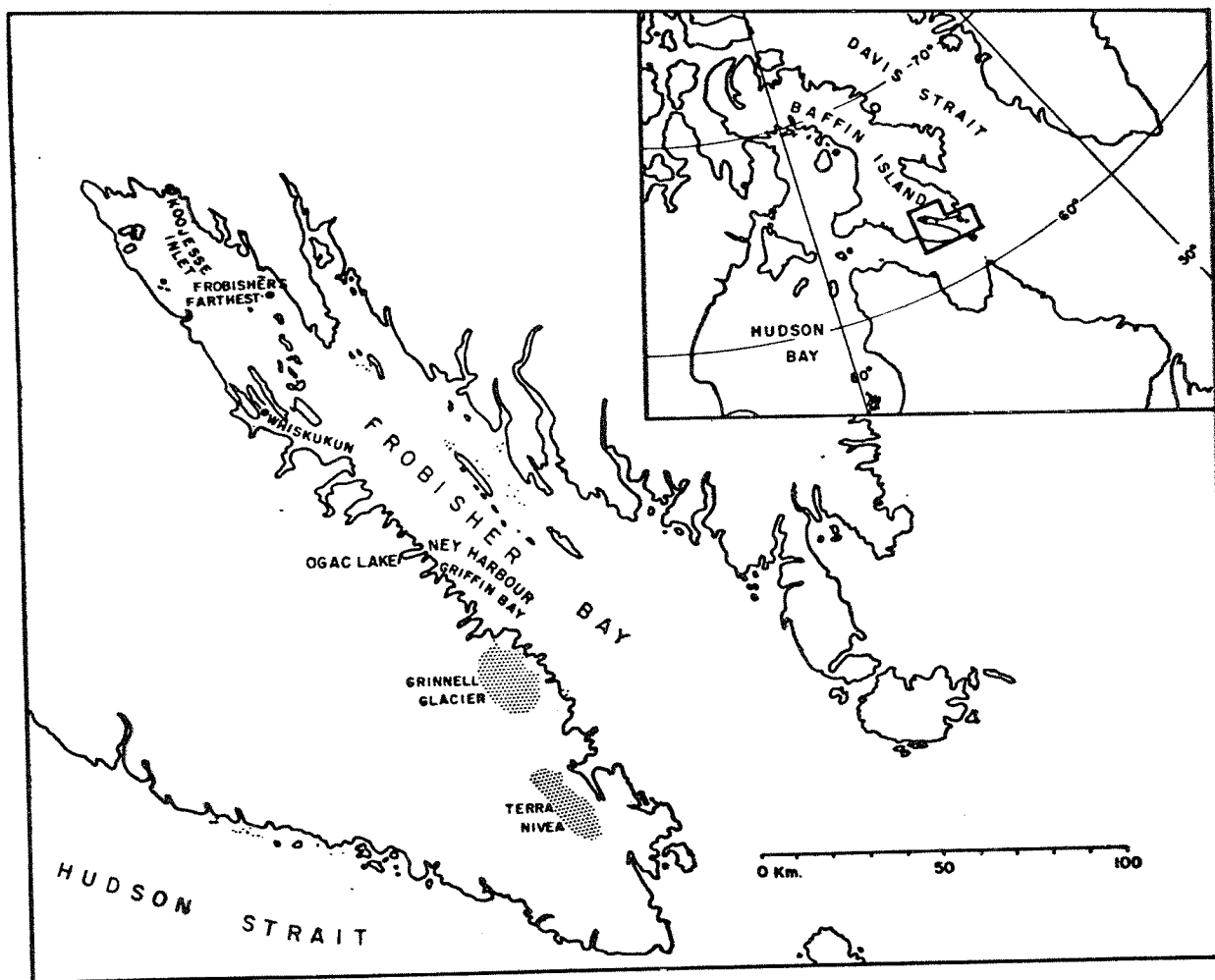


Figure 1. Map showing location of Ogac Lake.

sea and devoid of oxygen in its deeper waters. It was obvious from the setting of the lake that the highest tides could flow in, replenishing its salinity although such an inflow was not witnessed. A number of codfish were taken and confirmed as Gadus morhua L., the Atlantic cod. The fish averaged much larger (one of 128 cm.) than their nearest marine counterparts, which migrate north to the mouth of Hudson Strait. No cod have been taken in Frobisher Bay, and their presence is hydrographically unlikely. From the circumstances it seemed certain that the fish were relict, presumably from some warmer postglacial time.

Further study of this remarkable lake and its codfish was obviously called for, and an expedition was arranged by M. J. Dunbar under the auspices of the Arctic Institute of North America to visit the lake in 1952. A. D. Dawson and R. S. McCall were taken there aboard M/V "Calanus" on July 16 and picked up on August 22. They collected considerable material on the cod, plankton and benthos of the lake, made regular hydrographic stations, and were fortunate enough to witness the entry of the highest tides of their month's stay. An examination of the planktonic and benthonic material of 1952, some of which has appeared in the systematic and distributional accounts of the "Calanus" collections, revealed that it consisted of a rather depauperated selection of marine forms common outside. It was clear that the greatest interest of the lake was not faunistic, but ecological, and that a much more extensive study was desirable, preferably from the

beginning of the biological season before the breakup of the ice.

Having seen the lake briefly in 1951 and 1952, the author maintained a considerable enthusiasm for a more intensive study, but an expedition was not possible until 1957. On June 1 of that year the author and his wife were brought by Eskimos to the lake after a three-day trip by dog team from the airport at Koojesse Inlet near the head of Frobisher Bay, 120 km. from Ogac Lake. They were picked up by ship and returned to the airport on October 4, after four full months at the lake.

Clearly there were limitations on the activities of an expedition as small and isolated as the present one. All the equipment necessary for living and working in the period before the shipping season had to be taken in on two dog sledges. Immediately after breakup, only a small rubber boat was available to sample from, but important needs, including a powered canoe, were brought by ship on July 23. The season up to early August was punctuated by occasional visits by military helicopters, but thereafter no outside contacts were made. Breakages and shortages were sometimes hampering, and improvisation necessary. In general the program as planned was more or less carried out, but inevitably problems suggested themselves in the field which were beyond the scope of the available materials and equipment.

The material presented in this thesis is only part of that collected in 1957. The hydrographic and plankton

cycles were followed by regular sampling in the lake and in the sea outside, the benthos was collected quantitatively and qualitatively, and much time was spent on the codfish. Of the several parts of the study, the hydrography and zooplankton biology appeared to have some coherence, and were accordingly chosen for presentation here.

HYDROGRAPHY

General Hydrographic Character of Ogac Lake

Ogac Lake is a member of a class of waters which Strøm (1936) has studied extensively in Norway. Occurring as they do in lands rebounding from glaciation, a whole sequence of types can be found, from somewhat badly ventilated fiords to lakes well above sea level which contain trapped sea water in their depths (Strøm, 1961).

The south coast of Frobisher Bay, which still has two small ice caps (see Fig. 1) some 60 km. to the southeast of Ogac Lake, is almost certainly still rising, perhaps quite rapidly. Mercer (1956) found universal strand lines along this coast at about 20 m. A. T., but was convinced of the presence of much higher ones, up to 435 m. Other parts of the Canadian arctic are thought to be rising at 1-2 m. per century (Sim, 1960). Ogac Lake is poised at a particularly interesting stage in its isolation from the sea, for only the highest spring tides of the open-water season carry sea water into the lake. Many other such semi-isolated waters receive

their sea water irregularly or even catastrophically, but the large amplitude of the tides in Frobisher Bay is responsible for a regular, measurable and predictable amount of inflow during the season.

Since Ogac Lake lies in the drainage of a small river, there is much freshwater influence at its surface. The upper 1-3 m. may be completely fresh at times, but below this the water becomes increasingly saline with depth. Ogac Lake is in fact meromictic, with the many attendant peculiarities of hydrography, and is an example of coastal ectogenic meromixis in the terms of Hutchinson (1957).

Much more field work would be required before anything approaching a complete hydrographic description and analysis of Ogac Lake could be made. Since this body of water must be changing its character rather rapidly, historical studies especially are called for. What follows can be considered as a necessary framework for more particular hydrographic studies, and a background for some of the biological matters discussed in the second part of this study.

Morphometry

It will become abundantly clear in the appropriate sections that the morphometry of Ogac Lake has important effects on its hydrography and plankton biology. A reasonably thorough plane-table survey was made in August from which the bathymetric charts (Figs. 2, 3) are drawn up. The shoreline detail is drawn from an enlarged, vertical air photo.



Figure 2. Bathymetric chart of Ogac Lake. Depth in metres.

The lake has three distinct basins, which afforded interesting hydrological and biological comparisons. The lower and middle basins are separated by a sill with a minimum free passage of about 7 m., while the threshold depth between the middle and upper basin is less reliably estimated at about 12 m. (see Fig. 3).

The whole lake has an area of about 1,481,000 m.² (148 ha., 60 acres) and a volume of some 34,360,000 m.³. Several morphometric parameters are listed separately for each basin of the lake in Table I. The development of volume in the upper basin is greater than in the other two. The volume to bottom-area relationship is further clarified in Figure 4, as it has important hydrological consequences.

Tidal Inflow

The tidal cycle. The tides in Frobisher Bay are among the World's largest, with a maximum range of about 12 meters. Ogac Lake receives only the highest tides during the open-water season. It was not possible to keep records of the tides in 1957, owing to the lack of an accurate timepiece and suitable materials for measuring tides of large amplitude. However, tides have been analysed in three localities (shown on Fig. 1) in Frobisher Bay and the results are available as height corrections on the prediction for Diana Bay, Hudson Strait (Canada, 1956 and annually since). The latest estimates have kindly been made available by Mr. N. G. Gray, Dominion Hydrographer, and are listed in Table II. The

Table I. Important morphometric parameters of the three basins of Ogac Lake.

<u>Basin</u>	<u>Surface area</u> m ²	<u>Volume</u> m ³	<u>Mean depth</u> m.	<u>Maximum depth</u> m.	<u>Development of volume</u>
lower	186,900	2,020,000	10.8	28.0	1.15
middle	698,200	15,700,000	22.5	60.5	1.12
upper	596,100	16,630,000	27.9	50.0	1.67

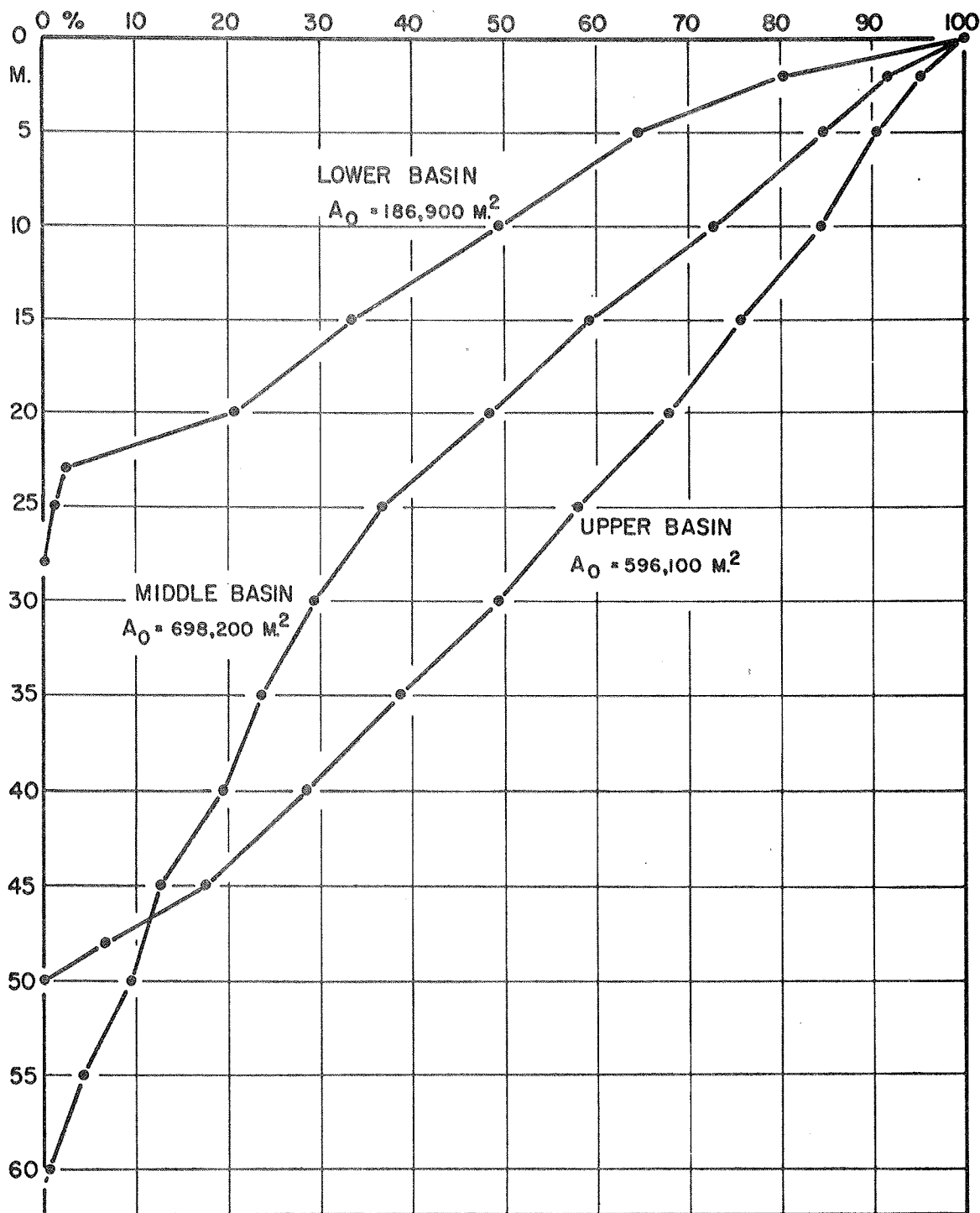


Figure 4. Relationship between area within depth contours and depth in the three basins of Ogac Lake. (as a percentage of surface area, A_0) and depth in the three basins of Ogac Lake.

Table II. Tidal height corrections for three localities in Frobisher Bay, to be applied to Diana Bay predictions (Canada 1956). The higher high-water levels at Diana Bay are 28.0 feet for mean tides and 34.3 feet for large tides. The lower low-water levels are 7.2 and 0.9 feet for mean and large tides respectively.

Locality	Lat.	Long.	Corrections for mean tides		Corrections for large tides		Height of high water above lower low water of mean tides			
			higher high water	lower low water	higher high water	lower low water	mean tides		large tides	
			feet	feet	feet	feet	feet	m.	feet	m.
Whiskukun	63°13'	68°03'	+5.2	+2.5	+6.4	+1.4	23.5	7.17	31	9.46
Frobisher's Farthest	63°29'	68°02'	+2.4	0	+2.8	-0.3	23.2	7.07	29.9	9.12
Koojesse Inlet	63°43'	68°31'	+3.4	+0.5	+4.3	-0.3	23.7	7.23	30.9	9.42

corrections give heights based on local datum, but when reduced to height above mean low water, high tides are shown to be almost equivalent in the three regions of Frobisher Bay. It is safe to suppose that the tide at Ney Harbour, 50 km. down the Bay from Whiskukun, will be of about the same range.

Another correction is needed before the Diana Bay predictions can be used to approximate the tidal cycle at Ney Harbour. The age of the semidiurnal tide differs by about 10 degrees at the two localities, and the spring tide should fall around 10 hours earlier at Ney Harbour (N. G. Gray, in litt.).

Heights of successive high tides at Ney Harbour in 1957 based on the above corrections are plotted in Figure 5. There is only slight inequality between the semidiurnal tides, but the new-moon spring tides may exceed the full moon tides by over 1.5 meters and the equinoctial tides in September may be higher than those of the June solstice by more than a meter. Figure 5 shows excellent accord between the hypothetical tidal cycle and the observed entry of water into Ogac Lake. A few direct measurements of successive high-tide marks in June and September suggest that the tidal range at Ney Harbour is, if anything, a little greater than shown in Figure 5.

Amount of inflow. Tidal water entering Ogac Lake must come in through a narrow gap of some 20 meters. Outside this gap the water may reach more than a meter above lake

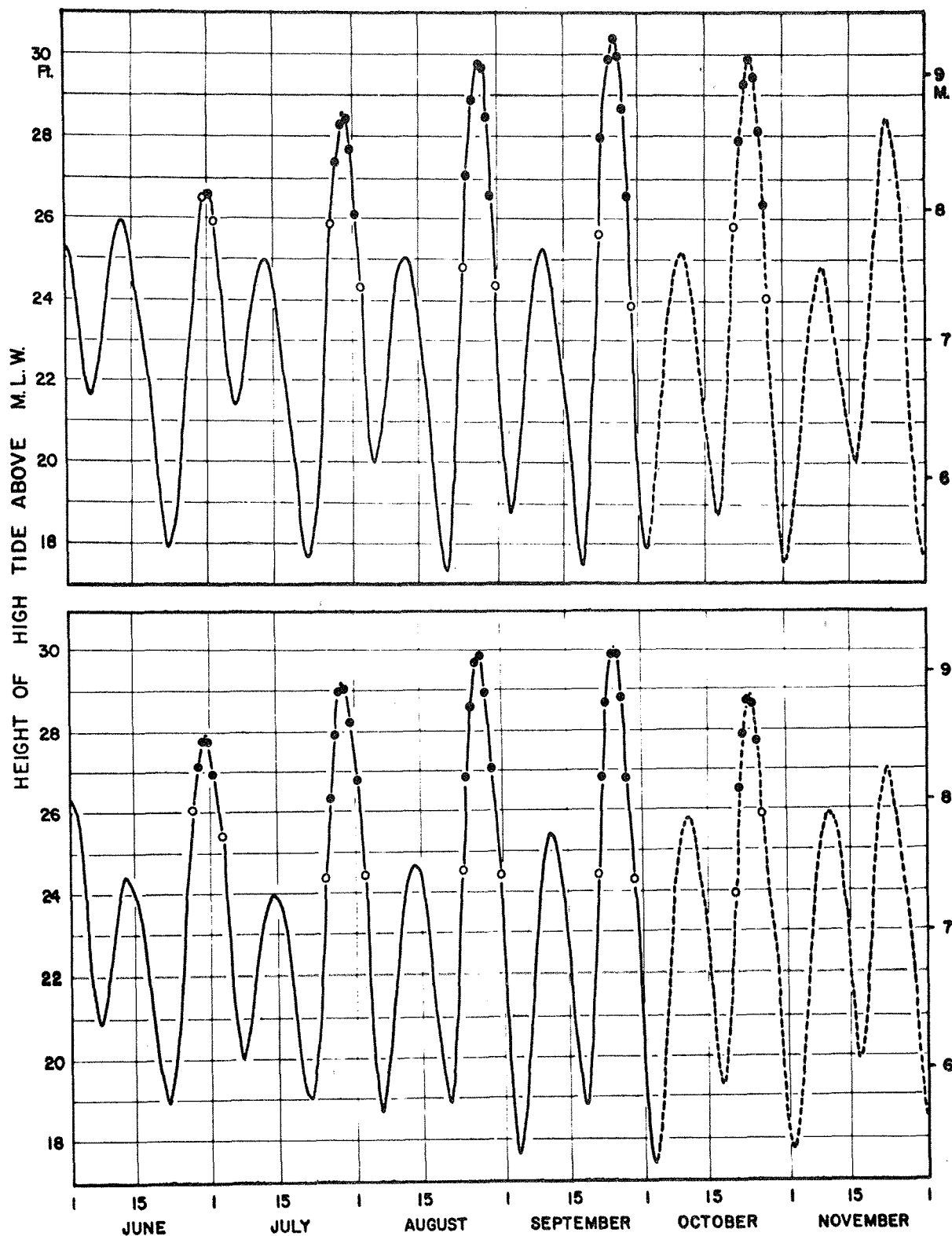


Figure 5. Calculated height of high tides in Ney Harbour between June 1 and December 1, 1957. Each semidiurnal series is plotted separately. Closed circles represent tides which entered the lake, and open circles those which did not. Tides not seen after October 4, but are presumed not to have entered the lake in late November because of ice barriers.

level at the height of the tide. The exact relationship between the predicted or observed height of the tide and the amount of water entering the lake must be empirically determined.

Attempts were made in August and September to measure the amount of inflow directly with a current meter. The high velocity of the stream (up to 2.1 m. sec.^{-1} in its widest section) and the irregular channel bottom were severe problems, and the results are of little value.

It is much simpler to determine the amount of inflow from change of lake level. The increase of lake level immediately after inflow can only derive from two sources--the tidal inflow and freshwater drainage into the lake. After the spring runoff, the freshwater drainage into the lake is very small. In August, 1952, rough estimates of current velocity and depth were made every 5 m. across a 42-m. section of the effluent. These revealed a discharge rate of about $0.3 \text{ m.}^3 \text{ sec.}^{-1}$, or about $1,100 \text{ m.}^3 \text{ hr.}^{-1}$. This would result in a rise of lake level of only about 0.7 mm. per hour if the outlet were blocked, as when the tide is entering. In the summer of 1957 the flow in the deep parts of the outlet was too slow to turn a meter, but indication of the maximum probable contribution of freshwater influents was gained indirectly from observations during the late-September tides. Surface waters of the lake were incompletely discharged in the twelve-and-a-half hours between successive tides, and immediately after the highest tide on September 25, the lake had reached a maximum of about 61 cm. above the datum of three days earlier, before the tidal

series began to enter. Thus it was possible to measure the rate of fall of the lake level from different heights during the tidal series, and the following values were obtained on rainless days:

<u>Av. ht. above datum</u>	<u>Rate of fall</u>
23 cm.	6 mm. hr. ⁻¹
32 cm.	12 mm. hr. ⁻¹
43 cm.	22 mm. hr. ⁻¹

The datum level in late September was very low, and the contribution of fresh water to the lake perhaps even smaller than that recorded in August, 1952 (above). The largest recorded increase in lake level after rains in the summer of 1957 was about 11 cm., although slightly greater increases might well have gone unrecorded. Clearly the maximum contribution of fresh water to the rise of the lake during tides can safely be concluded to be less than 2 or 3 mm. per hour, and since the observed rise of the lake after tidal inflows varied between about 5 and 105 mm. per hour, the contribution of non-tidal water to the rise can be ignored in summer. When the water cut through the ice blocking the outlet on June 17 the lake was about 0.5 m. above the summer level, and dropped by about 0.3 m. on June 19. However, summer levels were not reached until after the late-June tides. It is possible that the contribution of fresh water to the rise of the lake was much greater during this season of melting, perhaps of the order of 10 mm. per hour.

During the 1957 season, due to pressure of other

work, the increase of lake level was observed only on 29 of the 40 occasions when tidal water entered. It is important to know the amount of inflow on occasions when it was not monitored. The relationship between predicted height of the tide and the observed rise of lake level is given in Figure 6. The scatter is quite large, and it is evident that much of the error is due to meteorological distortion of the tides, for there is less deviation on days which were recorded as calm or near calm.

Records were also kept of the duration of tidal inflow, sometimes when the rise of lake level was not measured. It might be expected that the relationship between observed duration and observed increase of lake level would be close, but Figure 7 shows even greater scatter than Figure 6. Presumably, while almost all the water which actually enters the lake does so at the height of tide when there is a large head of water in the fiord outside, the duration of inflow is easily influenced by such factors as lake level. Figure 7 indicates that the duration of inflow was persistently shorter in the late-June tides, even on the one calm occasion. This may be attributed to the very high lake levels then, although it should also be noted from Figure 6 that the freshwater inflow in June does not seem to have greatly abetted the rise of the lake during the tides.

The amount of inflow has been calculated from Figure 6 for 11 tides in August and September when it was not measured; 7 of these were on calm days, suitable for other

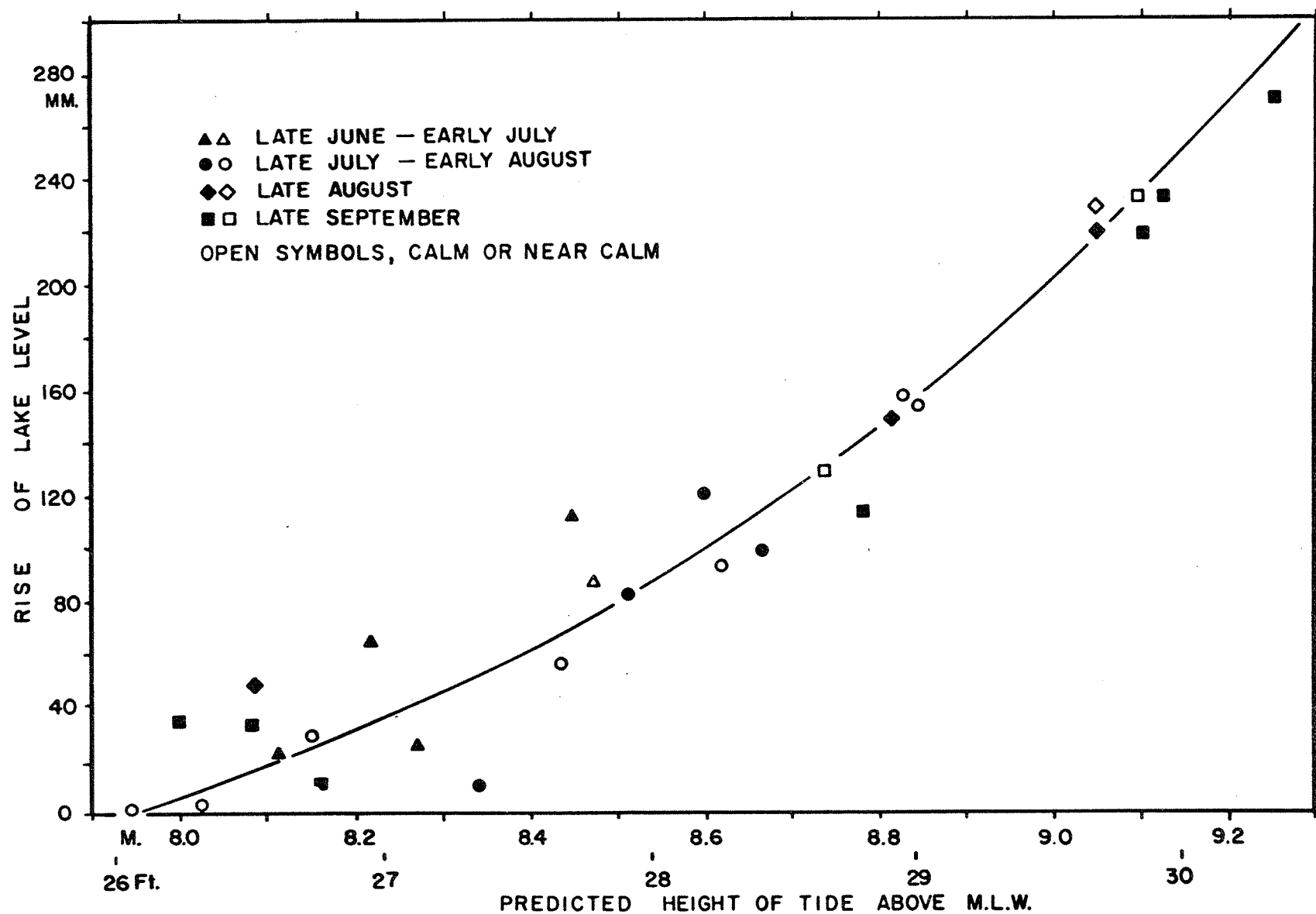


Figure 6. Relationship between predicted height of tide and observed rise of lake level.

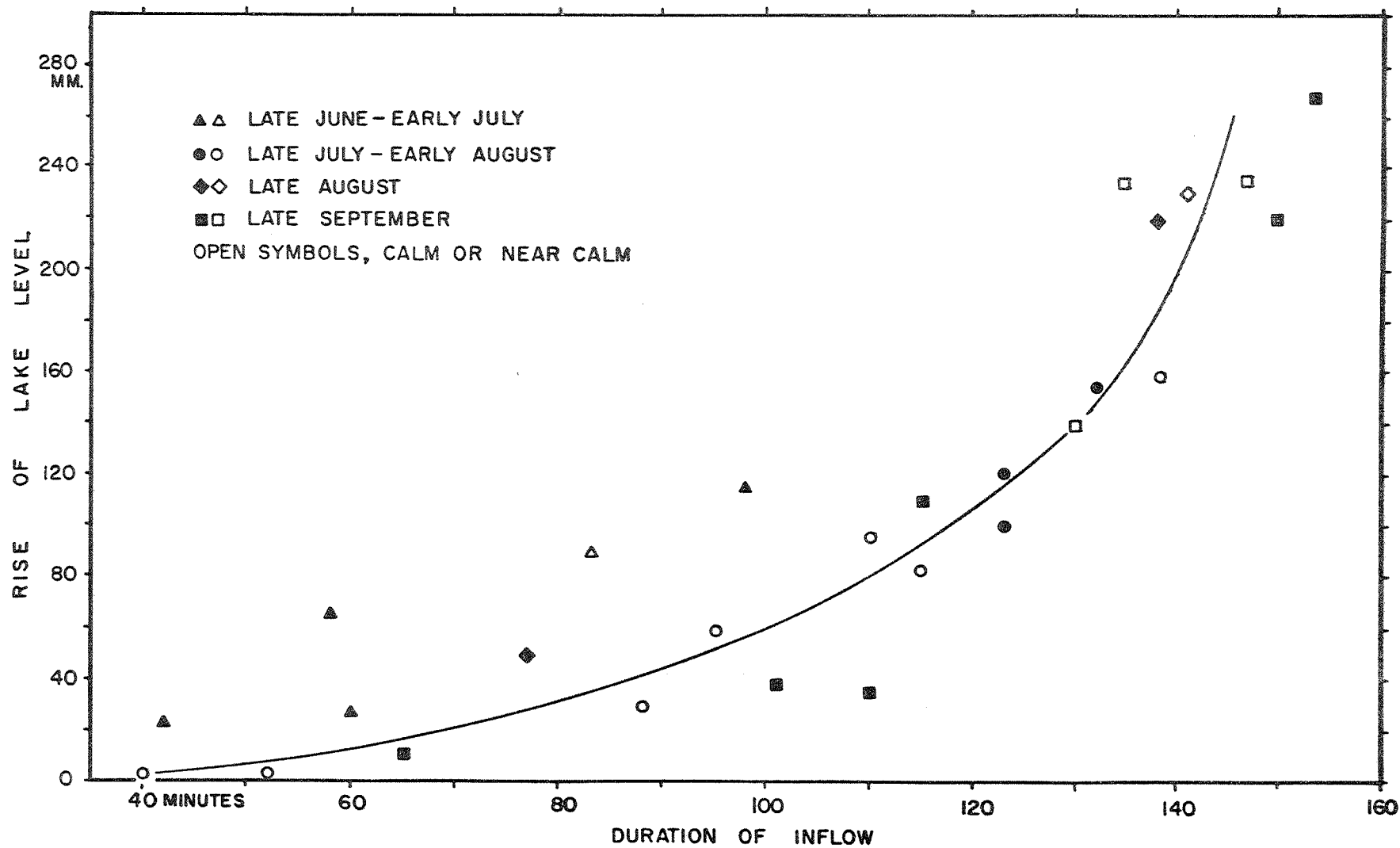


Figure 7. Relationship between observed duration of tidal inflow and observed rise of lake level.

work, and the estimates should be quite reliable. The late-October tidal heights have likewise been converted to amount of inflow, with less assurance of accuracy. The observed or calculated rise of the lake is simply multiplied by the area of the lake ($1,480,000 \text{ m.}^2$) to give volume of inflow. The volumes entering the lake in the open season of 1957 are listed in Table III. About $8,400,000 \text{ m.}^3$, or about one-quarter of the lake's volume, entered in 1957, most of it during the August and September tides.

Temperature and salinity of inflow. The quality of the tidal inflow is just as important as the quantity in maintaining the marine character of Ogac Lake. The seasonal changes of salinity and temperature in the near-surface water of Ney Harbour are listed in Table IV. Not only is there a decrease in salinity and increase of temperature in summer, but the surface waters are much more strongly stratified then. We might expect that the salinity and temperature of the water entering the lake when Ney Harbour is stratified would vary with the height of the tide.

Figure 8 shows that the threshold salinity of a large inflow on June 30 considerably exceeded that of a smaller inflow the next day, while in late September, when surface water was not as markedly stratified, the salinity of a small tide differed little from that of a large one. Since little water actually enters the lake near the beginning or end of an inflow, it seems safe to use average threshold values or even single observations from mid tide as indications of the

Table III. The amounts, salinities and temperatures of tidal water entering Ogac Lake during 1957. Each spring tide series is divided into components where the densities of different tides fell into more than one distinct group (within 7 units of σ_t). Ranges bracketed after means.

Tidal Series	Volume of inflow m^3	Salinity ‰	Temperature °C	Density σ_t
June 28 p.m. to July 1 p.m.	.07 x 10^6 .23 x 10^6 .17 x 10^6	4.4 (4.0 - 4.8) 21.5 (18.5 - 23.8) 30.0	0.82 (0.80 - 8.5) -0.51 (-0.45 to -0.55) -0.60	3.5 (3.1 - 3.8) 17.3 (14.9 - 19.1) 24.1
July 26 p.m. to Aug. 1 p.m.	.07 x 10^6 1.12 x 10^6	14.6 (8.8 - 16.7) 25.1 (24.5 - 25.8)	1.81 (1.78 - 1.83) 1.60 (1.42 - 1.90)	11.7 (7.0 - 13.4) 20.0 (19.6 - 20.7)
Aug. 24 p.m. to Aug. 30 a.m.	2.36 x 10^6	no records	no records	no records
Sept. 22 a.m. to Sept. 28 a.m.	2.57 x 10^6	32.1 (29.8 - 32.9)	-.11 (0.45 to -0.68)	25.8 (23.9 - 26.4)
Oct. 22 a.m. to Oct. 27 p.m.	1.80 x 10^6	no records	no records	no records

Table IV. Temperature and salinity of near-surface waters of Ney Harbour during 1957.

	Depth	June 7	June 23	July 6	July 21	Aug. 7	Aug. 20	Sept. 6	Sept. 25
		$\frac{^{\circ}}{_{\circ\circ}}$	$\frac{^{\circ}}{_{\circ\circ}}$	$\frac{^{\circ}}{_{\circ\circ}}$	$\frac{^{\circ}}{_{\circ\circ}}$	$\frac{^{\circ}}{_{\circ\circ}}$	$\frac{^{\circ}}{_{\circ\circ}}$	$\frac{^{\circ}}{_{\circ\circ}}$	$\frac{^{\circ}}{_{\circ\circ}}$
Salinity	0 m.	ice	ice	1.95	7.5	27.2			
	1 m.	ice	ice						
	2 m.	31.2	5.8	8.9					
	3 m.		33.3						
	4 m.								
	5 m.				30.2	32.1			
Temperature		$^{\circ}\text{C}$	$^{\circ}\text{C}$	$^{\circ}\text{C}$	$^{\circ}\text{C}$	$^{\circ}\text{C}$	$^{\circ}\text{C}$	$^{\circ}\text{C}$	$^{\circ}\text{C}$
	0 m.	ice	ice	0.20	2.20	1.25	2.50	3.18	1.17
	1 m.	ice	ice			0.35	1.78	2.64	0.17
	2 m.	-0.82		0.78		0.17	1.39	2.00	-0.06
	3 m.		-1.08		-0.38	0.08	0.78	1.81	-0.06
	4 m.					0.00	0.39	1.61	-0.06
	5 m.				-0.37	-0.30	0.10	1.33	-0.07

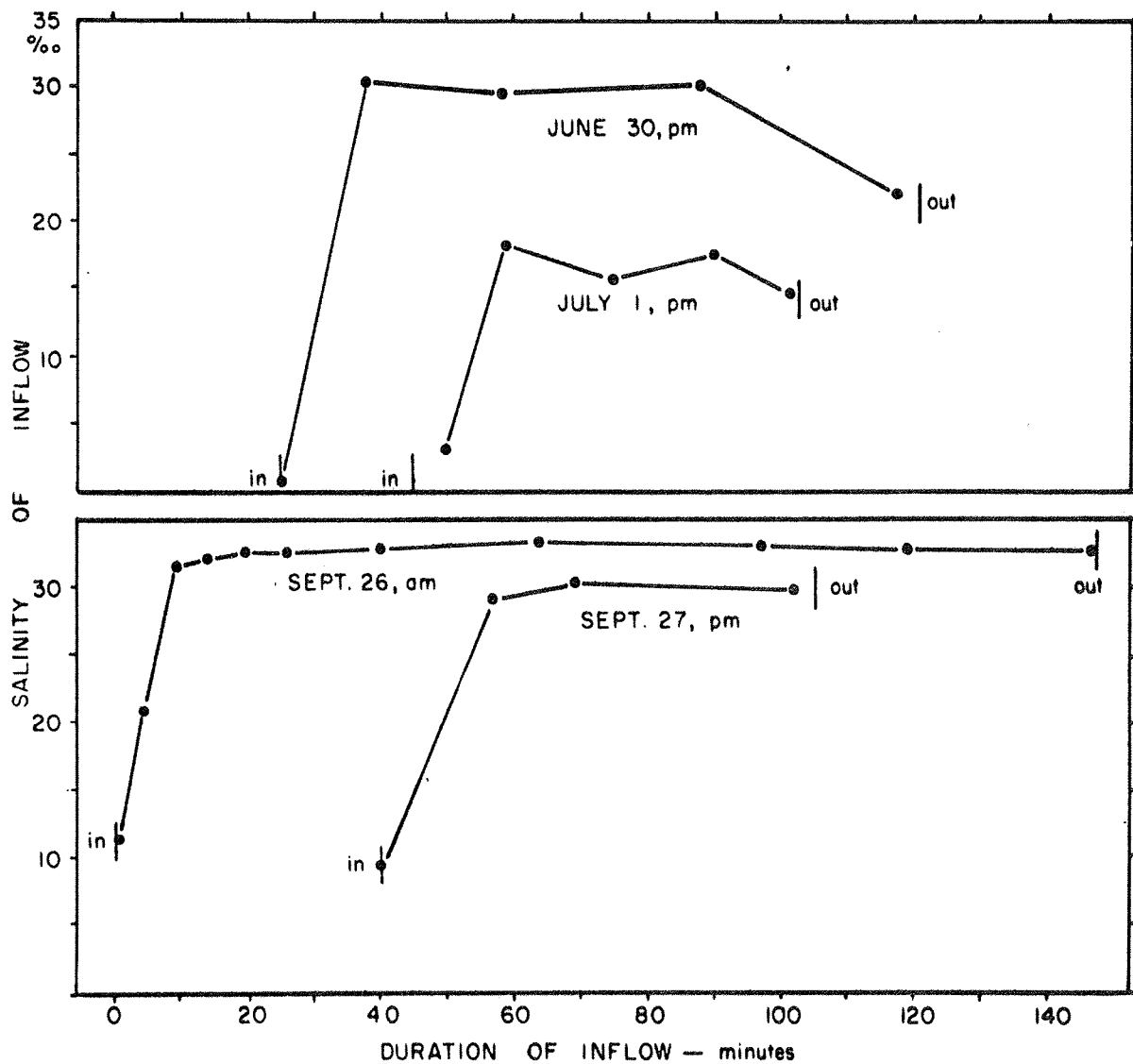


Figure 8. Salinities of large and small tidal inflows in early summer and in autumn.

salinity or temperature of the whole inflow. Such values are used to show the relationship between volume of inflow and its temperature and salinity in Figure 9. From these observations it is obvious that the September tides sent in far more highly saline water than tides earlier in the season. The curves in Figure 9 have been used to calculate the average temperatures and salinities of each tidal inflow of the spring-tide periods of late June, late July and late September. These tides have been grouped into major components on the basis of their density, and are listed in Table III. Unfortunately pertinent observations were not made for the August tides.

The density of the inflow determines its fate in the lake. After losing some salinity by mixing at entering, the tidal water flows into an equivalent density stratum in the lower basin. If this stratum is shallower than about 7 m., then tidal water can be forced over the sill into the middle basin and seek its equivalent density layer there; if this layer lies above about 12 m., then tidal water can continue on and penetrate the upper basin (see Fig. 3). Since the density is overwhelmingly determined by salinity, the extent and level of tidal penetration can most easily be determined by marked temperature changes in the lake. This will be shown in the discussion of the thermal regime (pp. 48-53).

Meromixis and the Salinity Balance

The effect of fresh water running into Ogac Lake is compensated by tidal inflow. Figure 10 depicts a series

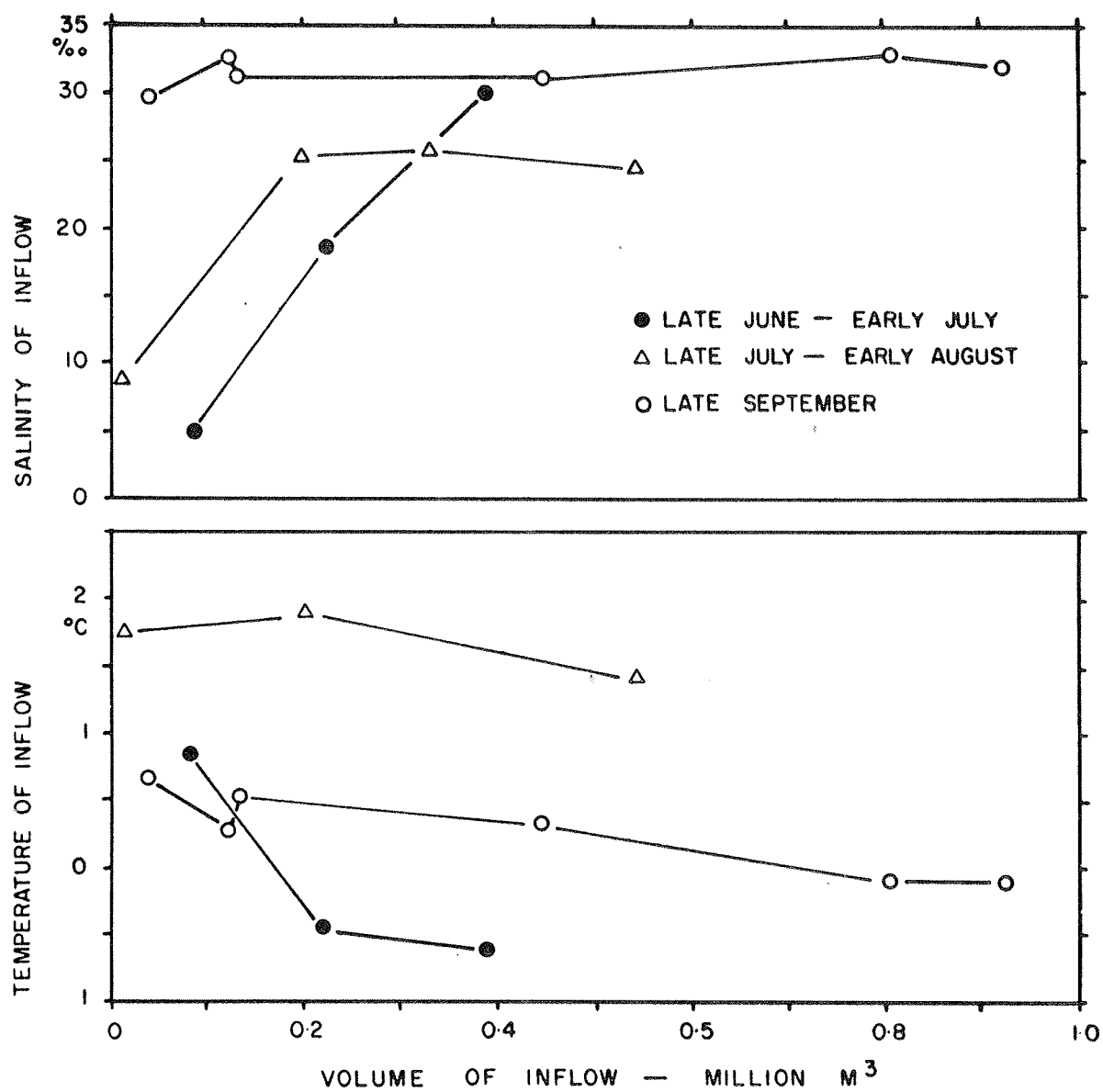


Figure 9. Relationship between volume of inflow and its temperature and salinity during different tidal series.

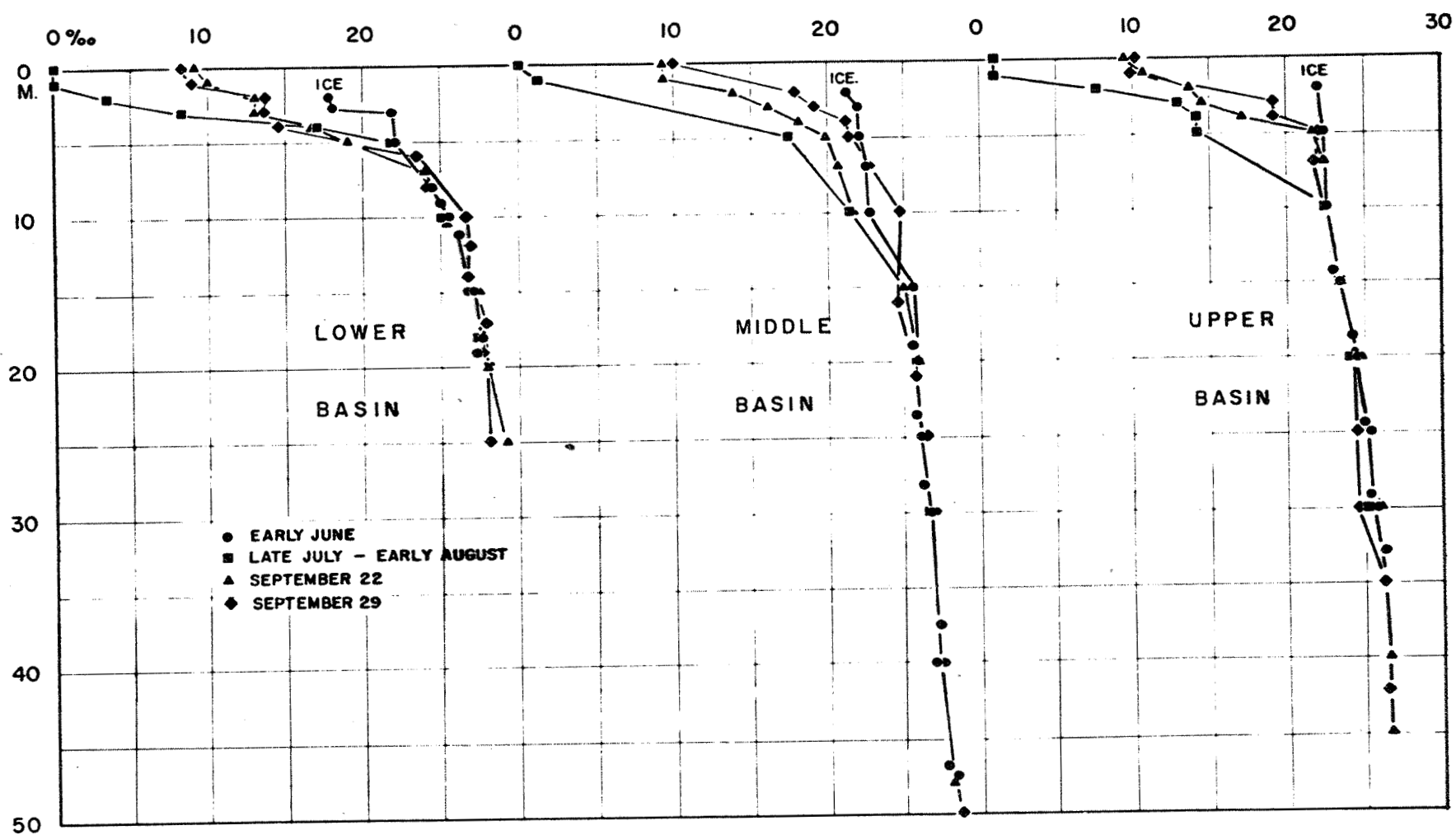


Figure 10. Vertical distribution of salinity in Ogac Lake during the 1957 season.
Some measurements from below 20 m. in mid June added to "early June".

of salinity curves from the three basins through the season. The salinities are based on hydrometer measurements, with occasional checks by titrated samples, and some impression of the inaccuracies of the data is given by the scatter of points in deep water in early and mid June.

The downward mixing of fresh water tends to increase the stability of the waters just below the surface during the summer. Temperature has a smaller effect, but likewise increases stability during the warming season. Since tidal inflows seek their own density layer, they do not cause much vertical mixing. It is clear from the selected density (σ_t) curves in Figure 11 that the lake is persistently meromictic. Except for an upper meter or two of fresh water present during part of the summer, no holomictic layer was found in the 1957 season.

The changes of salinity through the season can give a measure of the amount of salt which is lost from the surface waters by mixing and restored by the tidal inflows. The salinity of the ice cover was not determined. Water at the surface of an ice hole in the middle basin on June 4 before any melt water had entered was about 9 ‰; probably the ice was almost freshened by the freezing process. At any rate, since its salinity was not determined, and since the surface water was subject to short-term salinity changes, the analysis which follows deals only with water 2 m. and deeper.

Freshening below 2 m. by late July and early August was probably almost completed. The tides of late July affected

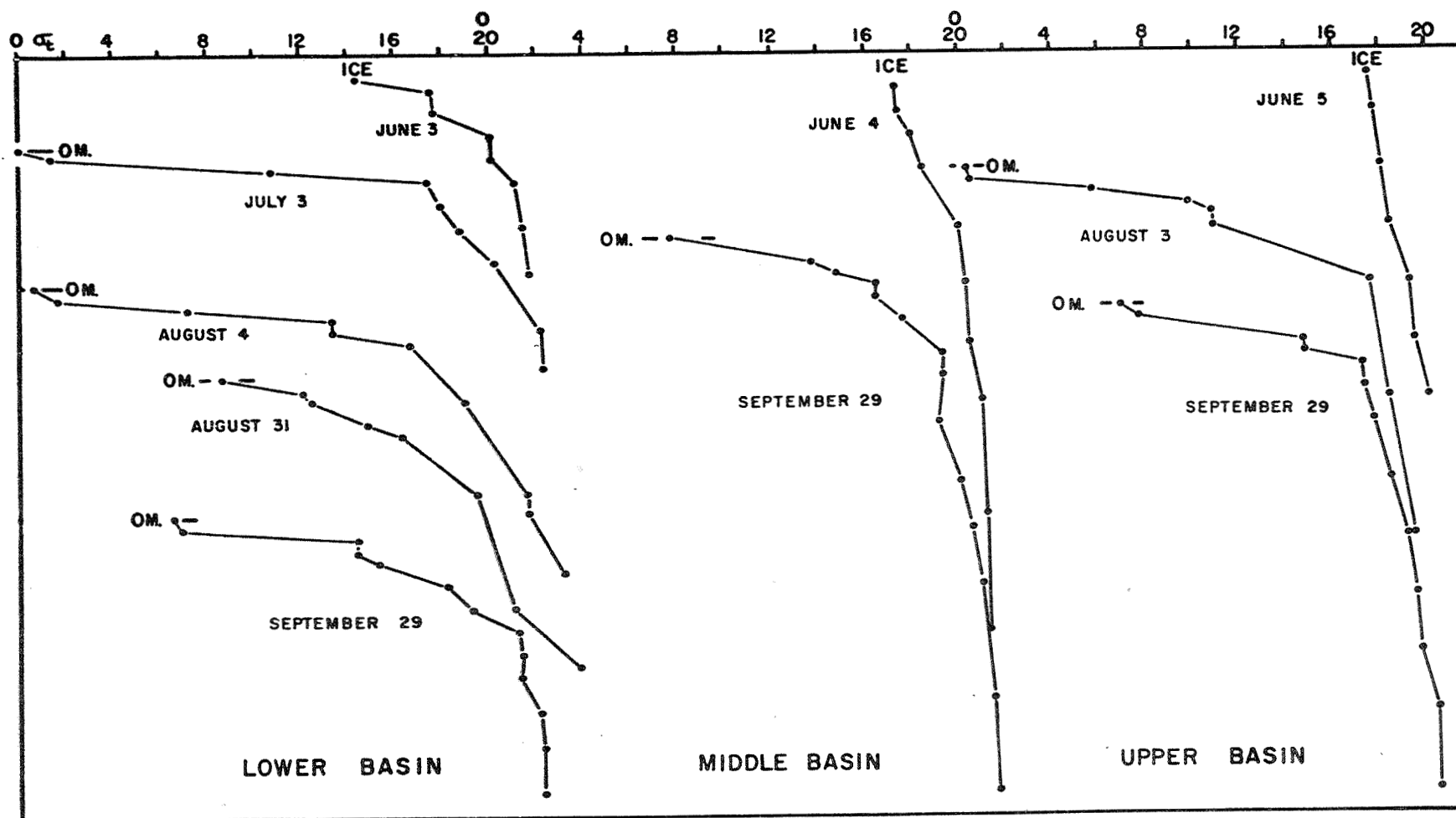


Figure 11. Selected vertical density (σ_t) curves from the 1957 season.
The few slight inversions due to error in hydrometer measurements.

the salinities in at least the lower basin, and measurements are not available from the upper and middle basins just prior to the late-August tides. By integrating the depth-specific volumes and reductions of salinities at 1-m. intervals, the loss of salt can be calculated as 27,300,000 kg. in upper, 30,800,000 kg. in the middle, and 3,400,000 kg. in the lower basin. In losses per unit surface area these become almost equivalent at 45.8 kg. m.^{-2} in the upper and 44.2 kg. m.^{-2} in the middle basin, but a much smaller 18.4 kg. m.^{-2} in the lower basin. Almost all the fresh water comes from the Ogac River entering at the head of the upper basin. The middle basin receives only a minor freshet at its lower end, and can be expected to depend on the same rate of exchange of fresh water at its surface. The lower basin receives two small but permanent streams, yet does not seem to be affected by this increase of fresh water. No doubt the differences in loss of salinity are due to wind exposure of the three basins. The lower basin certainly does not offer as much reach for the wind, especially the strong winds which tend to follow the axes of the fiord and the upper and middle basins.

It should be possible to derive coefficients of eddy diffusivity from the downward mixing of fresh water, although the measurements are widely spaced at critical depths for accurate estimates. Further, there is evidence that lateral transport might render the results spurious. Figure 10 indicates that significantly greater reduction of salinity occurred at 10 m. and perhaps deeper in the middle basin.

This deeper penetration of comparable amounts (per m.²) of fresh water is at least partly explicable by morphometric advantages for downward mixing in the middle basin. It is obvious from Figures 2 and 4 that the rate of decrease of volume is greater at pertinent depths in the middle basin than in the upper basin. In effect, through lateral exchange, equivalent amounts of fresh water would be forced into relatively smaller volumes in the middle basin, and would result in greater reductions of salinity at depth.

By mid September the salinities had returned almost to the June values, partly as a result of decrease in water level, and loss of fresh water from the surface, and partly due to the late-August tides. Tides serve to increase the salinity of the lake in two ways. If the salinity of the inflow is greater than the average salinity of the lake, then it will contribute to the salinity balance by its own concentration. However, by displacing less dense surface waters out of the lake it increases the salinity in proportion, not to its concentration, but to its volume. The August tides may have moved the salinity curves at 2 m. nearer the surface by an average 1.7 m. through the latter effect.

The tidal inflow in late September was cold and highly saline (Table III) and had a profound effect on the salinities of the lake. Mixed tidal and lake water filled the depths of the lower basin. Water at about 7 m. with a salinity of about 25 ‰ was displaced from the lower basin over the sill into the middle basin, where it increased salinity markedly above 15 m. In the middle basin there was little change in the shallows, but at 25-30 m., although

the scatter of earlier measurements is rather large, there seems to have been a distinct reduction of salinities following the late-September tides. Here again water in a position to be displaced over the sill (at about 12 m.) had a salinity of about 25 ‰ in the middle basin, so that the freshening effect, if real, demands an explanation. Only one mechanism would appear to account for this, and that is a turbidity current. In the first place, the vertical salinity gradient in the zone centered on the 25‰ level is less steep and therefore less stable in the upper basin. Also, although soundings are not as complete as might be wished (Fig. 3), there is some bathymetric support for a turbidity-current hypothesis. Water spilling over the sill into the upper basin would run down a considerably steeper slope in seeking its own density level than would water spilling into the middle basin. At least some of this flow could have picked up bottom material as well as fresher water from the shallows, and its sediment load and momentum could have carried it to depths below 25 m., where the bottom appears to level off in the upper basin.

After the tides of late September there was still a deficit in the salt balance of the lake. Again by integrating volumes and salinity changes between early June and the end of September, the loss of salt below 2 m. can be calculated as 14.9 kg. m.⁻² in the upper, 2.2 kg. m.⁻² in the middle, and 8.1 kg. m.⁻² in the lower basin. It cannot be exactly calculated to what extent the salinity would be

recovered through the unwitnessed late-October tides. We can safely assume that their salinity would be the same as in the late-September tides (also close to water immediately under the ice of Ney Harbour at the end of winter--Table IV). The predicted amount of inflow ($1,800,000 \text{ m}^3$) would displace water at about 3.3 m. up to the 2 m. level. From the data on Figure 10 it can be calculated that this water would have an average salinity of about 14.6 ‰ , which can be considered displaced by incoming water with a salinity of 32.0 ‰ to give a positive salinity balance, with some $19,400,000 \text{ kg.}$ or 13.1 kg. m^{-2} more salt present in the lake than in early June. Actually it is unlikely that the tidal water would be thus evenly distributed over the lake; much of the tidal water after mixing with the shallower lake water probably would have flowed over the layers already made dense by the late-September tides, and thus tended to enter the upper basin, where the salinity deficit was greatest.

Doubtless the salinity cycle varies from year to year, according to the timing of the high tides, the amount of runoff early in the season, and the effects of sporadic precipitation on the salinity of the tidal water entering the lake. No marked trend is shown in comparisons of salinities from 1951, 1952, and 1957 (Table V), although over the longer term the lake is presumably freshening.

Thermal Regime

General characteristics. The temperature curves of

Table V. Comparison of salinities in Ogac Lake in 1951 and 1952 with salinities in late July or early August 1957.

	<u>1951</u>	<u>1952</u>					<u>1957</u>	
	<u>Aug. 4</u>	<u>July 22</u>	<u>July 28</u>	<u>Aug. 4</u>		<u>Aug. 11</u>	<u>Aug. 18</u>	<u>late July - early August</u>
Lower Basin	‰	‰	‰	‰	Tide	‰	‰	‰
10 m.	26.99	26.58	26.35	26.53		26.71	26.49	25.3
17 m.		27.95	27.66	27.72		27.59	27.45	27.5
18 m.	27.47							
Middle Basin								
10 m.	22.32	22.32	22.14	22.29	Tide	22.32	22.32	21.5
25 m.	26.10	26.74	26.60	26.85		26.22	26.26	25.2
50 m.	26.95	27.27	27.00	27.23		27.12	27.20	28.3
Upper Basin								
10 m.		22.47	22.30	22.83	Tide	22.36	22.34	22.5
25 m.		25.70	26.02	26.02		25.88	25.73	25.2
45 m.		26.77	26.20			26.49		26.5
50 m.							26.27	

Figure 12 reveal the striking differences between the thermal properties of Ogac Lake and those of the sea outside and of a nearby freshwater lake. The higher temperatures of the lakes are of course due to their small size and landlocked nature, while the extraordinary vertical distribution of temperature in Ogac Lake is an effect of tidal inflows, preserved by the great vertical stability of the lake.

Each basin of Ogac Lake is hydrographically distinct and fairly uniform below the level of the sill separating it from its neighboring basin (Fig. 13). The lower basin, which is most influenced by tidal inflow, maintains colder temperatures than the other two.

The ordinary difficulties of following temperature changes in lakes are compounded in the highly stratified Ogac Lake. When changes of temperature with depth are very rapid, slight errors in determining depth lead to large errors of temperature measurement. Changes of lake level, for example, were only irregularly recorded. Further, it is very likely that isothermal surfaces were affected by internal seiches, and there is perhaps a hint of this in Figure 13. Unfortunately, these problems were not studied in 1957, and the surface of the lake must be taken as datum for the series of vertical temperature records.

Total energy delivered in the 1957 season. In the analysis of the thermal properties of Ogac Lake it is important to have at least rough estimates of the total incident radiation during various periods of the 1957 season. No instrumental

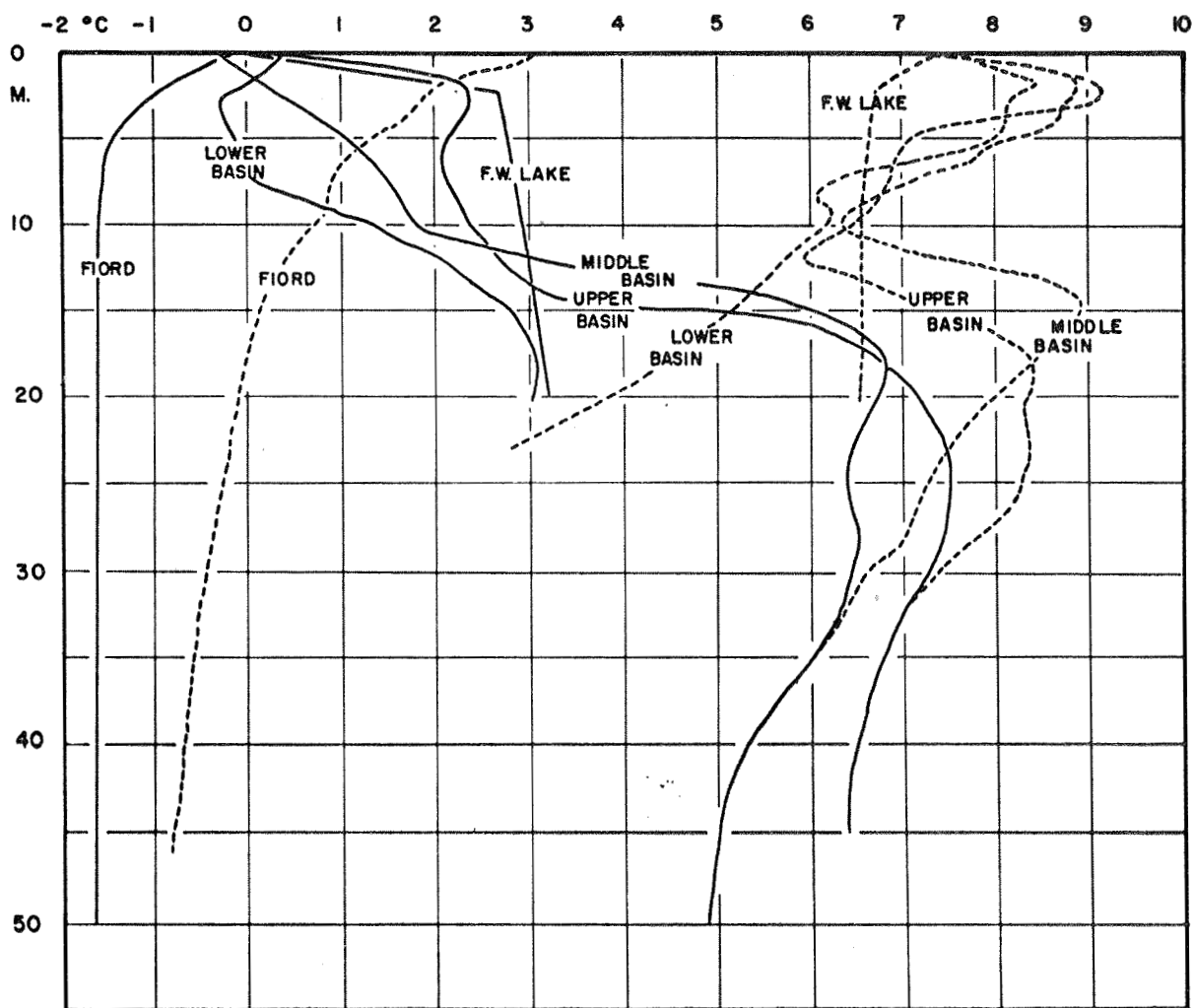


Figure 12. Vertical distribution of temperature in Ney Harbour, the three basins of Ogac Lake, and in a nearby freshwater lake, at the end of winter (early June in Ogac Lake and Ney Harbour; July 10 in the freshwater lake) and at the height of summer warming (August 17 in Ogac Lake, August 11 in the freshwater lake, and September 6 in Ney Harbour).

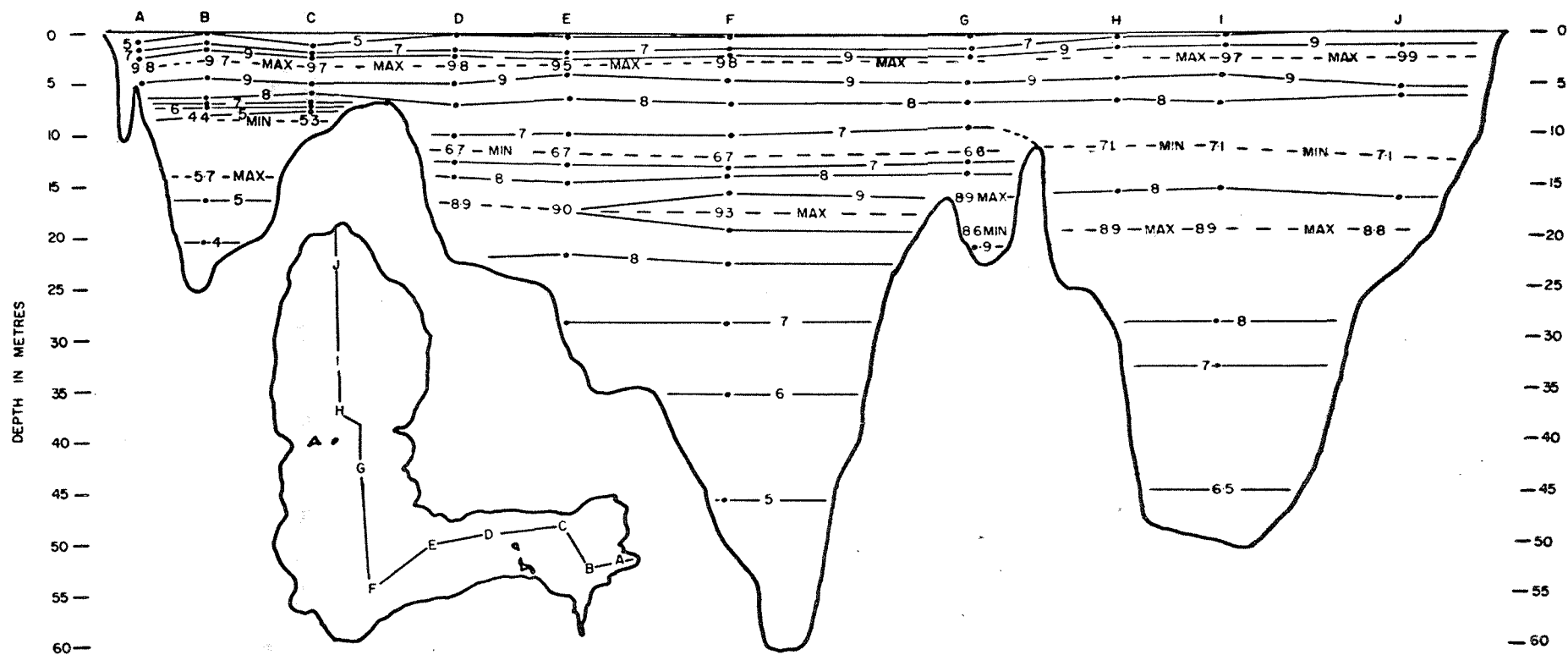


Figure 13. Temperature section through Ogac Lake, September 21, 1957.

observations were made, but approximations can be derived from theoretical figures of clear-day insolation corrected for cloud cover.

The most satisfactory estimates of total incident radiation on clear days appear to be those of Mateer (1955), who maps mid-month isopleths for all of Canada. His estimates, especially for June and July, considerably exceed those from other recent sources (List 1951, Roden 1959, Smayda 1959), but must be considered realistic for the present study, since some pertinent measurements were available to Mateer from Frobisher Bay, 120 km. from Ogac Lake.

Records of clear and overcast days were kept, but the types of overcast, from which quite accurate corrections can be derived, were only recorded occasionally. Mateer (1955a), without dealing with cloud type, relates average cloudiness (fraction of daytime sky obscured by cloud) to percentage reduction of insolation. Other relationships between sunshine and insolation were not available to him from the arctic. Strictly speaking Mateer's analysis should apply to synoptic records which include partial cloud-cover, the extent of which was not often noted at Ogac Lake. But, since the effect of open cloud on insolation may be positive or negative, probably little bias is introduced by treating days or portions of days as either clear or overcast, and deriving the average cloudiness for each day accordingly. The curves given by Mateer for Aklavik (lat. 68°) and Churchill (lat. 59°) are quite close, and the correction for Frobisher Bay (lat. 65°) can be taken

as intermediate. In this manner the total incident radiation at Ogac Lake has been estimated between early June and late September. The daily estimates are unlikely to be accurate, but probably combine to give quite acceptable figures of amounts of radiation delivered between series of temperature measurements (usually about 2 weeks apart). These amounts are listed in Table VI. The insolation of June and July was well above average for the Frobisher Bay area (comparable with expectations in central Baffin Island), while the August average was slightly low and the September high, judging from maps in Mateer (1955a).

Some of the incident radiation will be reflected and contribute no heat to the lake. From Roden (1959) this variable quantity is considered to average 7.5% for the latitude of Ogac Lake, and the radiation entering the lake is determined from this correction.

Gross annual heat budgets. When observations were begun in early June the daytime temperatures were just beginning to rise above freezing. Thus changes of lake temperature from this time until the height of summer warming, corrected for the melting of ice, should give the annual heat budget with some claim to accuracy.

There are some peculiarities of the lake which require consideration. First, although deeper waters continued to warm in the lake (due to insolation, to be discussed below) after the middle of August, the surface waters were at their warmest then, and the heat content of the lake was at its

Table VI. Total incoming radiation at Ogac Lake during the 1957 season.

<u>Series</u>	<u>Lower Basin</u>			<u>Middle Basin</u>			<u>Upper Basin</u>		
	<u>Dates</u>	<u>Total Energy</u> cal.cm ⁻²	<u>Av. per day</u> cal. cm ⁻²	<u>Dates</u>	<u>Total Energy</u> cal.cm ⁻²	<u>Av. per day</u> cal.cm ⁻²	<u>Dates</u>	<u>Total Energy</u> cal.cm ⁻²	<u>Av. per day</u> cal.cm ⁻²
1-2	June 4 to June 20	10,400	631	June 4 to June 18	8,500	606	June 5 to June 18	7,700	592
2-3	June 20 to July 3	8,200	629	June 18 to July 2	9,300	664	June 18 to July 4	10,100	634
3-4	July 3 to July 18	9,100	607	July 2 to July 19	9,900	583	July 4 to July 20	9,400	586
4-5	July 18 to Aug. 4	9,000	527	July 19 to Aug. 3	8,000	532	July 20 to Aug. 3	7,700	548
5-6	Aug. 4 to Aug. 17	3,900	303	Aug. 3 to Aug. 17	4,500	324	Aug. 3 to Aug. 17	4,500	324
6-7	Aug. 17 to Aug. 31	5,000	357	Aug. 17 to Aug. 31	5,000	357	Aug. 17 to Aug. 31	5,000	357
7-8	Aug. 31 to Sept.21	6,500	311	Aug. 31 to Sept.21	6,500	311	Aug. 31 to Sept.21	6,500	311

greatest. Secondly, although no correction is normally made for the temperature of influents in the heat budgets of lakes, tidal water flowing into Ogac Lake has an important effect in reducing the temperature of the lake water.

The temperature changes between early June and mid August are shown in Figure 12. By integrating these and volumes at one meter depth intervals, heat budgets for the water have been determined as 7,500 cal. cm.⁻² for the upper, 8,140 cal. cm.⁻² for the middle, and 6,040 cal. cm.⁻² for the lower basin. To these must be added about 1,200 cal. cm.⁻² for the melting of ice, which averaged 148 cm. in thickness on two basins and on the fiord outside before being affected by melting, and which can be considered fresh (p.27). The late-June tides had little thermal effect, as water very slightly below 0° merely displaced ice-water from the surface. In late July tidal water with a temperature of about 1.6° (Table III) displaced about 0.8 m. of surface water, which averaged about 9.9° between July 27 and August 3. Almost all the effect was in the lower basin, and from these values it can be calculated that about 670 cal. cm.⁻² should be added to that basin. No correction can be made for the heating of sediments or for the warming of the ice sheet prior to melting, but the annual heat budget as calculated, which amounts to some 8,950 cal. cm.⁻² for the whole lake, can be compared with those available from most lakes (Hutchinson 1957, Table 53).

It is of interest to compare the heat budget of the meromictic Ogac Lake with that of a freshwater lake. Temperatures

were recorded and a plane-table survey made of a small, unnamed kettle lake about 500 m. upstream from the upper basin on the Ogac River. This lake is quite comparable to the lower basin of Ogac Lake, being somewhat smaller (109,000 m.² to 187,000 m.²), shallower (maximum and mean depths of 24 and 8.9 m., to 28 and 10.8 m. respectively in the lower basin), and very similar in form (development of volume 1.11 in the small lake and 1.15 in the lower basin of Ogac Lake).

The ice thickness on the freshwater lake was not measured, but we can presume it to have been the same as on Ogac Lake. Temperatures were not taken before July 10, when the ice was waning rapidly, to disappear on July 17. Most of the heat prior to July 10 was probably taken up by melting ice, and the water temperatures below a few meters therefore almost at winter minimum. From the summer temperatures (Fig. 12), the freshwater lake is to be classed as subpolar and probably dimictic (Hutchinson, 1957). It is possible in fact that the lake mixed irregularly during the season. Its heat content was greater on August 11 (bottom 6.61°) than on July 26 (bottom 5.41°) and September 2 (bottom 5.58°), but had increased again on September 17 (bottom 6.13°) before the low of October 1 (bottom 4.48°). However, we will not be far wrong in considering the temperatures on August 11 to have been maximal. From these considerations an annual heat budget for the freshwater lake has been estimated at about 4,830 cal. cm.⁻². This figure may be taken as minimal, but it is clear that the advantage

which the relatively unstratified freshwater lake has in mixing heat to depths is counteracted by its greater tendency to lose heat gained near the surface.

Radiation heating. From the sections on meromixis and the salinity cycle it will be clear that Ogac Lake is highly resistant to downward mixing. While no attempt was made to derive coefficients of downward transport at various depths it was suggested that little or no fresh water was mixed from the surface to depths below 5 m. in the lower, 15 m. in the middle, and 10 m. in the upper basin (Fig. 10). No doubt vertical exchange occurs to a small degree between deeper strata, but the implication is that much or all of the warming which took place in deeper water was due to radiation.

Unfortunately, no Secchi disc readings were made during the 1957 season, but an indication of the clarity of the lake is given by the fact that a plankton net (with a white canvas mouth) was noted to disappear at about 14 m. in the middle and 19 m. in the upper basin on August 3. If certain ideal conditions obtain, then there are two further indications that radiation is the sole source of heating.

First, if water above a given plane can be considered optically uniform in time, then the amount of energy passing through the plane will be directly related to the amount of radiation absorbed at the surface. Figure 14 indicates a quite satisfactory relationship, at least for the deeper water of the middle and upper basins. The lower basin, being most disturbed by tides, and having the largest and most varied

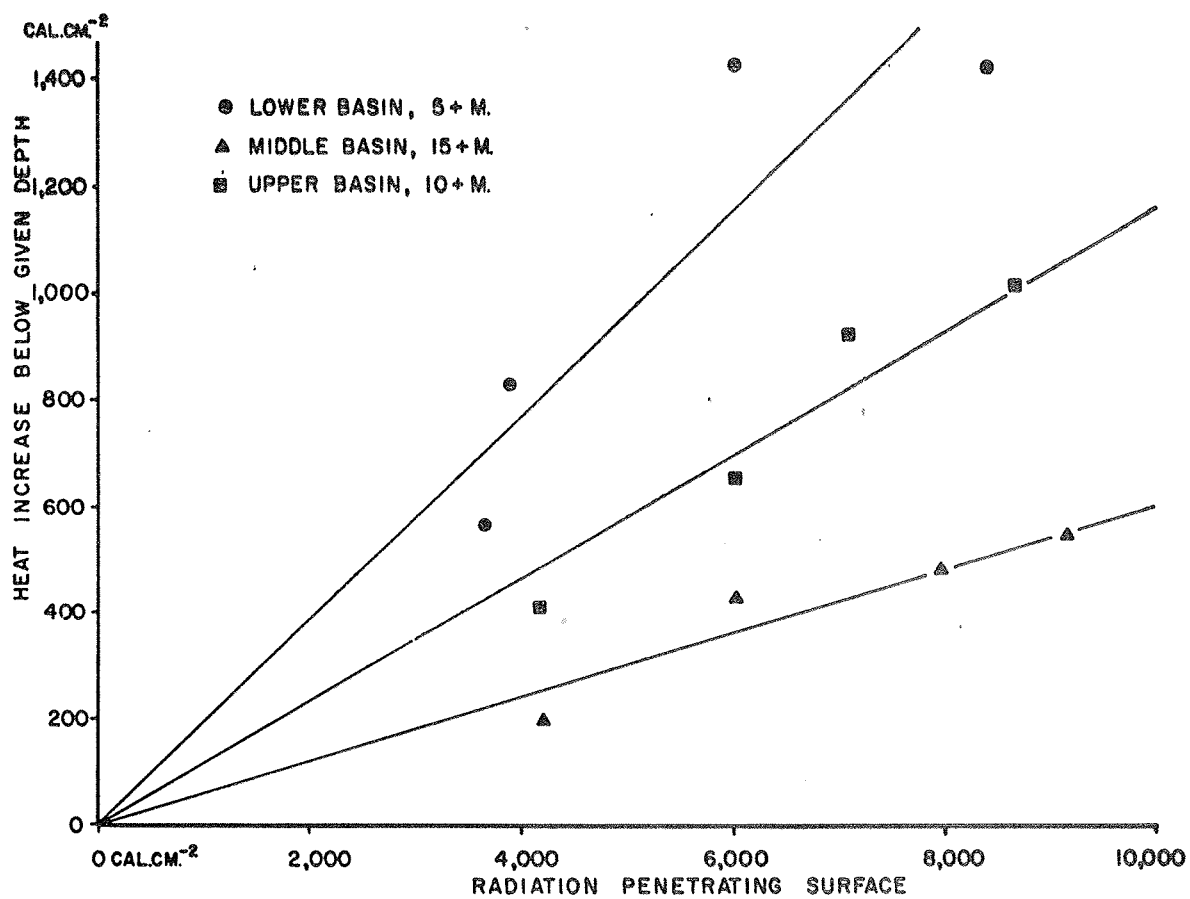


Figure 14. Relationship between calculated energy penetrating the surface during four periods in the open water season and observed heat increment below given depths in the three basins. The four periods chosen were undisturbed by tidal inflows.

plankton crops, was least likely to fulfill the conditions of optical homogeneity. Also, even although no fresh water was apparently mixed below 5 m. between early June and late July, vertical exchange of heat across this shallow plane later in the season was certainly more likely than across the deeper planes of the other two basins.

A second indication of radiation heating can be gained from an examination of temperature changes with time at different depths. Without direct measurements of energy penetration or knowledge of horizontal extinction coefficients, a detailed explanation of vertical temperature changes would be presumptuous. Nevertheless, it is believed that such changes can be accounted for in a qualitative way.

Figure 14 implies that about 11.5% of surface energy reached 10 m. and 6% reached 15 m. in the lake. Such penetrations are quite close to those for "average ocean water" given by Sverdrup et al. (1942), who also tabulate heating due to absorption of radiation. It can be seen from Figure 15 that the heating curves for "average ocean water" do not fit the observed increments at all well. If the hypothesis that no vertical exchange of heat occurred below 10 or 15 m. is to be maintained, then these deviations must be explained.

In the first place, it is to be noted that the heating curves apply to a boundless ocean. A great deal of energy entering Ogac Lake must be captured by the bottom, and, unless a strong differential can be maintained, some or most of this energy must be delivered to the water. The only direct

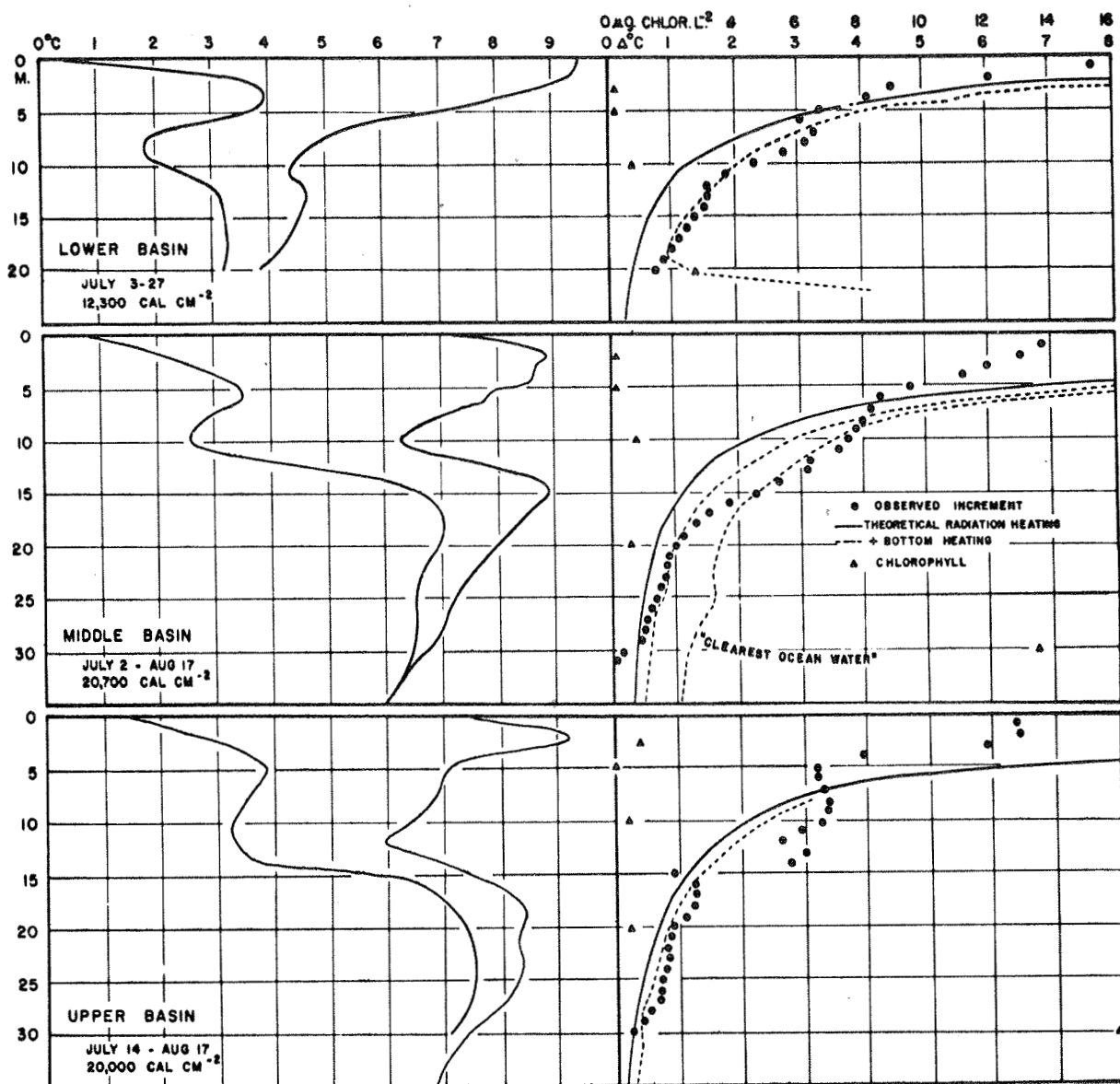


Figure 15. Temperature changes in the three basins during the open-water season and theoretical increments based on radiation heating. (See text).

evidence for such an effect is from bathythermograph records of temperatures in deep and shallow water made on September 21 (Fig. 16). The evidence from these curves is that there is strong local warming over sufficiently shallow bottoms, which means that heat is not in fact evenly distributed by horizontal exchange. However, as an indication of the maximum effect, the heating curves of Figure 15 are shown as corrected on the assumption that all heat delivered to the bottom at a given depth is distributed throughout the water at that depth. It can be seen that these curves too fail to describe satisfactorily the observed temperature increases, although they may help account for the somewhat greater heating of the water column in the middle and lower basins, where ratios of bottom area to water volume are larger. There is no justification for assuming that there are differences in the extent of horizontal exchange at various depths. The theoretical heating curves of Figure 15 would apply in optically uniform water, but it is probable that there are strong vertical differences in the absorption of radiation. What is needed is very clear water near the surface to permit maximum penetration of radiation to the next few meters, followed by more turbid water to absorb most of the remaining energy, followed by increasingly absorbent water to capture the last of the radiation between 20 and 30 m., at least in the middle and upper basins. This almost certainly describes the condition of water in Ogac Lake, where the fresh, colorless and lifeless surface waters must transmit almost as pure water, and where the increasing opacity with depth is reflected in the

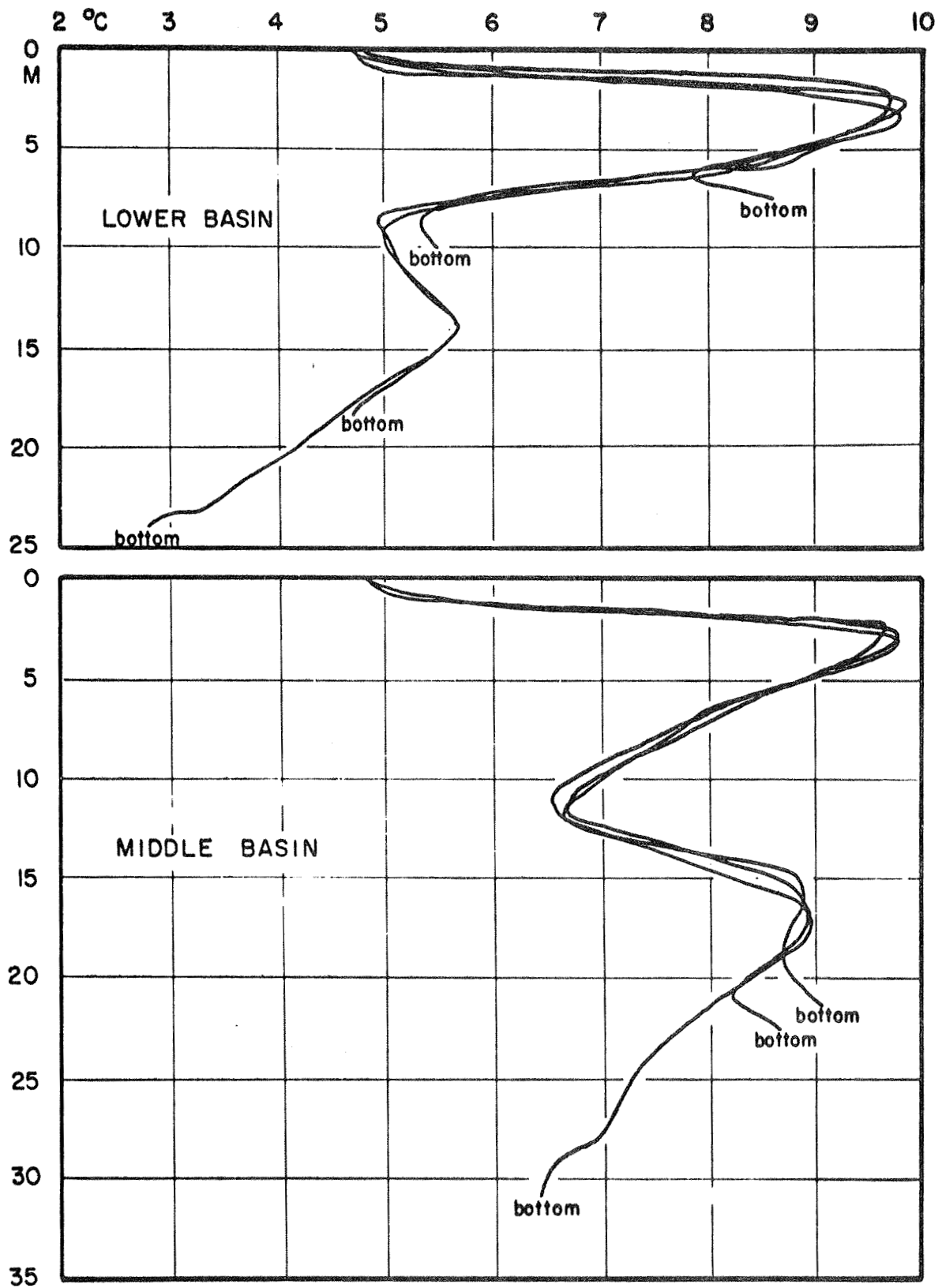


Figure 16. Evidence of local radiation heating over the bottom, September 21.

vertical distribution of chlorophyll, with the very high values below 20 m. probably associated with large amounts of suspended detritus (p.71). As an indication of the amount of heating which could occur in transparent shallower water, the heating curve for "clearest ocean water" (Sverdrup et al. 1942), corrected for heat from the bottom, is shown for the middle basin in Figure 15.

Temperature effects of tides. Radiation alone cannot account for the highly anomalous temperature curves in Ogac Lake. Possibly slight maxima and minima might result in a stratified system from clear and turbid zones in the water, or by horizontal transmission of heat from bottoms of varying slopes. However, the strong inversions found in the lake are easily explained by reference to the tidal inflows.

The temperature effect of each tide is shown graphically on Figure 17a, b, and c. Except for the late-August tides, temperature records are available from immediately before and after each series of inflows. Since the density of an inflow is overwhelmingly a function of salinity, so that it tends to seek its own salinity level in the lake, the temperature effects of the tides are quite startling.

The quantity of the inflow in late June was apparently insufficient to have a noticeable effect even in the lower basin. In late July, the tidal water appears to have entered at two levels (not seemingly equivalent to the large and small components of the tide on Table III). The effect was slight in the middle and not discernable in the upper basin. The

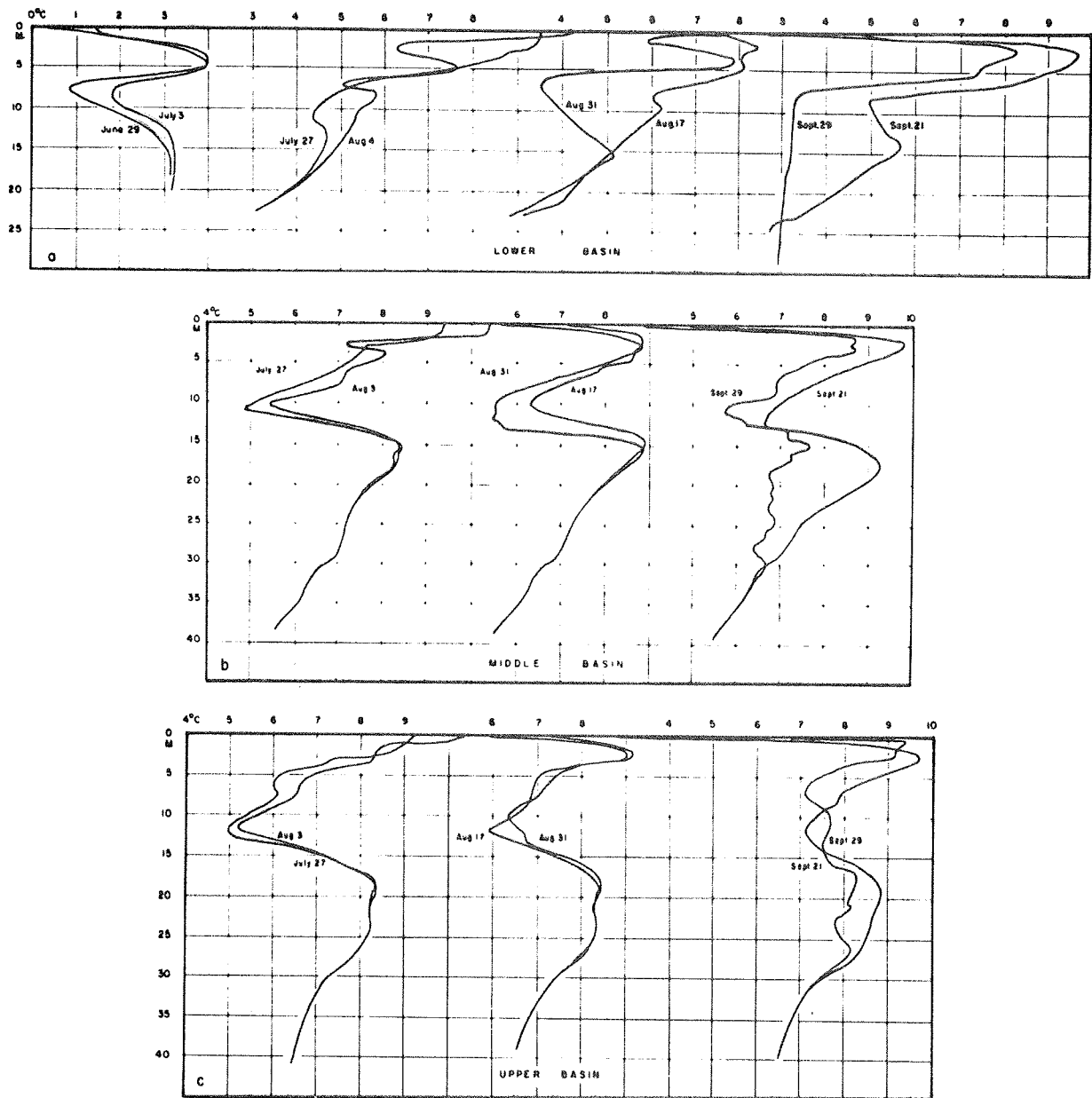


Figure 17. Vertical distribution of temperature in the lower, middle and upper basins before and after each tidal series.

large August inflow caused a distinctive inversion below 5 m. in the lower basin. Water flowing over the 7-m. sill entered the second basin at about 10-15 m. to expand vertically the extent of the temperature minimum. The effect in the upper basin, as might be expected, was much smaller, and little net temperature reduction occurred.

The late September inflow was cold and dense, and had a complex influence, quite unlike that of preceding tidal series. The depths of the lower basin were filled with colder water, but water flowing over the 7-m. sill seems to have entered a number of strata in the middle and upper basins. To explain such an effect, one must assume that flow into the basins was interruptive and of varying quality. In late August, although some non-tidal water was undoubtedly displaced from below, the main part of the inflow found its level at about 7 m., whence it had the opportunity of flowing smoothly into the middle basin. In September the inflow was denser, and flowed into and mixed with the water of the lower basin, to "fill" it from the bottom up. Each successive tide must have displaced denser water, and the temperatures of these displacements must have varied markedly, judging from conditions around 7 m. on September 21 (Figure 17a). After the deeper water of the lower basin had been made denser, tidal water had the opportunity of flowing over this water and into the middle basin. Perhaps this was most likely at the beginning and end of an inflow, when the water was slightly less dense.

The complicated vertical pattern of temperature

changes in the middle and upper basins is compounded by horizontal differences (Fig. 18). In general, the further away from the lower basin, the less marked are the anomalies and changes in the temperature curves. Presumably what began as a laminar flow across the sill from the lower basin would have lost much of its character and momentum as it progressed up the lake at its own density level.

The effect of the unobserved late-October tides would be most critical in the thermal regime of the lake. It has been suggested in the section on salinity that much of the tidal water then probably flowed over the layers in the lower basin already made dense by the late-September tides, and thus penetrated the other two basins. Because of salinity differences, the water would penetrate deeper in the upper basin. Such a mechanism would lead to temperature curves similar to those at the beginning of the 1957 season (Fig. 12). Although back radiation and limited convective mixing in winter could lead to near-surface cooling, the strong gradient at 10-15 m. in the middle and about 15 m. in the upper basin must have resulted from the penetration of cold tidal water to these depths in the autumn of 1956.

Since it appears (p.32) that there was little difference in the salinity structure of the lake between 1951, 1952 and 1957, it is probable that the same sort of tidal penetration occurs regularly each season, and that the marked temperature minimum during summer in the middle and upper basins is perpetuated as an interaction of solar radiation and

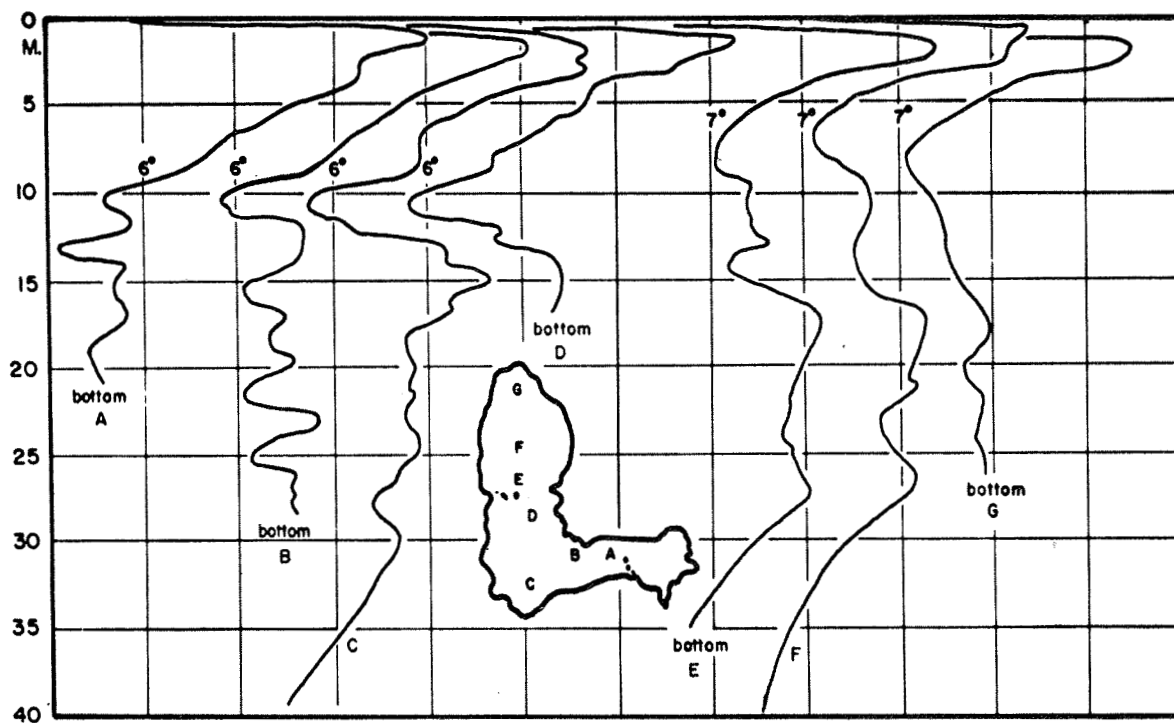


Figure 18. Vertical distribution of temperature at several stations in the lake on September 29, after the tides. [Vertical lines 1°C apart.]

autumnal tide influx. Unfortunately, temperature records from 1951 and 1952 are too widely spaced in depth to tell us anything of the shape of the temperature curve.

Oxygen

Vertical distribution. Meromixis is normally accompanied by marked effects on the vertical distribution of oxygen. Figure 19 depicts oxygen curves at the end of winter in the three basins. The fall of oxygen with depth was greatest in the lower and least in the upper basin. Oxygen was absent at all times below 32.5 m. in the upper and 30 m. in the middle basin, and was very nearly absent at 25 m. in the restricted "deep" of the lower basin.

It seems likely that the extent of oxygen reduction with depth is related to the morphometry of the three basins. More of the oxidizable seston from the trophogenic layer will reach the bottom at shallow and intermediate depths in the lower and middle basins than in the upper basin (see Fig. 4). It is of interest in this respect to point out that much of the bottom above the depth at which the water column became anaerobic was foul and devoid of macrobenthos. (Sometimes a thin oxidized zone overlaid reduced mud at quite shallow depths.) The minimum depths at which foul bottoms were noted were 20 m. in the lower, 25 m. in the middle, and 27 m. in the upper basin. Presumably water just above these bottoms was anaerobic, but samples were not taken to confirm this. The reduced sediments no doubt result from the oxidation of captured

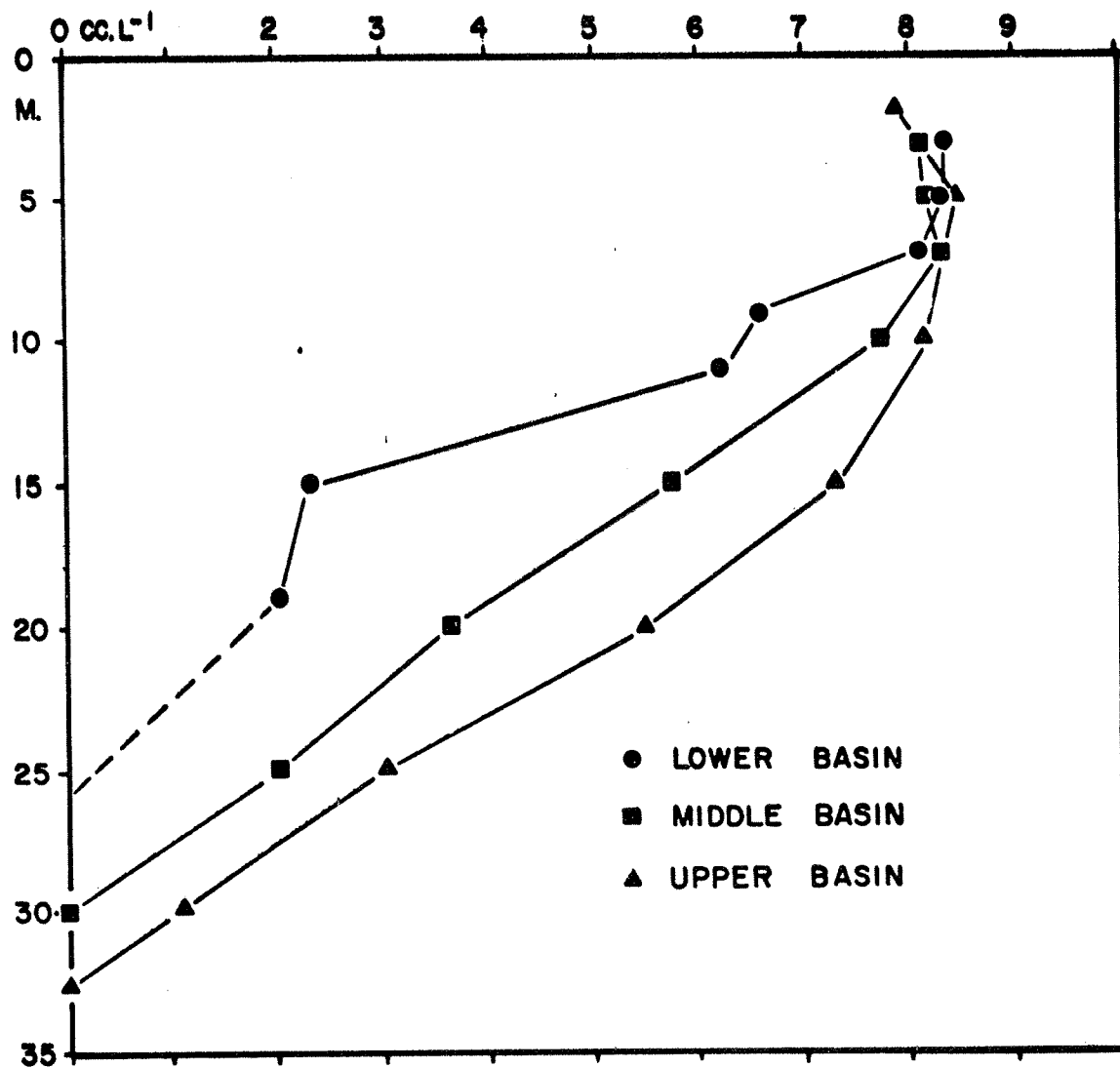


Figure 19. Vertical distribution of oxygen in the three basins in early June.

seston, and indicate the means by which oxygen is decreased at shallow and intermediate depths by morphometric factors.

As usual when oxygen is lacking in seawater, the sulfates are reduced, and for this reason large amounts of hydrogen sulfide are found below the aerobic levels of the lake. No specific study of the distribution of H_2S was made, but it could easily be smelled even in the water at the boundary of the anaerobic layer.

The oxygen cycle. The annual cycle of oxygen is outlined on Figure 20. Since there is very little downward mixing from the surface, oxygen changes below a few meters must be considered largely biogenic. These productive and consumptive changes will be discussed in a general way here, but certain details will periodically be referred to again when plankton cycles are dealt with.

In all basins, oxygen concentrations remained more or less unchanged through June. The oxygen from algal populations, which developed under the ice in all basins, was apparently consumed by the increase of numbers and possibly activity of the zooplankton. In the upper basin, where the diatom flowering was smallest (p. 74), the production of young plankton predators was also considerably smaller (pp. 125, 137); this may account for the maintenance of higher oxygen values there. There was little change in oxygen in the middle and upper basins in early July, although net-phytoplankton dwindled and large numbers of nauplii of the dominant grazing plankter, Pseudocalanus minutus, began to develop then. Sustained algal

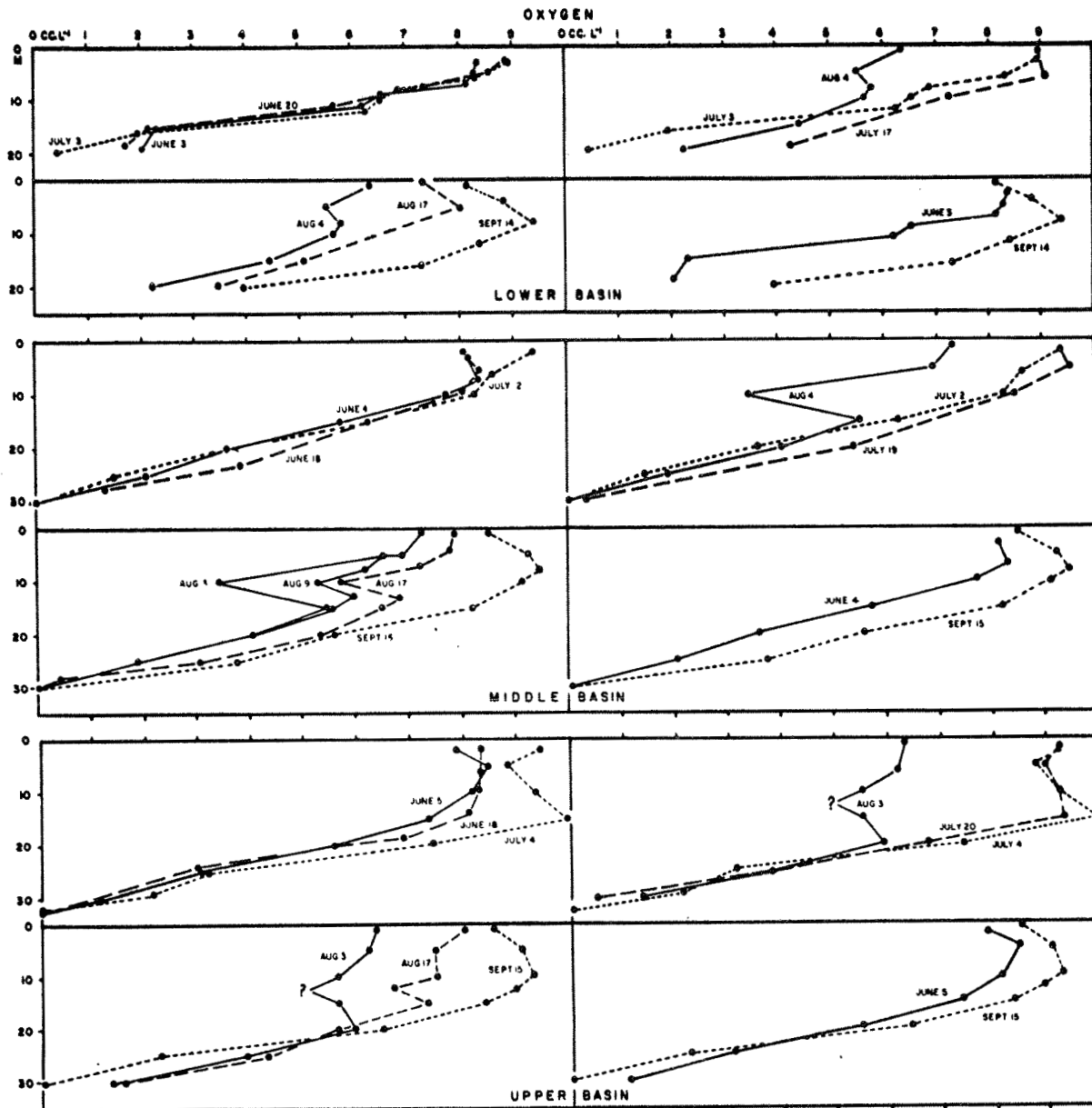


Figure 20. Seasonal cycle of oxygen in the three basins.

production in the lower basin, not yet matched by the reproduction of grazing forms (p. 87), seems to have been responsible for the increase of oxygen in deeper waters of the basin.

After mid July, there was a great drop in oxygen, traceable to the reproduction and growth of the various zooplankton species and decrease of primary production. The lower basin sustained much larger quantities of zooplankton at this time, but this was apparently compensated by the continuing high phytoplankton populations for the oxygen decrease was less severe there.

Finally the slow recovery of oxygen after early August can be traced to mortality of zooplankton as well as the increase of phytoplankton, particularly dinoflagellates and smaller species of diatoms. Primary production, however low, apparently kept ahead of oxygen consumption in the latter part of the open-water season, but respiration alone must have proceeded slowly during the winter if values comparable with those found in early June were reattained.

The cause of the oxygen minimum at mid depths.

Occurrences of metalimnetic minima of oxygen are well known in freshwater lakes. Often they may be attributed to localized oxidation of falling seston, or to morphometric effects (Hutchinson, 1957). Recently Shapiro (1960) has given ample evidence that such a minimum in Lake Washington results from respiration by large populations of non-migrating copepods.

In Ogac Lake, distinct minima occurred at 10 m. in the middle basin and 12 m. in the upper basin in early and mid August. A smaller, short-term minimum occurred at about 5 m.

in the lower basin on August 4 (Fig. 20). Reference to Figure 12 will reveal that marked temperature minima were found at exactly 10 and 12 m. in the middle and upper basins respectively. The causality is obviously indirect, and it appears certain that the oxygen minimum in Ogac Lake results from zooplankton activities. Pseudocalanus minutus (see p. 101), the most important herbivore, is largely responsible. The species appears to respond to temperature as such, and not to any large algal supply at the level of the temperature minimum, which might otherwise have compensated for oxygen respiration. The ephemeral notch in the lower basin is not as readily explained. It may be related to the influx of tidal water at about 7 and 2.5 m. during late July (Fig. 17a), on either side of the minimum.

ZOOPLANKTON BIOLOGY

General Character of the Plankton and Scope of this Study

Although most of the plankton collections of 1957 have been quite fully analysed, only a portion is dealt with in this study. The material collected falls naturally into several classes, each one of which might bear considerable study.

Most zooplankton species encountered in the lake are residents, and carry out their entire life cycles there in isolation from the sea. Unlike many estuaries, "ponds" and lagoons of temperate and tropical regions, in Ogac Lake there is no specialized brackish fauna to dominate the zooplankton,

although rare brackish elements may occur. The zooplankton consists of a rather impoverished selection of arctic marine forms, some with a wide distribution in the sea. Among the copepods, the calanoid Pseudocalanus minutus and the cyclopoid Oithona similis are overwhelmingly the most common. A few specimens of Metridia, Cyclopina, and two or three harpacticoids (probably epibenthic) seemed to represent rare copepod residents. The chaetognath Sagitta elegans was the most important predacious form, but the medusa Aglantha digitale was quite common. Another hydromedusan, Melicertum octocostatum, was rare, and the large scyphozoan Cyanea, although seen regularly in the lake, was rarely sampled by the nets. Other than these species, a few protozoans and rotifers of the genus Synchaeta made up the autochthonous, holoplanktonic zooplankton.

Although not all species have been fully identified as yet, there appears to be little of systematic or zoogeographic interest in the holoplankton. There is no true relict in the sense of the resident Atlantic cod (p. 3), with the possible exception of the medusan M. octocostatum, which has not hitherto been recorded from the Canadian arctic, but which is well known from brackish fiords in Norway and from West Greenland, and which may be an essentially brackish species from more southern waters (Russell, 1953). Some of the qualitative collections from just over the bottom may contain more of taxonomic interest.

There appears to have been no freshwater zooplankton inhabiting the surface of the lake in 1957. Since the freshwater

layer was not always present, and was only 1-3 m. thick at most, this lack is not surprising.

There is also, of course, a large meroplankton. Since the benthos, too, is limited in species, the lake offers an ideal medium for the identification and study of larval stages. There is much of biological interest in this material, including strong but unprecedented evidence that veliger larvae (probably of Saxicava) spend almost a year in the plankton in these warm and unproductive waters. The meroplankton has largely been analysed, but cannot properly be dealt with separately from the parent benthos, and so is not considered here.

A third class of zooplankton in the lake is allochthonous. Each tide in 1957 brought in numbers of species which were not represented in the resident plankton. Large Crustacea--Mysis oculata, Themisto libellula, and several gammarids--fell prey to the voracious codfish which schooled at the outlet at high tides, and were never taken in the plankton nets in the lake. Others, like Ctenophora, were found dead or in fragments after the tides. Still others, like Calanus glacialis, often the most common animal in the inflows, appeared in some numbers in plankton hauls taken immediately after the tides, but had largely disappeared two weeks afterwards; probably Calanus was intolerant of low salinities at least (Marshall and Orr, 1955). Only Pseudocalanus minutus of the species in the lake was well represented in tidal inflows, and will be discussed further (p. 106). The allochthonous zooplankton certainly merits consideration in the

economy of the lake, even if only as food or general organic enrichment. But since a full analysis would involve reference to plankton and their cycles in the waters outside, such a discussion is deferred.

As stated above, four species dominate the zooplankton--P. minutus, O. similis, S. elegans, and A. digitale--and offered a large material for study. All are widespread in arctic and other seas, and have a considerable literature. Advantages of studying these animals in the lake include the ease of taking complete samples (between the anaerobic level and the surface), physical and biological differences between the three basins, the slow growth of the animals, and the general simplicity of the ecosystem. Ogac Lake in fact is a natural laboratory for the study of the life history, trophic relations, and other features of these animals in greater detail and accuracy than is possible in the sea. The study of these four animals is the core of the thesis.

The phytoplankton was inadequately sampled and has not been fully identified. It is presented in this study to the extent necessary for background to the zooplankton biology. Some of the phytoplankton species are brackish and some subarctic or boreal (A. S. Bursa, pers. comm.) and there may be interesting taxonomic possibilities in the lake. The brief account of phytoplankton given below contains several hints on possible controls of succession and productivity. It is planned to give primary productivity further attention in the field.

An ultimate aim of the study of Ogac Lake will be to

express exchanges within the entire plankton ecosystem in energetic terms. The sections which follow will make clear that such an aim is not unreasonable in the lake, with its limited population of slow-growing zooplankton. However, before any such analysis is commenced, collections of specimens suitable for calorific analysis, direct measurements of primary production, and perhaps assessment of the respiratory activities of the zooplankton, would be necessary. This field work is planned for the future.

Sampling Methods

Since sampling was to begin well before the departure of ice, it was necessary to devise a program of regular plankton collection by vertical net hauls. The marked physical and biological stratification of the lake likewise indicated that only sampling of all depths, as with vertical hauls, would be representative.

Although a metered Clarke-Bumpus plankton sampler was available, it was decided that regular sampling was best carried out with nets 30 cm. in diameter, both for larger catches and to ensure the capture of larger and more agile plankters. Since very fine-mesh nets, especially when clogged, are of low and variable efficiency of filtration, a mesh of No. 6 (aperture 0.239 mm.) was chosen for the standardized vertical hauls. It is doubted that the plankton was ever sufficiently thick to affect the efficiency of this net by clogging. The quantitative basis to the collections was given

by a constant hauling rate of 0.5 m. sec.^{-1} , usually estimated by counting. Every effort was made not to change the rate of raising the net through different strata, even if the rate was felt to be slightly fast or slow. The few hauls which deviated from the standard hauling rate by more than 0.1 m. sec.^{-1} were discarded and repeated.

While the No. 6 net retains larger plankters adequately, many smaller forms may pass through its meshes. These were sampled with a 30-cm. net of No. 20 mesh (aperture 0.076 mm.). No net is adequate for the phytoplankton or smaller holozoic forms, but this mesh is generally believed to retain the smallest copepod nauplii, benthonic larvae, and others of comparable size.

The vertical hauls were made biweekly from early June to late September in the center of the lower basin and in the deepest parts of the middle and upper basins. Each series in all basins consisted first of two combined hauls with the No. 6 net and two with the No. 20 net, from 20 m. to the surface. One or two combined hauls with the No. 6 net were made at the same times from below the anaerobic level to the surface in the middle and upper basins, except unfortunately during the first series in June. Due to lack of bottles it was not possible to take fine-mesh samples during the last series on September 29.

Although deep hauls were made regularly with the coarse-mesh net, the entire water column of the middle and upper basins was not normally sampled by the fine-mesh net

except on two occasions in the middle basin. Prior to the 1957 expedition, it was noted from plankton samples taken in 1952 that the lake was relatively lifeless below about 20 m., and particularly lacking in herbivorous zooplankton. Since one of the concerns in 1957 was phytoplankton-zooplankton relationships, it was imagined that deeper hauls might give a false impression of the food available by sampling ungrazed populations of phytoplankton. This rationale seems somewhat less valid in retrospect and, except for a shortage of sample bottles, a series of deep hauls with the fine-mesh net should have been taken as well. However, the 1957 season did produce ample confirmation that the small and young forms of zooplankton were almost all found above 20 m., and therefore well sampled by the fine-mesh net.

Sixty-seven plankton samples from the regular series were analysed. The whole coarse-net samples were first searched for larger organisms (mainly A. digitale, S. elegans and large bottom larvae) which were measured when pertinent and removed. Subsamples were taken from these thoroughly mixed samples by a large-bore suction pipette and volumes determined in small graduated cylinders. The sizes of subsamples were varied according to the makeup of the sample, but were usually greater than 10% and never less than 6%. Complete counts were attempted of all zooplankters in these subsamples under the dissecting microscope. Sometimes this required sub-subsampling for small and abundant forms. Arbitrary subsamples were removed from the fine-net samples. Again a complete accounting of the contents

usually involved further subsampling. Proportions of naupliar stages and counts of the smallest forms were determined by concentrating subsamples, then pipetting well mixed fractions onto slides for analysis under the compound microscope. Finally, phytoplankton was assessed under the compound microscope, relative to the previously counted nauplii and other small forms appearing on the slides. It is well known that sampling error is greatly increased by partial or "field" counts of samples under the microscope, and this practice was only resorted to when counting phytoplankton at its peaks of abundance. An attempt was made to identify all species of zooplankton, but the phytoplankton was categorized in larger groups, down to genera in some cases.

All the larger organisms were measured from the whole samples, and thirty or more individuals from the pertinent species or stages in the subsamples were measured when possible. The measurements taken are given in the discussions of each species which follow.

The fine-mesh net was always used in conjunction with the standardized vertical hauls of the coarser net, thus affording a means of getting quantitative estimates of smaller organisms. To do this, we must assume that animals of an intermediate size and agility are adequately collected by both fine and coarse nets. In Ogac Lake, the older copepodites and adults of Pseudocalanus minutus seemed of a suitable size and abundance to act as intermediaries. Their suitability was verified as follows. Where counts in the subsamples were

sufficiently large (30 or more), the numbers of a given stage from the fine-mesh subsample were expressed as a proportion of the number counted from both nets. By tests of significance of difference between proportions it was found that while copepodite stages IV, V and VI (adults) were sometimes sampled to a significantly different extent by the coarse and fine-mesh nets, there was no bias to suggest that stage IV was retained less than V, or V less than VI by the coarse net. Stage III showed perhaps a slight tendency to be undersampled, but there was a persistent and invariably significant undersampling by the coarse net of stage II and I copepodites. For these reasons combined numbers of P. minutus stages IV through VI were considered safe to make counts of smaller forms in the fine-mesh net equivalent to counts of larger forms in the coarse-mesh net. Usually quite large numbers were available: of 24 conversions, 11 were based on counts from both nets of over 100, 12 on counts of over 50 (sometimes the whole sample) from the fine and over 100 in the coarse net, and one involved the entire fine-net sample of 32 individuals of P. minutus. The sampling errors were thus kept reasonably small.

It remains only to convert numbers in the standardized vertical haul to numbers per unit area (the proper unit when the entire water column can be accounted for). Although small-mouthed nets (of the "Wisconsin" or "Hensen" sort) of No. 6 mesh are known to be 100% efficient in filtering a water column when towed at 0.5 m. sec.⁻¹ (Ricker, 1938), a conical net like those used at Ogac Lake was tested from M/V "Calanus"

in September 1960, in southern Hudson Bay and found to be less efficient. Here too the net was not likely to be affected by clogging. The No. 6 net to be standardized was suspended adjacent to a Clarke-Bumpus sampler, modified and open for vertical use, and fitted with the same mesh. The whole unit was lowered slowly (so that no back-revolutions on the sampler could be seen in the first few meters of descent) to 50 m. The paired nets were raised vertically at a constant speed, and the whole operation repeated seven times. The samples thus obtained from the "same" column of water were examined for numbers of larger (IV - VI) P. minutus and Calanus, neither of which will pass through the No. 6 mesh (see above). From the quantitative Clarke-Bumpus samples we can determine the numbers of these copepods per unit volume or area of the 50-m. water column, and therefore the number expected to be captured by a 100%-efficient net of the same diameter as the sort used. Obviously the scatter revealed in Figure 21 makes such estimates of limited accuracy, but it seems safe to conclude that the efficiency of a net raised at 0.5 m. sec.^{-1} will be of the order of 60%. All the samples taken at Ogac Lake and expressed in numbers per m.^2 are corrected accordingly.

The biweekly series of plankton hauls was supplemented by irregular samples. An important group was collected on August 21 from 10 depths in the middle basin by horizontal tows with the Clarke-Bumpus sampler fitted with a No. 10 net and bucket. Further series were begun to determine the extent of vertical migration, but were thwarted by instrument troubles.

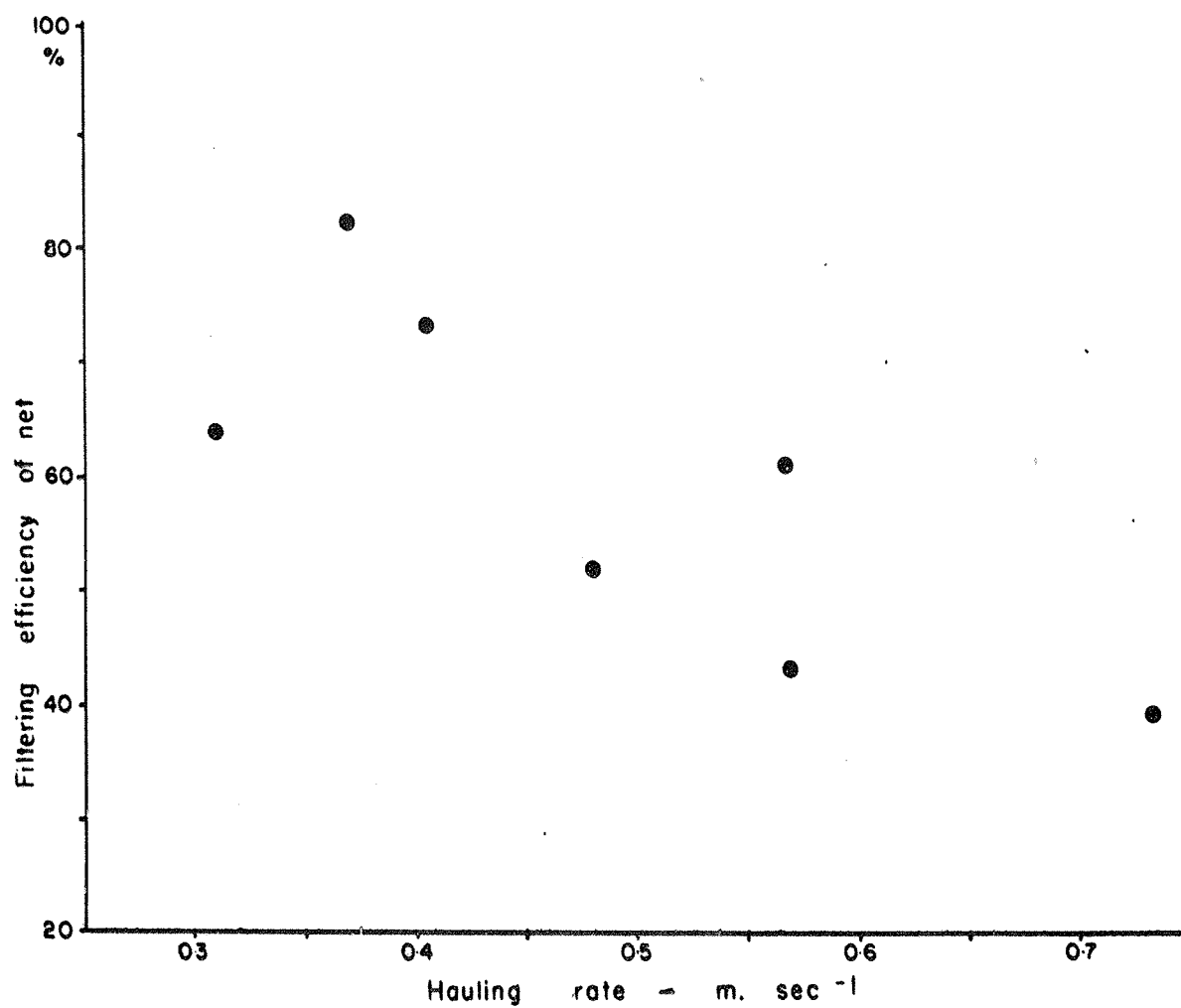


Figure 21. Efficiency of the conical, 30-cm. net of No. 6 mesh used at Ogac Lake, when towed at different rates. See text for explanation.

Water samples of 500 cc. were taken from selected depths between late June and late September and suction filtered through fine paper filters. The samples were stored frozen for over 2½ years after return from the field before being acetone-extracted and read on the Klett-Summerson photometer. The results may therefore give only relative values of chlorophylla through the season.

Phytoplankton

The assessment of phytoplankton was unsatisfactory, particularly as no direct measurement of primary production was made. We must rely on net collections and limited chlorophyll data. However, the material collected is sufficient to outline the phytoplankton cycle, in which the qualitative aspects prove to be of significance to the zooplankton biology which is the main concern of this study.

Phytoplankton has been studied in landlocked fiord waters of Norway (e.g., Braarud and Hope, 1952), but in these settings allochthonous phytoplankton and other complications have to be reckoned with, and the work has little direct bearing on the circumstances of Ogac Lake.

Chlorophyll. The seasonal values of chlorophylla are listed in Table VII. The samples are too widely spaced in both time and depth to present an accurate picture of primary production through the season.

Chlorophyll values were relatively greater throughout the open-water season in the lower basin, especially at 20 m.

Table VII. Seasonal chlorophylla content of various depths in Ogac Lake and in the fiord outside between late June and late September. Values in $\mu\text{g. per litre.}$

<u>Basin</u>	<u>Depth</u> (m.)	<u>June 24</u>	<u>July 2-4</u>	<u>July 17-20</u>	<u>Aug. 3-4</u>	<u>Aug. 17</u>	<u>Aug. 31</u>	<u>Sept. 15</u>	<u>Sept. 29</u>
Lower	3	-	0.4	-	-	-	-	-	-
	5	-	0.2	0.3	0.0	-	0.3	-	-
	10	0.5	0.3	0.8	1.1	1.6	1.3	0.0	1.3
	20	-	3.0	1.5	3.8	-	5.6	-	0.1
Middle	2	-	0.4	-	-	-	-	-	-
	5	-	0.0	0.0	0.2	-	0.6	0.0	-
	10	0.1	1.2	0.1	0.9	0.0	0.0	0.3	-
	20	-	1.1	0.0	0.6	-	0.4	1.2	-
	30	-	-	18.7	8.4	-	-	-	-
Upper	2-3	-	0.9	-	0.0	-	-	-	-
	5	-	-	0.0	0.0	-	1.0	0.3	-
	10	0.3	0.4	0.5	0.0	0.7	0.2	0.3	-
	20	-	0.6	0.2	0.6	-	1.0	1.6	-
	30	-	22.9	16.4	8.0	-	-	-	-

<u>Ney</u> <u>Harbour</u>	<u>Depth</u> (m.)	<u>June 23</u>	<u>July 6</u>	<u>July 21</u>	<u>Aug. 7</u>	<u>Aug. 20</u>	<u>Sept. 6</u>	<u>Sept. 25</u>
	0	-	-	-	1.2	-	-	-
	5	0.0	-	0.7	3.7	0.3	-	-
	10	0.0	1.5	0.5	2.6	2.8	-	-
	20	-	-	-	3.6	0.5	0.4	0.6
	25	-	1.2	0.1	-	-	-	-
	30	-	-	-	2.9	0.7	-	-
	50	0.8	0.5	1.3	2.4	0.6	-	-

In the upper and middle basins there was a decline after the beginning of July, and perhaps a slight recovery towards the end of the season. The values in the fiord outside reached their maximum in early August, rather higher than at shallow depths in the lake.

One interesting feature deserves comment. Chlorophyll values from the middle and upper basins at 30 m. are at least an order of magnitude greater than at any other depth. Any phytoplankton at 30 m. would probably be above the compensation point in these clear waters (see p. 42) but would be at or below the anaerobic level. The populations of grazing zooplankton decreased below 20 m. (pp. 101, 122), but there is no suggestion of much greater phytoplankton quantities in two fine-mesh hauls from below the anaerobic level (see p. 76). This combined with the relatively small changes in oxygen below 20 m. in the middle and upper basins (see Fig. 20) suggests that the high values at 30 m. represent "dead" chlorophyll, sinking out of the trophogenic layer. The decline in quantity between early July and early August probably reflects the decreasing production in the trophogenic layer as well as sinking from and degradation in the anaerobic layer; the last process might be quite slow.

It was hoped that the chlorophyll values even if relative would serve to give some measure of absolute primary production, in combination with the fairly well plotted changes of oxygen in the lake. However it has become quite obvious on analysis that chlorophyll values from a few depths

are not safely integrated to give values for the whole water column. The importance of marked vertical differences in primary production in the sea has recently been stressed by Sorokin (1960), and such vertical differences are doubtless much greater in the highly stratified Ogac Lake.

Net-phytoplankton cycles. With all their deficiencies, the net samples undoubtedly give a much more faithful account of the cycle of phytoplankton production in Ogac Lake than do chlorophyll values.

Figure 22 depicts counts of phytoplankton between early June and mid September. There are striking differences in the composition and abundance of the phytoplankton of the three basins.

In the lower basin there was a large flowering of Nitzschia commencing in mid June and extending through early July. Fragillaria spp. (including possibly other ribbon-shaped genera) followed with a peak in early July. Only then did Chaetoceros become the dominant diatom, whose numbers were sustained at a high level throughout July and August. Other diatoms, mostly of small size, were not taken in very large numbers. A few silicoflagellates were taken at the height of the Chaetoceros, and large dinoflagellates, particularly Ceratium, were significant after July. There was recovery in the mixed diatom population at the end of August, after the decline of Chaetoceros.

In the middle basin Nitzschia was all but absent, but Chaetoceros was present in enormous numbers in mid June,

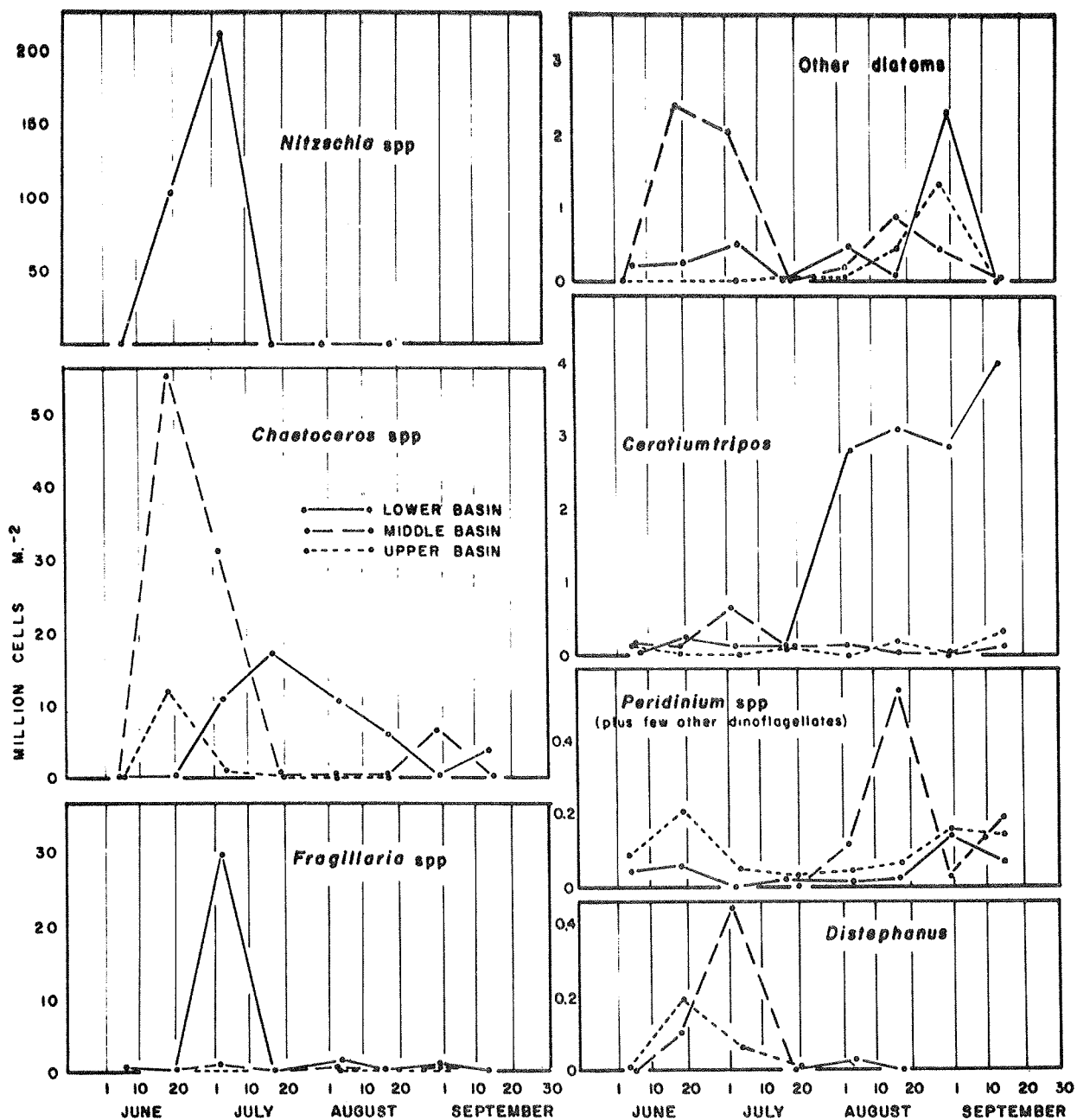


Figure 22. Counts of phytoplankton cells taken by the No. 20 mesh net in vertical hauls from 20 m. to the surface in the three basins.

and almost finished by mid July. A population of small pennate and centric diatoms accompanied this maximum. The tiny silicoflagellate, Distephanus, probably mostly passed through the meshes, but was unlikely to have been a significant primary producer. There was a marked increase of dinoflagellates in mid August. Although Ceratium did not take part in this increase above the 20 m. level, it was the only phytoplankter which was much more abundant in deep water in August (see below). There its population may have matched that of the lower basin. Other diatoms, mostly small pennates among which Asterionella was prominent, recovered after the beginning of August, and a distinct maximum of Chaetoceros followed upon the late August tides.

The cycle in the upper basin was initiated by a burst of Chaetoceros. This may have reached a peak before June 18, for many spores were present then, but at any rate was of considerably lower amplitude and shorter duration than the Chaetoceros flowering of the middle basin. Phytoplankton was sparse in early August but there was a development of small "other" diatoms from the middle to the end of August.

The early peaks and declines of Chaetoceros in the upper and middle basins were matched by the drops in chlorophyll after early July (Table VII). Similarly the sustained Chaetoceros population in July and August parallels the persistently higher chlorophyll values in the lower basin in summer. In each basin, also, the decline in oxygen (p. 56, Fig. 20) follows the reduction of the major spring flowerings

of Nitzschia-Fragillaria in the lower basin and Chaetoceros in the middle and upper basins. The seasonal low in primary production appears to have been in mid to late July. The recovery of oxygen after the beginning of August may be partly attributed to increases of dinoflagellates and "other" diatoms. This last category was certainly undersampled by the nets, as it consisted largely of a variety of small pennate diatoms. However, it seems from these comparisons that the fine-mesh net, although by no means expected to retain all plant cells equally well, did not miss any major component of the phytoplankton cycle. The importance of the nanoplankton has recently been reviewed by Yentsch and Ryther (1959), who stress the insufficiency of net samples in Vineyard Sound. There is general belief that the percentage of phytoplankton biomass caught by a fine-mesh net is greater in northern waters. Tiny diatoms rather than flagellates made up the major portion of the nanoplankton sampled by Yentsch and Ryther, and the same seems true of Ogac Lake.

Possible effects of grazing. Although there is a marked correlation between production of the dominant herbivore P. minutus and the flowerings of Chaetoceros (see pp. 82-97), grazing in its turn does not appear to have been primarily responsible for the declines of phytoplankton. In the first place, grazing by P. minutus fails to account for the maintenance of Chaetoceros in the lower basin and its rapid decline in the other basins. Also, many of the Chaetoceros after the peaks in the middle and upper basins were spores, indicative of inimical

conditions for further growth. Finally, with one or two exceptions the plant crops were not notably larger below 20 m. following the Chaetoceros peak in the middle basin (Table VIII) although it will be shown that herbivorous zooplankton was much scarcer below this depth. Most of the Chaetoceros below 20 m. on July 17 were spores, and certainly not in numbers approaching the earlier peaks. Ceratium was much more common at depth (apparently matching the population in the lower basin), but this large flagellate rarely falls prey even to Calanus (Marshall and Orr, 1955) and is therefore unlikely to have been kept grazed down by the smallish herbivores in the upper waters of the lake.

Nutrients, morphometry, and the effect of tides. As a rule the arctic diatom succession consists of two major modes--an early peak of "shade" Pennatae, adapted to low illumination and probably high nutrients, and often developing under the ice, followed by open-water Centriceae (Bursa, in press). The dinoflagellates usually appear in the open-water season.

In Ogac Lake the succession in the lower basin, where the pennates Nitzschia and Fragillaria developed under the ice and were succeeded in summer by the centric Chaetoceros, most resembles the usual arctic marine pattern. In the middle and upper basins the pennate mode was absent, and Chaetoceros flourished early under the ice. While phytoplankton cycles, in view of demonstrations of minor metabolites, antibiosis, and other complexities, are not to be explained lightly, it may be that the main differences between the successions in the

Table VIII. The numbers of phytoplankters collected on two dates in the middle basin by sequential hauls with the No. 20 net raised from 35 m. and 20 m. respectively.

<u>Date</u>	<u>Depth</u>	<u>Number per m²</u>					
		<u>Chaetoceros</u>	<u>Fragillaria</u>	<u>Other Diatoms</u>	<u>Distephanus</u>	<u>Peridinium</u>	<u>Ceratium</u>
July 19	20-0 m.	250,000		15,000		30,000	115,000
	35-0 m.	1,480,000	115,000	50,000	5,000	65,000	700,000
Aug. 3	20-0 m.	370,000	405,000	195,000		115,000	165,000
	35-0 m.	445,000	375,000	140,000		85,000	2,370,000

lake have a simple basis. The lower basin receives the most sea water, offers the greater opportunities for nutrient recovery (see below) and is almost certainly richer in nutrients at the end of winter than the other more isolated and stable basins. Fragillaria and Nitzschia may have been permitted their normal development through this more marine quality of the lower basin. On the other hand, the ice was thinner and wasted earlier in the middle and upper basins, and light penetration must have been sufficient to support the "open-water" Chaetoceros in these presumably more nutrient-poor waters.

While Nitzschia may be precluded from the upper and middle basins because of shortage of nutrients in spring, it appears that the decline of Chaetoceros in its turn may be a result of nutrient depletion. The direct evidence for this is limited. Phosphate was measured in 1952 (Table IX) but the results as absolute figures are considered unacceptable, due to technical troubles (Dr. A. D. Dawson, pers. comm.). While there is no trustworthy indication that phosphate was limiting in the upper waters, it is interesting to note that the values were persistently several times higher in the deeper aerobic waters of the lake. Presumably either phosphate was not as fully used at these depths or was being regenerated from falling seston before the latter was beyond reclaim in the anaerobic water. That nutrient material is lost from the aerobic level, as in all meromictic lakes in which it has been studied, is further indicated by the high values of chlorophyll at 30 m. in the middle and upper basins, where it does not likely represent

Table IX. Measurements of dissolved inorganic phosphate (in $\mu\text{g. at. l.}^{-1}$) from Ogac Lake in late July and early August, 1952.

	m.	<u>July 28</u>	<u>Aug. 4</u>	<u>Aug. 11</u>
Lower Basin	0	0.1	0.1	0.7
	10	0.4	0.5	0.6
	17	2.0	2.1	1.4
Middle Basin	0	0.2	0.1	0.6
	10	0.5	0.4	0.6
	25	2.1	2.0	1.0
Upper Basin	0	0.1	0.1	0.7
	10	0.4	0.4	0.8
	25	1.8	1.9	1.4

living plants (p. 71).

The lower basin not only receives more invigorating water from the sea, but may have distinct morphometric advantages for the maintenance of primary production. The basin is shallower, and the water is aerobic almost to the deepest parts. Whether the reduction of the sediments underlying oxygenated water (p. 53) aids this process or not (Hayes and Phillips, 1958), nutrients, and even viable cells, have much more opportunity of being brought back into the water column of the lower basin by lateral exchange. This lateral recirculation may well have prevented the early decline of Chaetoceros found in the other two basins.

While the lower basin receives the most sea water and supports the most sustained production of phytoplankton, there is a seeming contradiction in the immediate effects of the tides of late August and late September. On August 31 there was a distinct maximum of Chaetoceros in the middle basin, but not in the other two basins. On September 29, although the fine-mesh net was not used, Chaetoceros appeared abundantly in the coarse-net samples from all basins. The samples cannot be made quantitatively equivalent to the net-phytoplankton cycle in Figure 22, but the population was definitely larger in the middle basin, as in late August. This effect also may have a morphometric explanation (see Fig. 2). Water entering the lake from Ney Harbour flows down a steep, boulder-strewn slope, almost lacking in soft sediments, to enter the lower basin at the appropriate density level. Water continuing on to the

middle basin must flow over a fairly extensive area of the sill and down a shallower, muddy slope in seeking its density level. Such a flow could recover much nutrient material and viable cells, and deliver them to the water column. Water flowing into the upper basin would already have been enriched, but might have gained little from the steeper slope at the threshold of the upper basin (the putative density current discussed on p. 31 would have carried slope material below the depth where it could have been used). This explanation of the greater post-tidal development of Chaetoceros in the middle basin has the further advantage of not detracting from the argument that the lower basin was morphometrically more suitable for a sustained nutrient recirculation.

It is clear that the sinking of material from the trophogenic layers of the middle and upper basins can result in permanent loss of nutrients to the anaerobic depths. The spring flowering of Chaetoceros in these basins may indeed be largely supported by nutrients recaptured and distributed by the latest inflowing tides of the season (presumably late October in 1957). At that time of year, and under the new ice, the phytoplankton populations would no doubt be too light-starved to take advantage of the nutrient supply, which would remain unutilized until spring. The lower basin, while receiving a smaller supply of nutrients from the bottom for immediate use, would build up a higher nutrient supply in winter, both through slow recovery from the bottom, and through degradation of the organic content of the larger amount of sea

water which it receives in autumn.

The Biology of Pseudocalanus minutus (Krøyer)

Annual cycle. Seasonal abundance of the six naupliar and six copepodite stages of P. minutus in the three basins is given in Figure 23. The copepodite and adult cycle is given in greater detail in Figure 24, which includes data from the last day of sampling (September 29) when the coarse net used sufficed to catch the older stages (see p. 66).

A glance at Figure 23 will at once reveal marked differences between the three basins. Egg production and the ensuing development of nauplii are remarkably well correlated with phytoplankton conditions in the three basins, specifically with net-sampled Chaetoceros, as shown clearly in Figure 25. However, there are a number of further subtleties which demand an inquiry.

It is known that individual female Calanus may produce several clutches of eggs with intervals between, and it has been suggested by Marshall (1949) that P. minutus may also spawn more than once. However the times of such spawnings overlap in the sea, and the resultant broods (a term which loses value in the literature by being used as equivalent to "generation") cannot be traced. In Ogac Lake, where populations are slower developing and relatively synchronous, such broods seem quite apparent. The eggs of P. minutus may be found attached in ovisacs to the females or free, as groups or individual eggs, in the sample. It may be that a single,

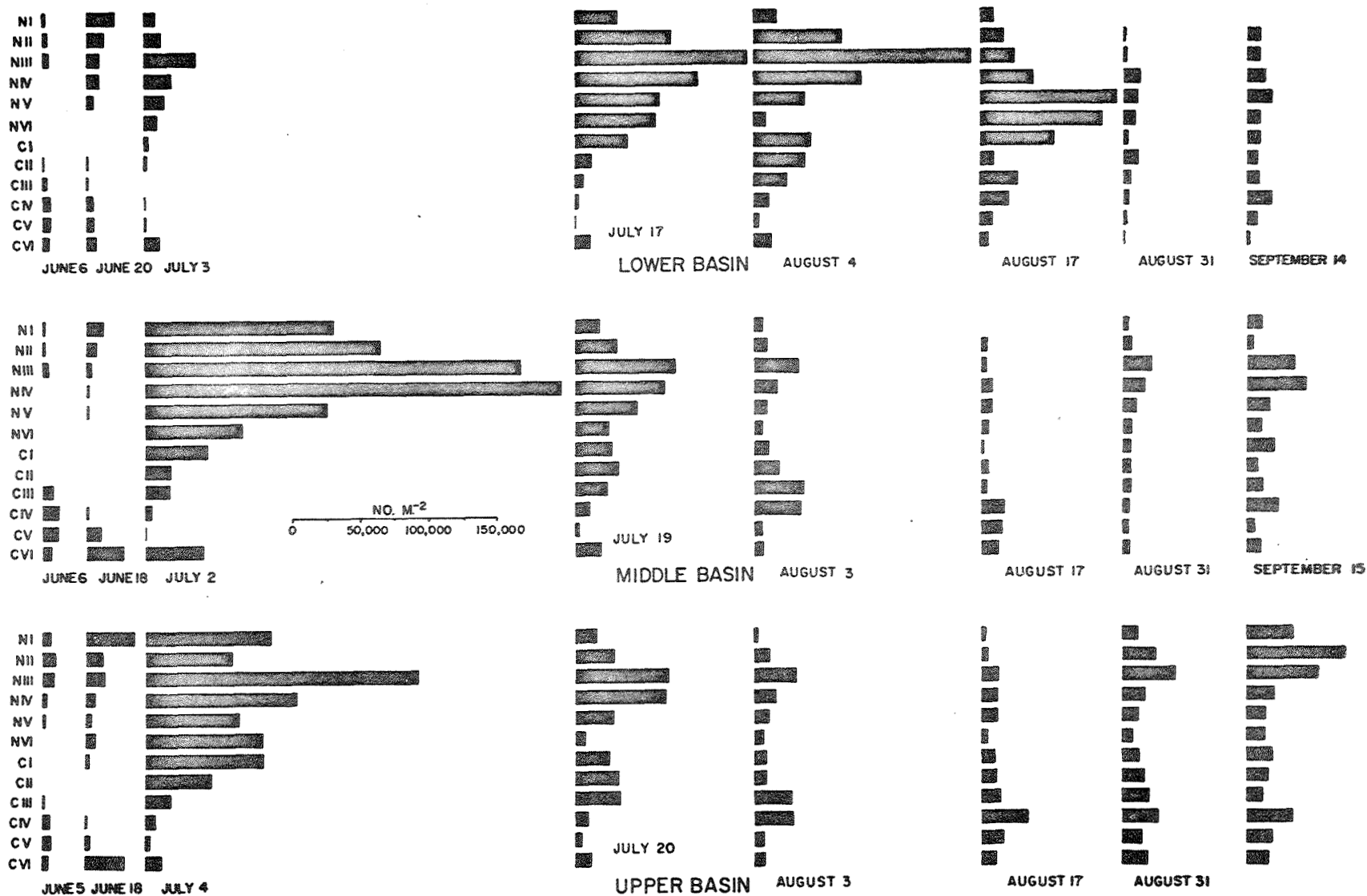


Figure 23. Numbers of all stages of *Pseudocalanus minutus* through the season.

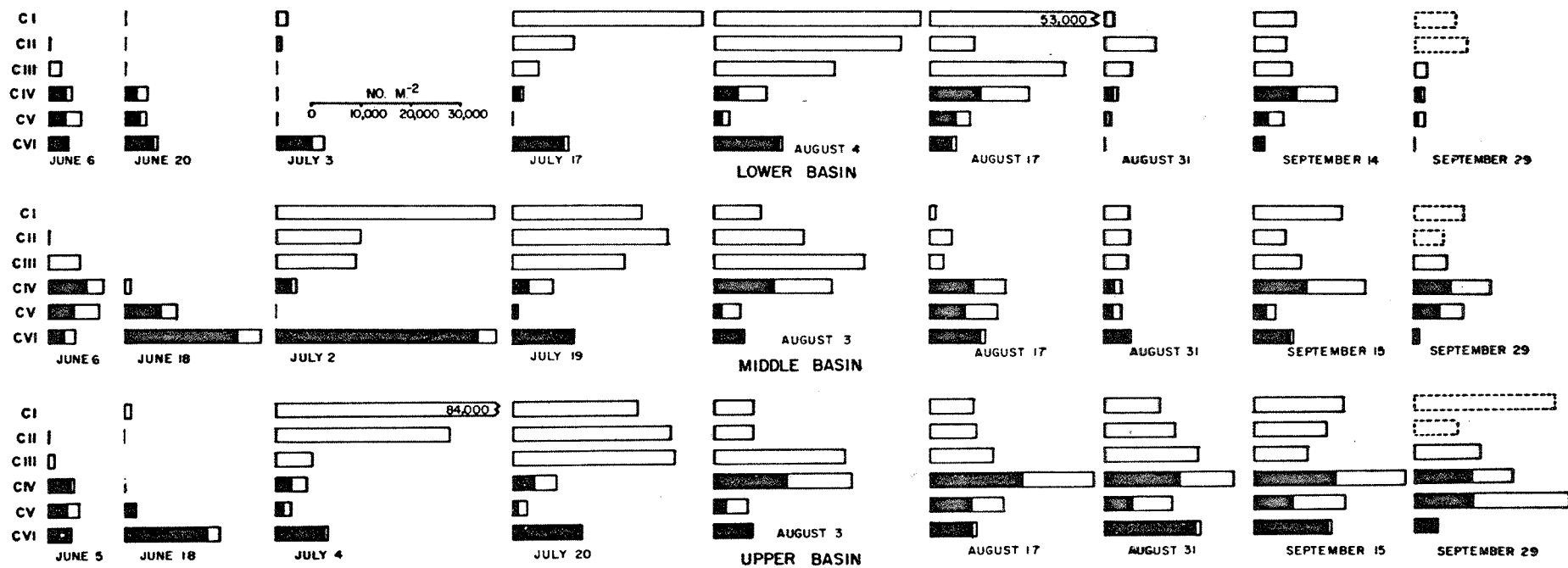


Figure 24. Numbers of the copepodite stages of *P. minutus* through the season. Females of stages IV to VI shown in black. Copepodites I and II on September 29 estimated (see text).

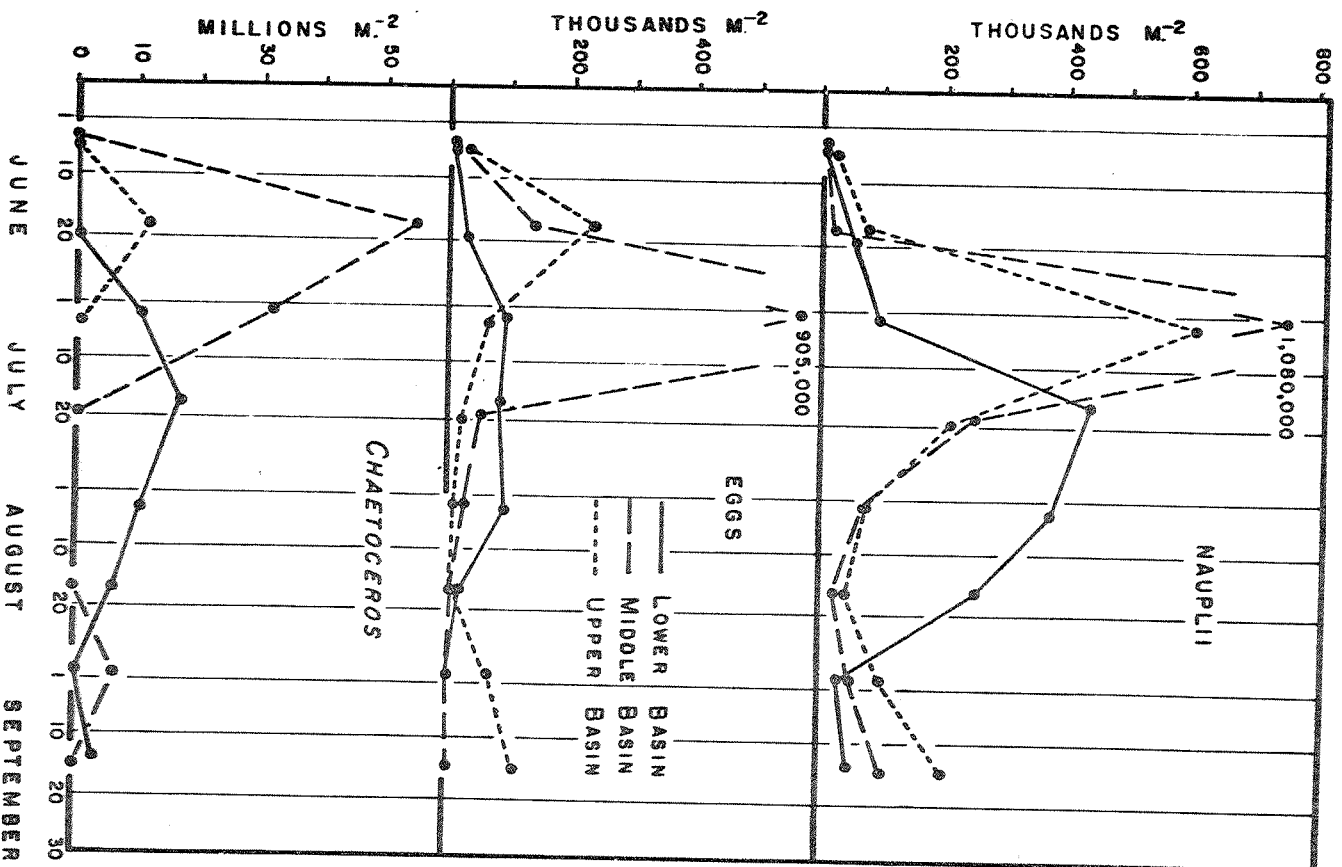


Figure 25. Relationship of reproduction and abundance of nauplii in *P. minutus* with abundance of the diatom *Chaetoceros* in the three basins.

undisrupted ovisac constitutes a brood, but it is not known if the eggs became detached from the females in the net, or in the waters of the lake. It is assumed that the eggs, if free, do not sink out of the upper 20 m. of the lake before hatching, and are fully sampled by the fine-mesh net.

The cycle was most advanced in the upper basin, where the first brood appeared in mid June as a high density of eggs, some of which were entering the naupliar stages. This was in response to the highest recorded count in that basin of Chaetoceros, which was probably in decline by then (see p. 74). This same first brood appeared two weeks later as an abundance peak in nauplius VI and copepodite I. In the meanwhile, a second spawning produced the mode at nauplius III, and there was a small peak of nauplius I which possibly represents a third brood in early July (stage I is quite ephemeral, and quickly develops to III, where growth slows down in most calanoid copepods, so must represent a contemporary hatching). While food had been sufficient to produce two broods and a possible small third (food storage probably aids the adult females), it was by no means sufficient to continue supporting the broods. The first brood developed slowly through July and August, but metamorphoses of the second brood appeared halted, and its numbers decreased sharply through July and August. Of the third brood, there was not a sign. It would seem that the older first brood was much better fitted to survive in the conditions of depleted food.

In the middle basin the broods initially were much

larger, attributable to the larger adult population, but probably not to food (see below). The height of first spawning must have been between mid June and early July, expressed in the large mode at nauplius IV on July 2. The recorded Chaetoceros peak in mid June may thus have been close to the actual peak of the flowering. A second brood of nauplii was imminent on July 2, judging from the enormous number of eggs present. In mid July the first brood appeared as a mode at copepodite II, and the great egg number of July 2 had come down to a rather paltry peak at nauplius III. If there was a third brood between early and mid July, it was obliterated. Further development in the food-poor waters followed the pattern of the upper basin--slow growth of the first brood and attenuation of the second.

In the lower basin egg numbers increased more slowly, and did not approach a maximum until early July. Nitzschia, which was present in large numbers in mid June, did not appear to stimulate egg production. This would seem to be good indirect evidence for selective feeding, and it is interesting to note that Harvey (1937), in an early demonstration of selective feeding, found that "Nitzschia"¹ was poorly filtered by Calanus. Only a few nauplii were present in early July, and the numbers of eggs then represented the first brood, and apparently developed in response to recent increase in Chaetoceros. The first brood appeared next with a mode at nauplius III in mid July. A second brood was expressed as a peak of nauplius

¹ Possibly Phaeodactylum, but of the same general size and form as Nitzschia.

III in early August. A third brood appears not to have developed. Both first and second broods in this basin continued to grow through mid August, in response to the maintained supply of Chaetoceros.

The correlation between the timing of egg production and food supply as well as the effect of continuing food on survival of the young is well known in marine P. minutus. However, there are certain intrinsic factors in reproduction which have not been clearly revealed in the several studies of the marine form.

In the first place, only two broods (the third is certainly small, if it exists) appear to be spawned by each female of this species in Ogac Lake. At first glance this might be attributed to the failure of the food supply after late June or early July in the upper and middle basins, but the same phenomenon appears in the lower basin, where food was available after the spawning of the second brood. The limitation is intrinsic, and the second spawning is followed by the death of the females and their replacement by initially non-fecund females of the first brood. Reduction of numbers of females of the old generation is shown by early August in the upper and middle basin, and mid August in the lower basin (Fig. 24). The females of the new generation averaged smaller, and clearly had all but replaced the old generation mid August in all basins (Fig. 26).

A second limitation appears to be the number of eggs produced by a female. Without more frequent collections, this

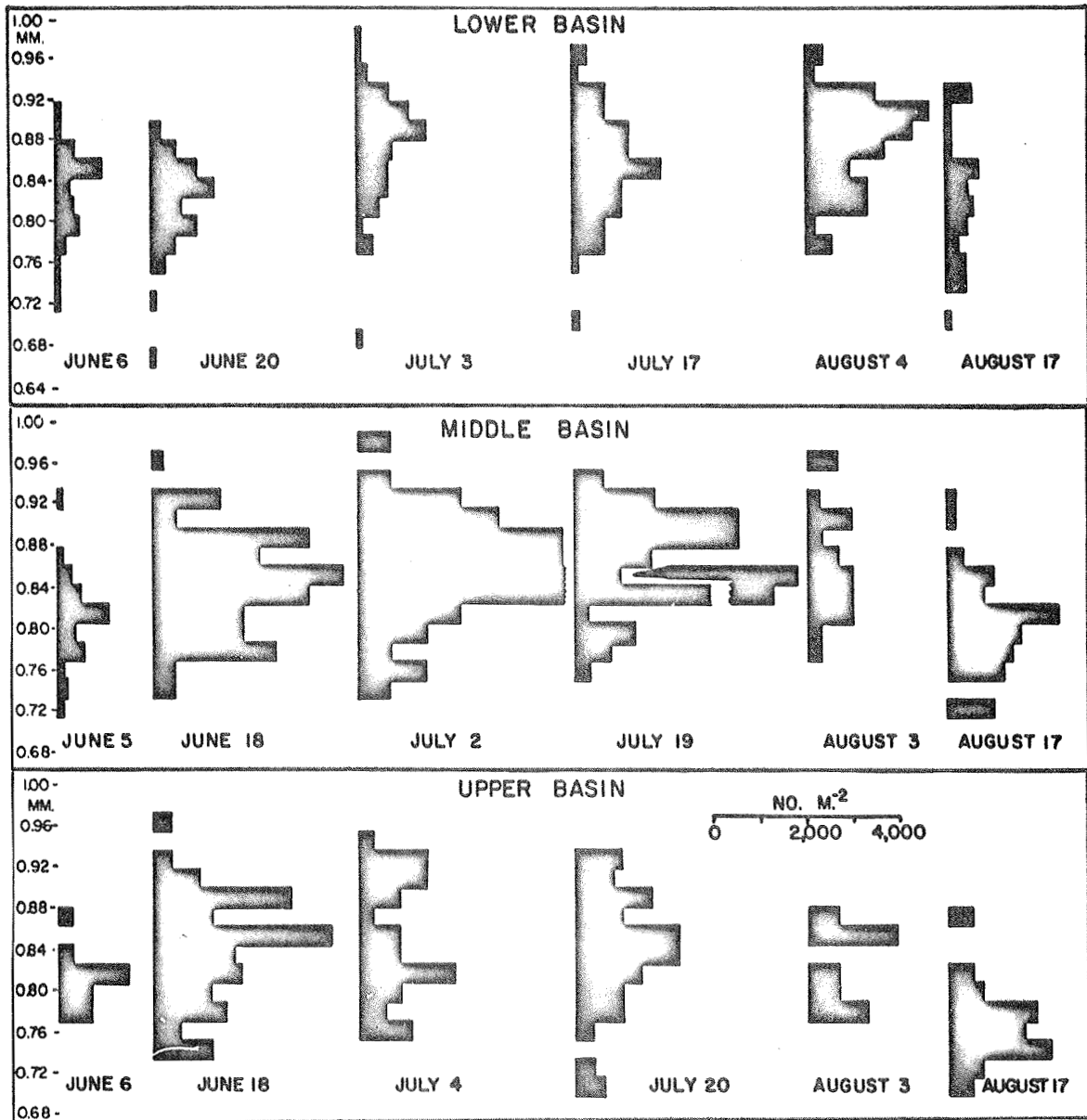


Figure 26. Size (cephalothorax length) distribution of stage VI ♀♀ *P. minutus* between early June and mid August in the three basins.

could not be determined exactly, but rough approximations of calculated natality are set out in Table X. The minimal stages between brood modes have their numbers divided equally between the two broods. Apart from errors of sampling, which are obviously large, the figures are further limited by the fact that the broods have suffered varying amounts of mortality, and one (eggs in the middle basin on July 2) may not have been completed. However, there is no indication in Table X that the larger Chaetoceros peak in the middle basin or the sustained flowering in the lower basin supported a higher natality. In Calanus (Marshall and Orr, 1955) there is good laboratory evidence for asymptotes in both rate of laying and size of the whole production of eggs when food is increased. Marshall (1949) made observations on P. minutus in Loch Striven which bear on this. By counting eggs per undisrupted egg sac she found that the highest numbers (around 35-40) per female occurred during the spring diatom maximum. Secondary diatom maxima had little if any direct effect on egg number, which declined steadily to about 10 per sac in autumn. Rather, egg number was correlated highly significantly with female size as such. It is interesting that the calculated natality (average of Table X) in Ogac Lake was 27, quite comparable with the maximum of 35-40 eggs per ovisac in Loch Striven, and not merely 10, the number produced by Loch Striven P. minutus of comparable size (ca. 0.85 mm.). Further aspects of size will be discussed separately (p. 102).

Although Fish (1936) has suggested that each female

Table X. Calculated natality in the two broods of Pseudocalanus minutus. Numbers of nauplii or eggs within each brood (delimited as explained in text) divided by number of females present at same time. Counts from subsamples of fine-mesh net hauls, from 20 m. to the surface.

Basin	First Brood					Second Brood				
	Date	Brood Mode	No. ♀♀	No. in brood	No. young per female	Date	Brood Mode	No. ♀♀	No. in brood	No. young per female
Lower	July 17	N III	43	2,084	49	Aug. 4	N III	37	1,002	27
Middle	July 2	N IV	94	1,948	20	July 2	eggs	94	1,507	17
Upper	July 4	NVI-CI	39	1,070	27	July 4	N III	39	1,734	45

P. minutus in the Gulf of Maine must produce several hundred eggs to account for the numbers of free eggs in the water, his sampling was less critical than Marshall's (1949), and in fact his tabulated data suggest no such high natality. It would be of value to know if the double brood is found in all populations of P. minutus, regardless of the number of eggs which make up these broods.

The fate of the two broods in August has been ascribed to food conditions. The second brood all but disappeared in the middle and upper basins, while the older first brood, reduced in numbers, began to enter adulthood before mid August. In the lower basin, where the cycle began later but was well sustained, both broods survived, the older being somewhat less advanced in mid August than those of the other basins.

At the end of August, however, changes occurred which seem not to have been part of this simple progression (Figs. 23, 24). In the lower basin both broods were drastically decreased, but the older copepodites and adults suffered considerably greater mortality. In the middle basin there was an increase of young nauplii but the older copepodites and adults of the first brood were disproportionately eliminated. In the upper basin the older brood maintained itself, while a group of new nauplii appeared--as in the middle basin. Obviously these changes demand explanations.

In the lower basin the end of the Chaetoceros production after mid August (Fig. 25) certainly would have resulted in the reduction of both broods, especially the second, as in

the other basins. The first brood presumably had insufficient time to develop into fecund females before this slowing down of its growth. In the upper and middle basins the first broods were considerably older and more developed in mid August, and some of the adult females must have produced the young nauplii found on August 31.

But what then explains the marked reduction of older copepodites and adults in the lower and middle basins and the status quo in the upper basin? The late-August tides seemingly offer the only possible mechanism. These tides had marked effects on the lower and middle basins, but little influence in upper basin (Fig. 17a, b, c). Further support for this cause is indicated by the fact that the tidal influx penetrated the middle basin at exactly that level (10 m.) where large numbers of older copepodites and adults, but very few younger stages, concentrated in late August (see p. 101). The nature of this inimical effect can only be guessed at, and the question will be returned to in connection with the effects of the late-September tides (below).

The differential mortality of these older stages in the three basins has secondary effects on the ensuing nature of the cycles. Reference should first be made to the phytoplankton conditions (Fig. 22). Only the middle basin showed a distinct maximum of Chaetoceros on August 31, although all basins showed recovery of other diatom populations in August.

In the lower basin there was slight growth of the decimated first and second broods of the summer generation.

There was perhaps some augmentation of young nauplii--a new generation--but phytoplankton was apparently insufficient to support much growth or maturation of the population.

In the middle basin the changes in mid September were curious. Where there were very few older copepodites in late August, there was a distinct mode at copepodite IV two weeks later. Two other modes at nauplius IV and copepodite I were conspicuous. It would seem that the Chaetoceros peak noted only in this basin on August 31 extended into early September and permitted growth of a second generation at that time. The mode at copepodite IV must have developed rapidly from the early nauplii which survived the August tides in the surface waters above the influx. The required rate of development exceeds any modal rate noted for the broods in spring, but the autumn young had two advantages not given to most of those produced in spring: they were present as young nauplii before the diatom maximum, and their very small numbers may have prevented local depletion of food during development. The modes at nauplius IV and copepodite I seem best interpreted as the two broods produced by females which survived and matured after the late August tides. The development rate of these two broods in the two-week period after late August is comparable with the modal rates during the spring. The small size of the broods appears to have been due to the paucity of mature females present; adults had increased by mid September (Fig. 24), but the egg density was still low (Fig. 25). The females of this generation

averaged smaller than those of the spring (Fig. 26), but the natality, which may have been lower (as in Loch Striven, discussed above), is incalculable, as we cannot assume that all adult females were gravid.

In the upper basin, quite another set of circumstances prevailed. There the population was spared the effects of the late August tides, and females continued to mature and build up a considerable supply of eggs (Fig. 25). However, the growth of the first brood produced in spring was on the whole negligible (mode unchanged from copepodite IV), and the development of second-generation broods was slow. The brood at nauplius III on August 31 appeared very much reduced at copepodite I on September 15, while a new brood appeared with a mode at nauplius II, a stage which indicates either very recent hatching or thwarted growth. Apparently the low food supply was sufficient to support reproduction of the matured females, but not the development of their broods.

Unfortunately the fine-mesh net was not used in the series following the late-September tides. The coarse net sampled older copepodites and, by using conversion factors from the three previous series in each basin, the numbers of copepodites I and II have been estimated as well (Fig. 24).

In the lower basin there was a decrease of older copepodites and adults comparable with that effected by the late-August tides. Chaetoceros increased slightly in mid September (Fig. 23) and may have supported the development of what appears to be the second brood produced in July (centered

at nauplius IV in mid September) to a mode at copepodite II. A second generation of nauplii might have been produced by the few remaining adults of the first brood utilizing the Chaetoceros of late September, but it is unlikely that these would have advanced much before or survived well after the onset of winter. The second brood produced in spring in this basin was probably therefore the major source of the adult population the following spring, and the reproductive cycle is essentially annual.

In the middle basin adults apparently died off, but other than this there was little change between mid and late September, presumably because of low food supply (Fig. 23). In this basin the copepodite population of the following spring would be derived almost entirely from the second generation in the summer--the older from a brood hatched before the late-August tides, and the younger from nauplii hatched after those tides; thus two generations were produced during the year.

No Chaetoceros peak was noted until after the late-September tides and there was accordingly little change in the copepodite population of the upper basin, except for a dying off of adults. It is possible that the unwitnessed late-October tides, which probably penetrated the upper basin much more strongly (p. 32), had a more severe effect in reducing the older copepodite population there. At any rate, although a few members of the first brood produced by females born in spring might have gained enough growth from feeding on the Chaetoceros of the late-September tides to winter over, it is

clear that most of the adults in spring are derived from young born the previous spring; the reproductive cycle is essentially annual.

The cause of death of the older copepodites and adults as a result of the late-August and late-September tides remains obscure. It might be speculated that the rapid temperature changes common to both tides were responsible. The late-August tides reduced temperatures in a thin stratum around 10 m. in the middle basin, where adults and older copepodites were concentrated. The late-September inflows, although resulting in greater net temperature reduction, entered the middle basin more erratically at several levels (Fig. 17b, 18). The temperature changes therefore may not have been as sudden at any given depth, which may account for the greater survival of copepodites. The temperature reduction in the lower basin was more profound, and may have been responsible for the greater mortality there (Fig. 24). Although the temperature changes implicated in this mortality are very small (2°C. or less) it is noteworthy that the vertical distribution of P. minutus is strongly affected by temperature differences of the same order, as will be shown below (p. 101). The adults seem particularly sensitive to these tidal effects. Where there is a breeding hiatus in winter, even in more southerly waters (Østvedt, 1955), P. minutus exists mainly as older copepodites. It would appear that adulthood is energetically a large step, and that it also may entail certain sacrifices of metabolic stability.

The life-history of P. minutus in Ogac Lake highlights the distinction between reproductive and production cycles. Although two generations per year occur in the middle basin and essentially one in the other basins, the peak of production is annual in response to the major diatom flowering in all three basins, and probably largest in the reproductively annual population of the lower basin.

In general the described reproductive cycles of P. minutus in the arctic are annual, and most resemble the pattern found in the lower basin of the lake, although two broods have not been demonstrated in the sea. A smaller second summer generation is suggested for several localities, most conspicuously in subarctic Ungava Bay (Fontaine, 1955); it is unlikely that this generation supplants the earlier one to establish a cycle of two generations per year as in the middle basin of Ogac Lake. In the high arctic (Digby 1954, Grainger 1959), individuals from this second generation in summer may overwinter as very young stages, develop as larger copepodites in the food-rich summer, and pass a second winter to breed when $1\frac{1}{2}$ years old. Digby found nauplii, apparently born in late autumn or winter, in small numbers through the winter in East Greenland. There is no suggestion that nauplii overwinter in Ogac Lake, where those found in early June (Fig. 23) are certainly young and recently produced.

Vertical distribution. Widespread observations (summarized by Marshall, 1949) on the vertical distribution of P. minutus suggest that it is not generally found in the

deepest waters, but that the older stages especially avoid the warmer surface waters. Wiborg (1944) obtained critical evidence from his study of the landlocked Norwegian Fiord, Nordåsvatn. The outer basin of this fiord is fairly well ventilated, but oxygen is seasonally absent below 20 m. in the inner basin. In both basins the nauplii and usually the younger copepodites were found in the surface layers, but distinct seasonal differences occur in the vertical distribution of adults and older copepodites, which are described but not explained by Wiborg. Later work on phytoplankton collected at the same time (Braarud and Hope, 1952) makes it quite clear that the times when adults and older copepodites are concentrated near the surface were also times when there were diatom maxima there. Østvedt (1955) described the annual vertical migration of this species between extreme depths (600 m.) and the upper 50 m. of the Norwegian Sea. The return to the surface coincided with the spring diatom maximum, and Østvedt believed it to be a spawning migration.

Unfortunately, evidence on seasonal changes in the vertical distribution of plankton in Ogac Lake is lacking, but a series of horizontal tows with the Clarke-Bumpus sampler was made on August 21. It can be seen from Figure 27 that while the highly stratified Ogac Lake little resembles the usual marine environment, this very stratification gives considerable insight into the factors controlling vertical distribution in the species. The upper and lower limits (1.5 and 28 m., where no specimens were taken) were obviously established

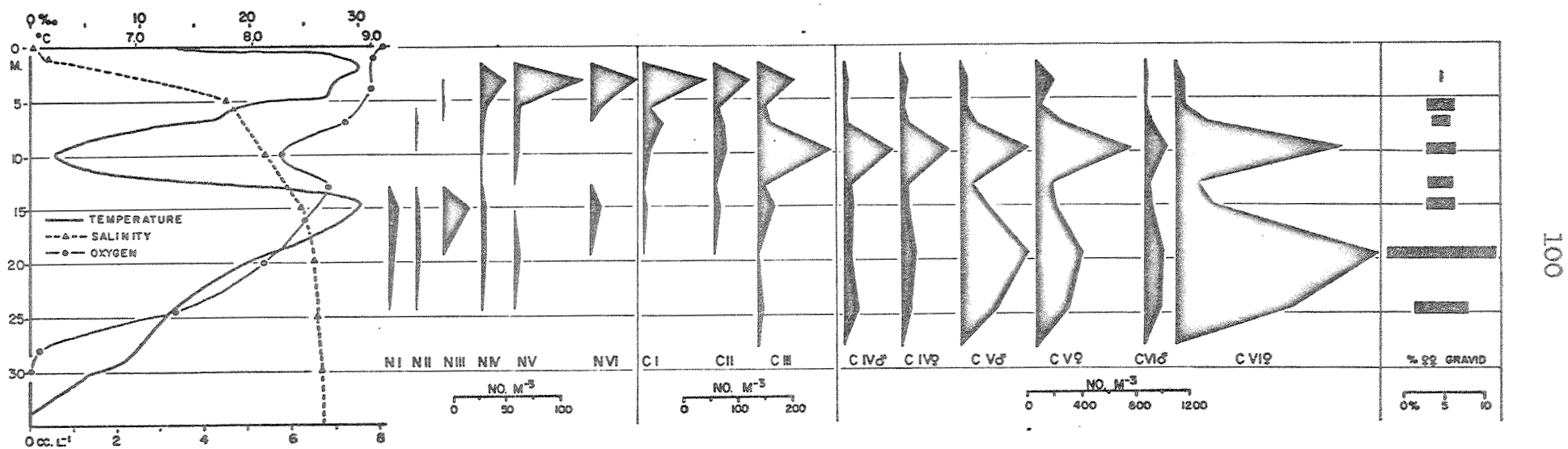


Figure 27. Vertical distribution of *P. minutus* in the middle basin on August 21.

by low salinity and oxygen lack respectively. Between these limits, temperature seemed to show considerable control.

The nauplii were presumably largely born at depth, where the majority of females and the highest egg numbers were found. (Eggs and at least early nauplii were all or almost all of the second generation at this date--see p.93). Quite in keeping with this, most of the deeper nauplii were younger. The nauplii moved surfacewards, but were seemingly balked by the strong negative temperature gradient from 15-10 m. The first two copepodite stages apparently developed with no change in reaction in the upper few meters but a definite tendency to go deeper appears in stage III. Whether the descent is controlled by phototactic or geotactic responses cannot be said. At any rate, it does not appear to be passive, for either the low temperature at 10 m. suppresses the downward movement, or the higher temperature just below this is a barrier to further descent; there is evidence that the latter effect is responsible for the distribution. Size differences (p. 106) suggest that exchanges of copepods between strata are limited. The oxygen minimum at 10 m. was first noted on August 3 and was still present, somewhat less pronounced, in mid August (Fig. 20). Its appearance thus coincided with the advent of numbers of older copepodites of the new generation (Fig. 23). Proportionately more copepodite V than IV and more VI than V were found below the 15-m. level, and more of the females at depth were gravid. These facts together suggest that the deeper population averaged older and that the positive thermal gradient from 10-15 m. was a barrier which

took time or persistence to penetrate in the downward movement.

It is to be noted that the initiation of the descent in stage III is incomplete. The bimodal distribution of stage III is quite different from bimodal distributions of the older stages and cannot be explained with reference to physical conditions alone. The population of copepodite III appears dimorphic in response, but whether this is due to differences which are present at the beginning of this stage or arise during it cannot be said.

Doubtless the older copepodites and adults, if unimpeded by thermal gradients, would continue to descend, and their behaviour in Ogac Lake may be compared with larger scale seasonal movements in the sea. The possible selective value of this descent will be discussed in relation to other features of the life history (p.109).

Size. The correlations between food, temperature and the size of several species of copepods have been given firm expression recently by Deevey (1960a). She studied the seasonal length variations of adult female P. minutus from localities where there is more-or-less continuous breeding through the year, and where size is therefore an expression of immediate or recent conditions. In Long Island Sound, where phytoplankton was never minimal for growth and reproduction, the size of P. minutus was strongly correlated with the widely ranging temperatures. In Loch Striven, where the temperature range was much narrower, phytoplankton and temperature together were influential. Copepods from arctic

waters, where development is slow, were not suitable for the correlations extracted by Deevey, but she supports earlier views that phytoplankton conditions should be the primary determinant of size in waters of such narrow temperature range.

The seasonal range in average cephalothorax length of adult female P. minutus was much smaller in Ogac Lake than in any of the populations analysed by Deevey. However, the rather subtle seasonal variations, as well as differences between the basins do seem explicable in terms of phytoplankton and perhaps temperature (see Fig. 28).

Both old and new generations of adult females are well represented in the samples. Their average length increased in the upper and middle basins in mid June, as recruits were nurtured by the contemporary Chaetoceros flowerings. The increase in size was noted two weeks later in the lower basin, correlated with the later Chaetoceros increase there. The majority of the old generation were presumably dead by mid August, and the break in size appears obvious in both Figures 26 and 28.

Only the older copepodites of the old generation were sufficiently sampled in early and mid June, and these showed the expected increase in average size in the middle and upper basins, and maintenance of size in the lower basin.

Of the new-generation copepodites, all stages in the middle and upper basins showed declines in size after the Chaetoceros peaks of June and early July. The older copepodites

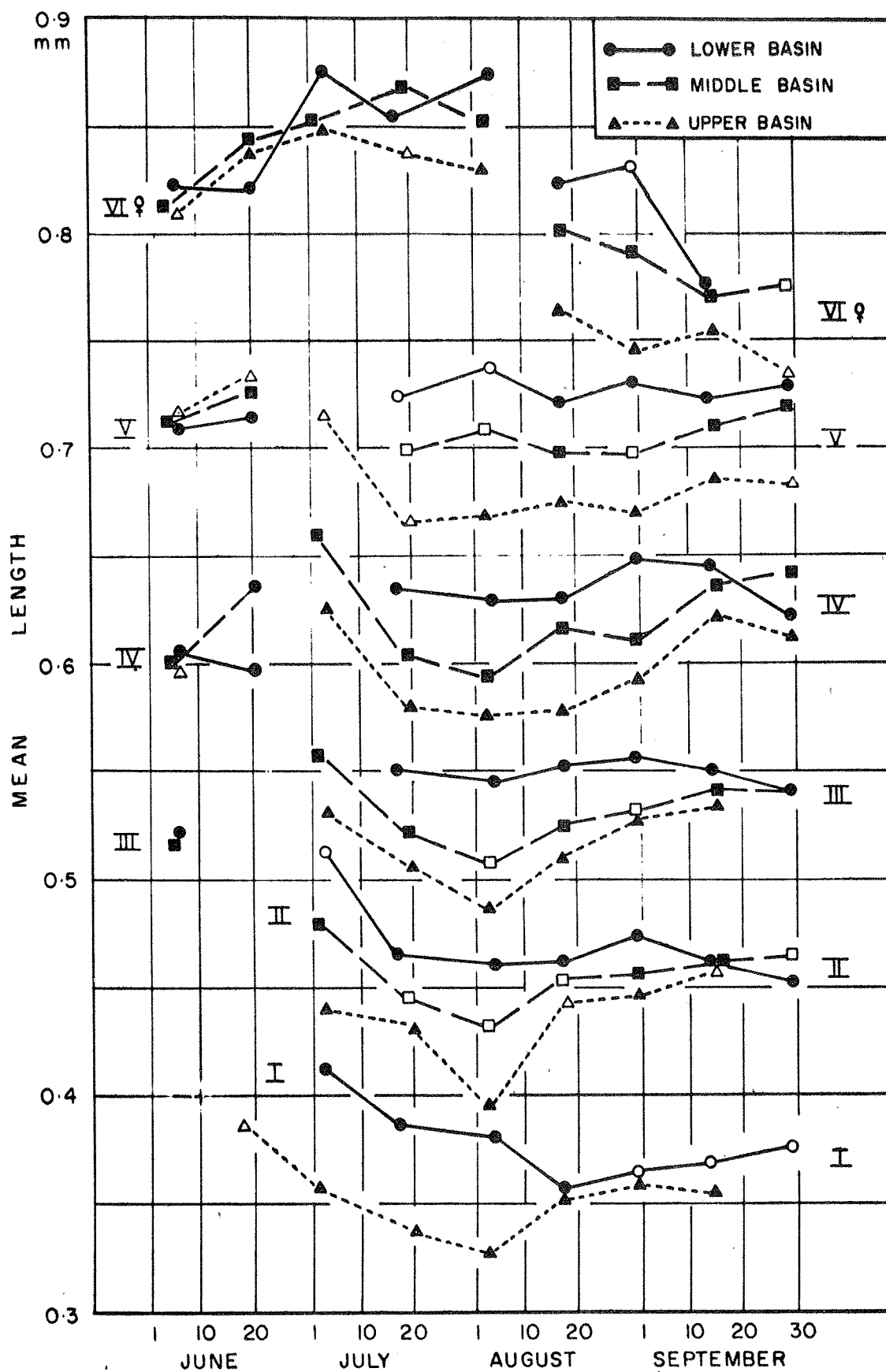


Figure 28. Seasonal variations in mean cephalothorax length of copepodites I to VI in the three basins. Open symbols represent mean of <30 specimens. Old and new generations separated by gaps in lines.

in the lower basin stayed generally constant in size between mid July and mid August, in apparent response to continuing food supply. Of the new generation in the lower basin, only stages I and II were sufficiently common to measure in early July, and it is not clear why they were larger than in mid July, as food conditions were seemingly no better on the earlier date. Possibly here we have an effect of temperature, for the surface waters warmed up considerably during the wasting of ice at this time.

There was a distinct recovery in size of the younger copepodites after early August in the upper and middle basins. This appears correlated with recovery of the "other" diatoms (Fig. 22), some of which may have sufficed the much reduced copepodite populations.

The consistent superiority of size of the younger copepodites in the lower basin over those of the middle, and those of the middle over those of the upper basin is almost eliminated by the end of September. The end of the summer Chaetoceros production in the lower basin is probably involved in this equalization, which would come about more slowly in the slower-developing older copepodites. An increase in size is especially pronounced in the middle basin, where Chaetoceros flourished after the late-August tides.

It is apparent that the seasonal changes in Ogac Lake are attributable to phytoplankton. If there are any effects of temperature differences (e.g., the lower basin was consistently cooler at depth) they seem to be masked by effects

of food. This supports Deevey's (1960a) view that food is primarily responsible for size differences when temperature range is narrow.

The marked anomalies in vertical distribution of P. minutus, discussed above, are matched by distinct, although less spectacular, differences in the size of copepodites at different depths (Fig. 29). There was a general increase of size with depth among the older copepodites, which averaged significantly longer near the lower limit than near the surface. There were, furthermore, distinct size minima at 5.7, 9.7, and 19.5 m. It is tempting to associate the smaller sizes at 9.7 and 19.5 m. with crowding and resultant food depletion, although this does not appear to apply at 5.7 m. That stage III did not appear to show the same pattern as the older copepodites is reasonable, since all molted from stage II which was concentrated at about the same depth near the surface, and thereafter migrated downward. These consistent size differences suggest that exchanges between different depths of older copepodites were in some degree limited, and it may be supposed that some or even most of the individuals at a given depth had molted at that depth.

Allochthonous populations. Each tide brought in populations of P. minutus from Ney Harbour. This was the only one of the four dominant species to receive any substantial additions from the sea. A complete account would require analysis of the annual cycle in the waters outside (not dealt with here), but a brief reference to these allochthonous

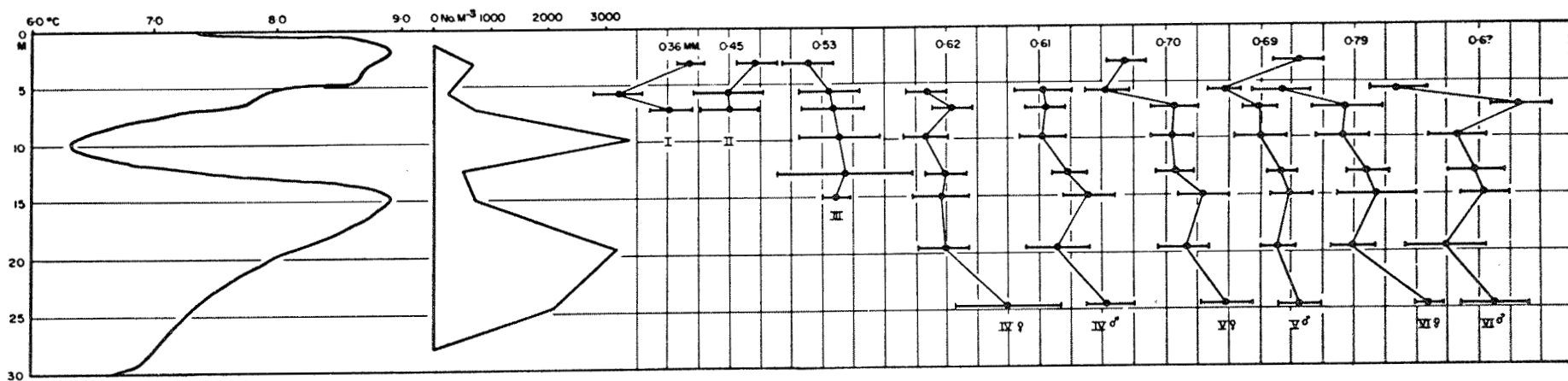


Figure 29. Cephalothorax length (mean and two standard errors of the mean) of *P. minutus* copepodites at different depths in the middle basin. Vertical lines 0.01 mm. apart.

animals seems desirable.

The outside copepodites always averaged much longer (from about 20-45%) than those of the lake, and the ranges of size only barely overlapped once, among stage I copepodites at the end of September. Nauplii could likewise easily be distinguished, but as these were not always measured, the two groups were not separated in the counts.

The allochthonous P. minutus were of course most abundant in the lower basin immediately after each tidal series. Immediately after the late-June tides, before the small resident population had begun much reproduction, 20% of the copepodite population had come from outside. At no other time did they exceed 4% of the population.

More important than the numbers brought in was their fate. The plankton in the lower basin was usually sampled about two weeks after each tide, by which time the foreign copepods had almost entirely disappeared, constituting at most about 5% of the numbers estimated just after the tides. The few specimens taken were all stages I, II or III copepodites and, although in no case lying within the size range of the indigenous stages, they were invariably smaller than the smallest allochthonous forms measured two weeks earlier. The conclusion is inevitable that these animals had moulted in the lake, with its higher temperature and poorer food supply.

It could be argued that some of the allochthonous stages had moulted several times to become indistinguishable in size from the equivalent indigenous stages. But it seems

far more likely that the outside P. minutus were in some way ill-adapted to the lake, and died off. There is perhaps a clue to this mortality in the middle basin. Tidal water penetrated the upper levels of that basin in late July, and a few allochthonous copepodites of all stages were collected there on August 3, and fewer in mid August. In the horizontal series of August 21 a total of 11 older (IV-VI) large copepodites were taken, all at 24.5 m., below the bulk of lake P. minutus. It appears that Ogac Lake did not satisfy the depth or temperature requirements of the marine P. minutus, but whether this difference was genetically or ontogenetically controlled can only be guessed at.

A possible adaptive complex of size, fecundity and vertical migration in P. minutus. The literature on diurnal and annual vertical migrations (summarized for the Crustacea recently by Bainbridge, 1961) is enormous, complex, and full of conflicting generalizations. One must be wary of new generalizations, but it is believed that observations in Ogac Lake and certain references to the behaviour of P. minutus elsewhere suggest an adaptive relationship between vertical migrations, size and fecundity.

P. minutus was one of the copepods exhibiting diurnal migrations in the Barents Sea, but not during periods of 24-hour daylight (Bogorov, 1946). This is in agreement with the general belief that the immediate stimulus to migration is light.

Other observations (summarized on p. 99) do not

indicate anything further of the nature of diurnal migrations, but suggest that the summer generations of P. minutus are generally near the surface, notably when diatoms are abundant there, but that older copepodites and adults avoid warm surface waters, at least during daytime. Animals of the overwintering generation, whether the last produced in summer (as in more southern waters) or the only one of an essentially annual cycle (as in Ogac Lake or the Norwegian Sea) descend as soon as they reach an older copepodite stage. This descent occurs well before the hydrographic winter.

It has been suggested that these descended copepodite stages are conserving their energy, and P. minutus (Østvedt, 1955) and other species are even said (without physiological evidence) to be "hibernating" by some authors. Where the biological cycle (specifically, diatom production) is essentially annual, the dangers of poor timing seem obvious. In Ogac Lake, where the period of Chaetoceros production is very circumscribed, the second spring broods of P. minutus in the upper and middle basins, laid perhaps a week after the first, failed utterly. Furthermore, the adults seem metabolically more subject to mortality, even when they have not produced eggs (p. 97). Animals continuing to live near the surface after the major diatom production was finished might achieve maturity, accelerated by warm temperatures, on ephemeral diatom flowerings, but the fate of their offspring would be in doubt. The selective advantage would appear to lie with those animals which retard maturity by seeking the cold depths. The

notable vertical descent of P. minutus in the Norwegian Sea (Østvedt, 1955) carries almost all the copepodites below 600 m., at which depth the break in the temperature curve occurs (at around 0°C.).

The relationships between temperature, size and maturation are well documented, but the relationship between size and fecundity has perhaps not received the full attention it deserves. In P. minutus the correlation between female size and number of eggs in the ovisac was shown by Marshall (1949) to be highly significant (0.98; 30 pairs of observations). Her tabulated data demonstrate a linear increase of egg number per ovisac from about 10 in females of 0.90 mm. to 37 in females 1.20 mm. long. If, as suggested above (p. 88), two broods (ovisacs) constitute the maximum output of this species then, all other things being equal, large size would confer an enormous selective advantage. Doubtless there is considerable geographical adaptation in the relationship between size, fecundity and temperature, as indicated by the fact that females in Ogac Lake comparable in size with the smallest females in Loch Striven produce much larger broods (p. 90). But we can presume that largest size and fecundity will be fostered by the coldest temperatures within the range to which the local populations are adapted.

One of the adaptive values of vertical migration, whether annual or seasonal, might therefore be its effect on fecundity. When food is scarce and surface waters warm, then fecundity and timeliness might best be ensured by leaving these surface waters altogether; perhaps this could be initiated

by nutritional conditions. When diatoms are abundant in warm surface waters, then size and fecundity may be increased by assimilating food captured near the surface in the cooler depths. In some coastal localities (including Ogac Lake) vertical descent may offer little or no advantage of lower temperatures. It can be supposed that this very widespread behavior is genetically conservative, and doubly difficult to modify locally in waters which are in continuous communication with the sea at large.

It is obvious that this hypothesis cannot itself account for many of the anomalies and variations in vertical migration of other marine animals. But the facts that temperature is known to be interrelated with size, maturation and fecundity in many poikilotherms, and that surface waters are almost universally warmer than deeper waters, are suggestive.

The Biology of Oithona similis Claus

The only other copepod of any productive consequence in Ogac Lake is Oithona similis. Like P. minutus it is common in all northern seas.

Annual cycle. The eggs of O. similis are carried in bilateral ovisacs, which may or may not be found attached to the genital segments of the females in the samples. Ovisacs were generally undisrupted, but when this had happened, individual eggs were easily identified. The egg counts in all three basins were greatest two weeks after the recorded peak (or near peak in the lower basin) of Chaetoceros (compare

Figs. 30 and 22). The number of eggs per female and the number per ovisac also lagged somewhat. The lag was greater in the number of eggs per female; this no doubt resulted from the fact that the adult female population at the beginning of the season contained many recent recruits (see Fig. 31), which were presumably not yet fully mature.

From Figure 30 it can be seen that the relatively later increase of egg production in the lower basin (high numbers reached by mid July) was reflected by the paucity of nauplii in that basin until the beginning of August. There were, on the other hand, small but distinct increases of nauplii in the upper and middle basin, beginning in early July. Two or three modes may be followed in these basins (Fig. 31) indicating quite rapid rate of growth. But the numbers of nauplii by no means matched the egg numbers present in early July; obviously there was enormous mortality of the early-produced nauplii in the middle and upper basins, and a less severe reduction of those produced later in the lower basin.

In the middle of July, there was a sharp drop in egg number in the middle and upper basins, although the number of females was generally maintained. The decrease of eggs seemed to stem mostly from a reduction of the proportion of females which were gravid, but also from a smaller average egg number in the ovisacs. This decrease was followed by a recovery in early August in the upper basin and probably in the middle basin (the lowered absolute egg number in the middle basin may be a result of sampling error, as the number

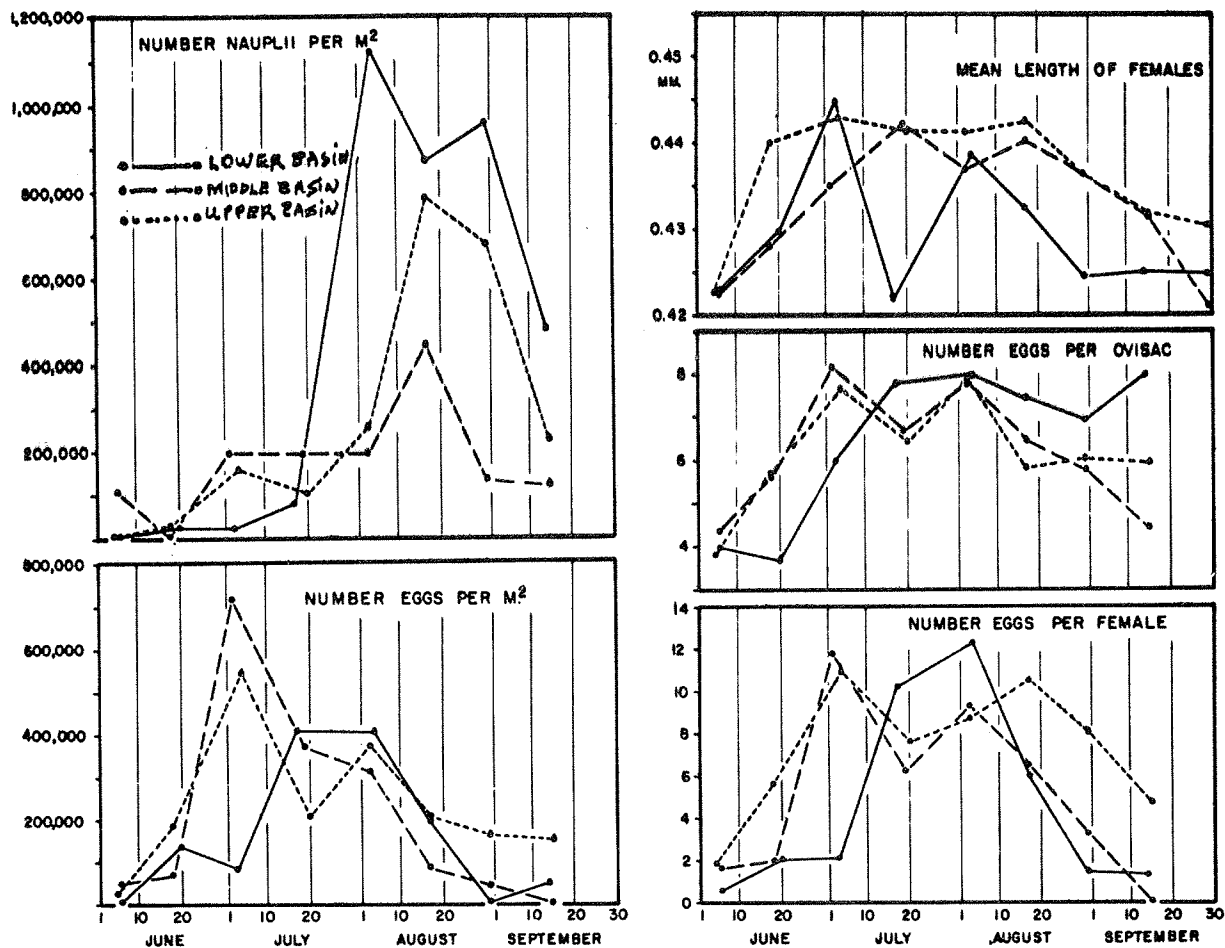


Figure 30. Reproductive status and size of adult female *Oithona similis*, and the numbers of nauplii through the season in the three basins.

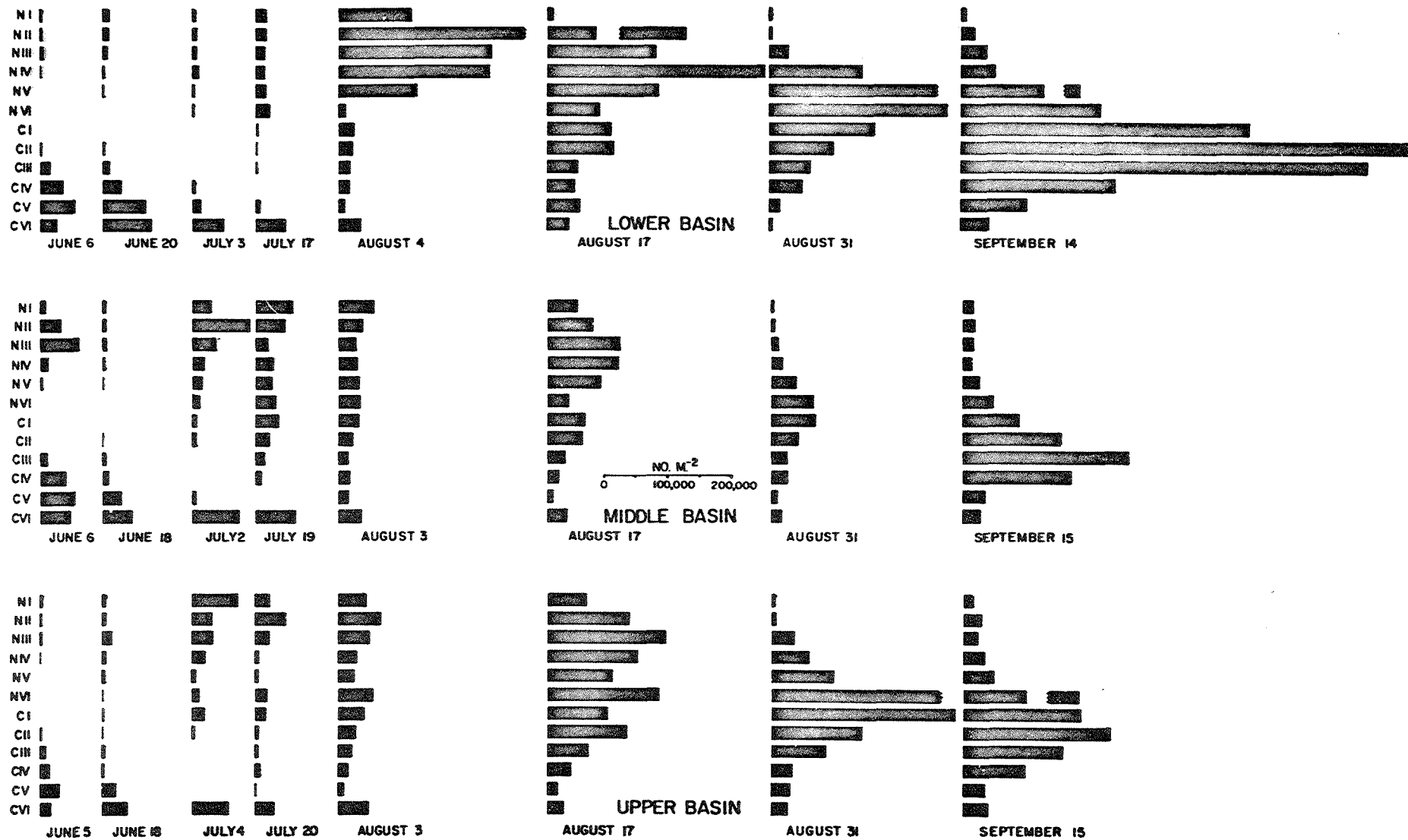


Figure 31. Numbers of all stages of *O. similis* through the season.

of eggs per female and per ovisac both increased, as in the upper basin).

The final decline in egg number in the three basins seems to have resulted largely from a decreasing proportion of gravid females, only slightly abetted by a drop in numbers of eggs in the ovisacs of those females which continued fertile. Curiously, the egg numbers in the lower basin, which increased latest, declined at about the same time as in the other two basins. In the lower basin, the decline seems wholly attributable to a decrease in the number of gravid females, as here the number of eggs per ovisac was maintained.

The decrease of gravid females in its turn apparently resulted from the death of the old generation and its replacement with the new. Changes in size can be used to indicate the recruitment of smaller females of the new generation (Fig. 30). O. similis in Ogac Lake averaged smaller than the minimal seasonal sizes recorded by Marshall (1949) in Loch Striven or Digby (1954) in East Greenland. The seasonal range of size of Ogac Lake was also very limited. Dwarf specimens, noted by Wiborg (1944) in Nordåsvatn and by Fontaine (1955) in Ungava Bay, also occurred in Ogac Lake. For some reason a larger number of these foreshortened animals were sampled in the lower basin in mid July, which explains the temporary but marked drop in size there. Otherwise the seasonal changes in size, although slight, follow a fairly consistent pattern in the three basins. The replacement of the old generation seems from size changes to have occurred first in the lower basin,

and this is supported by numerical changes in adults and older copepodites (Fig. 31). Since the number of eggs per ovisac did not decline in those few gravid females in the lower basin which persisted (Fig. 30), the interesting possibility is raised that the extinction of the old generation was accelerated by their sustained higher reproduction. Females in the other basins may have, contrariwise, continued egg production longer at a lower and decreasing rate.

The question of the number of broods and total egg production by this species cannot be answered satisfactorily. Since each female carried two ovisacs, and since the number of eggs per female never exceeded the quantity which could be carried in about 1.5 ovisacs, it seems probable that each female carried her eggs for some time and that there was a gap between the production of batches of eggs. But unlike P. minutus, in which distinct modes of abundance among stages of the second generation were preserved for weeks, with or without growth, C. similis developed a considerable "blurring" between modes which seemed clear early in the season. For example, two modes appeared in the upper basin on July 4, perhaps three on July 20, and two on August 3. Then three much larger modes could be noted on August 17, but thereafter only one was distinct. No connections can safely be inferred between modes of successive dates. Further, if we attempt to calculate natality in the lower basin, where high egg production was closely followed by high naupliar production, and where mortality can therefore be presumed minimal, we get unsatisfactory results. Both the

"first brood" centered at nauplius II on August 4 and the "third brood" on August 17 (presuming the first to be now at copepodite V and the second at copepodite II) are calculated to be roughly twice as large (36 and 26) as the mean contents of two ovisacs (16) at that time (Table XI). This seems irreconcilable on present evidence, but at least suggests that several pairs of ovisacs were produced by the females of O. similis.

Fish (1936a) states that in the Gulf of Maine in August the large number of larvae (ca. $35,000 \text{ m.}^{-3}$) and few females (ca. $3,000 \text{ m.}^{-3}$) indicates that several egg sacs must have been produced by each female. Fish does not give the number of eggs per sac, but the ratio of adults to young given could be accounted for by a single pair of ovisacs with the contents found in Ogac Lake. Marshall (1949) obtained counts of number of eggs per ovisac through the season in Loch Striven. As in P. minutus, there was significant correlation between number of eggs and female size, although size itself was seasonably less variable. The minimum egg number per ovisac (ca. 6) occurred in January, when the median female size (0.52 mm) was still longer than the largest seasonal mean size (0.44 mm.) in Ogac Lake. The summer maximum egg number per ovisac (ca. 18) far exceeded the maximum (ca. 8) noted in Ogac Lake.

The younger nauplii produced in the summer in all three basins seemed to grow especially rapidly, and from the end of August there was but a single mode, centered at copepodite II or III in all basins by mid September (Fig. 31). Those females

Table XI. Calculated natality within putative broods of Oithona similis in the lower basin. Counts from subsamples of fine-mesh net hauls from 20 m. to the surface. Calculated as in Table X.

<u>Putative Brood</u>	<u>Date</u>	<u>"Brood" Mode</u>	<u>No. of ♀♀</u>	<u>No. in "Brood"</u>	<u>No. young per ♀♀</u>
First	Aug. 4	N II	89	3,170	36
Third	Aug. 17	N IV	62	1,640	26

which reached adulthood during the summer do not appear to have been notably reproductive, and egg number showed a steady decline in all basins. The few persistent egg producers may have been largely members of the old generation in the upper and middle basins (see above), but the slight increases of egg numbers per ovisac and per m.² in the lower basin in mid September (Fig. 28) are probably attributable to the new generation. The reproductive cycle was however essentially annual in all basins, and it is doubtful that there was even a small, attenuated second generation produced late in the season.

Feeding. It is clear from what has been said that O. similis cannot be dependent on the same sort of food as P. minutus. While egg production and size increase of the females followed by about two weeks the initial Chaetoceros peaks in each basin, the females continued to produce eggs after the virtual disappearance of Chaetoceros, and nauplii thrived through August and September when the young of P. minutus suffered reductions in numbers and slow growth (compare, e.g., Figs. 31 and 23).

There is evidence that O. similis was feeding on at least part of that phytoplankton fraction which was undersampled by the nets--the small diatoms included under "other diatoms" on Figure 22. In the middle and upper basins, although large numbers of eggs were present, the development of nauplii was subjected to 1½ months of suppression until mid August. Nauplii appeared abundantly in early August in the lower basin, two weeks after eggs became common. In all basins the

naupliar bursts coincided with marked increases of the "other" diatoms. This seems strong circumstantial evidence that the nauplii were able to feed on the nannoplankton, which is under-represented in the "other" diatom fraction (see p. 75).

The relationship of small diatoms with growth and egg production by the adults is less clear. There seems to have been a substantial population of small diatoms at the appropriate time in the middle basin, but few in the upper basin. The "other" diatoms of the lower basin do not seem to have accelerated reproduction there. The distinct minimum of number of eggs per female and per ovisac in mid July (Fig. 28) certainly coincided with the seasonal nadir of any sort of primary production.

Since there was a lag of about two weeks between the major spring flowerings and the growth and egg production by female O. similis in all basins, the possibility that they could feed on the detrital residue of such flowerings might be considered. It is not desirable on such slender evidence to deal with the whole question of trophic relations of the zooplankton, or revive the ideas of Pütter (1909) even in the more sophisticated form of Fox (1957) and his associates. But it has been hinted in the literature that Oithona spp. can utilize material other than phytoplankton. Wiborg (1944) points out that although "no copepods have been found which are exclusively saprophile", Oithona spp. and certain other small forms increase in sewage-rich waters of Norwegian fiords. Lebour (1922) found diatom remains, but Marshall (1949) found only indistinguishable

debris in the guts of O. similis females. Other authors have commented on the maintenance of O. similis in apparent phytoplankton scarcity, such as through the arctic winter (Digby, 1954). It seems likely, however, that insufficient attention has been paid to the nanoplankton as a source of food, especially as small diatoms may be much less variable in quantity through the season (Yentsch and Ryther, 1959).

Vertical distribution. The little information available on the vertical distribution of this species suggests that it is essentially a near-surface form. It is the most abundant copepod in the upper 50 m. of the Norwegian Sea in winter, and remains common near the surface in summer after the migrant species return from the depths (Østvedt, 1955). Both Ussing (1938) and Digby (1954) attribute the summer reduction of young stages in the surface waters of East Greenland to grazing rather than vertical descent. Bogorov (1946) lists this as one of the species which does not make diurnal migrations in the Barents Sea, even in times of alternating daylight and darkness.

Figure 32 shows the vertical distribution of the various stages on August 21 in the middle basin. The pattern was quite different from that exhibited by P. minutus. On the whole, O. similis of all stages had their maxima near the surface, and their distribution in deeper water seemed less sharply affected by temperature.

The nauplii showed surface and deep maxima, both in warm levels. The mesh used (No. 10) on the plankton sampler

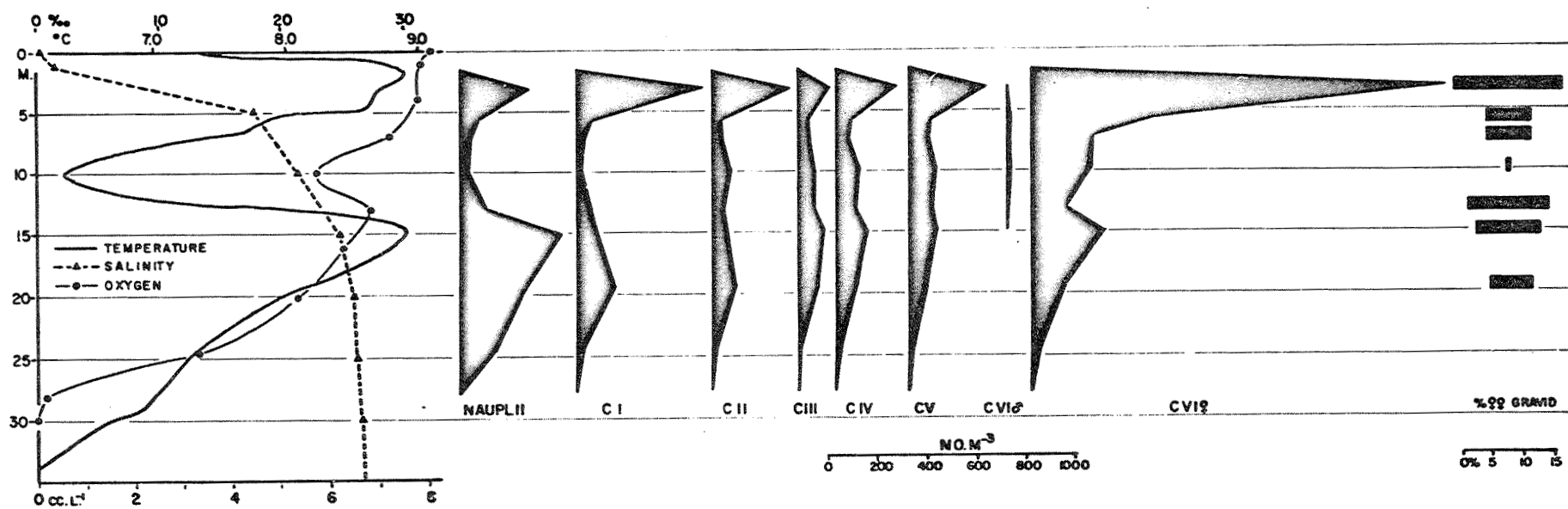


Figure 32. Vertical distribution of *O. similis* in the middle basin on August 21.

probably failed to retain the youngest nauplii adequately, but there was no suggestion that the deeper nauplii averaged younger, as was found in P. minutus; separate naupliar stages are therefore not shown in Figure 32. There is perhaps a slight suggestion of reaction change between copepodite II and III, the deeper maxima of the latter and older stages being found at the warm level. This can be contrasted with P. minutus (p.101), in which stage III and older copepodites descended from the surface and occupied cold depths.

The Biology of Sagitta elegans Verrill

This species, the dominant predator in Ogac Lake, is very widely distributed in coastal and oceanic waters of the northern hemisphere. In the Canadian arctic it is the only chaetognath normally met with.

The maturity stages used in this study are the three defined by Russell (1932). Essentially, gonads are not visible in stage I, II have small eggs, and III are mature. Animals which had partially or wholly discharged their eggs were included under stage III. Kramp (1939) counted further subdivisions among mature and near-mature animals, but his stages did not appear to shed any more light on the essentials of the reproductive cycle in Ogac Lake. As the animals were somewhat more transparent than usual in marine S. elegans, it was found unnecessary to heighten the visibility of the gonads by staining, as practised by a number of authors. Lengths were measured to the nearest 0.15 mm., and excluded the tail fin.

Annual cycle. The cycle is shown in Figure 33.

Unfortunately deep hauls were not made in the upper and middle basins until mid June, and older animals tended to be below 20 m. (see below). However, reproduction was just beginning in mid June, and samples then probably represented adequately the population at the end of winter.

Eggs and young were present in all basins in mid June, but the fate of the young which hatched differed considerably. Much the largest numbers of eggs and young were found in the lower basin and the smallest in the upper basin. This is certainly a reflection of the numbers of mature S. elegans present in each basin. Young in the upper basin grew in size considerably and maintained their numbers. Less growth had been gained in the middle basin, and a marked reduction of numbers was combined with insignificant growth in the lower basin. By July 20 the new generation was most advanced in the upper basin, where the overwintering generation might well have been extinct (the few stage III at this time could have been derived either from the new generation or from the large immature animals sampled on June 18 and July 4). At the same time the new generation in the middle basin averaged 1-2 mm. shorter and the old generation was still discretely represented. In the lower basin the new generation was just beginning to advance on July 17, after a month of stagnation.

It is obvious that the differences in timing in the three basins were related to the reproductive bursts of P. minutus, which were in their turn dependent on the maxima of

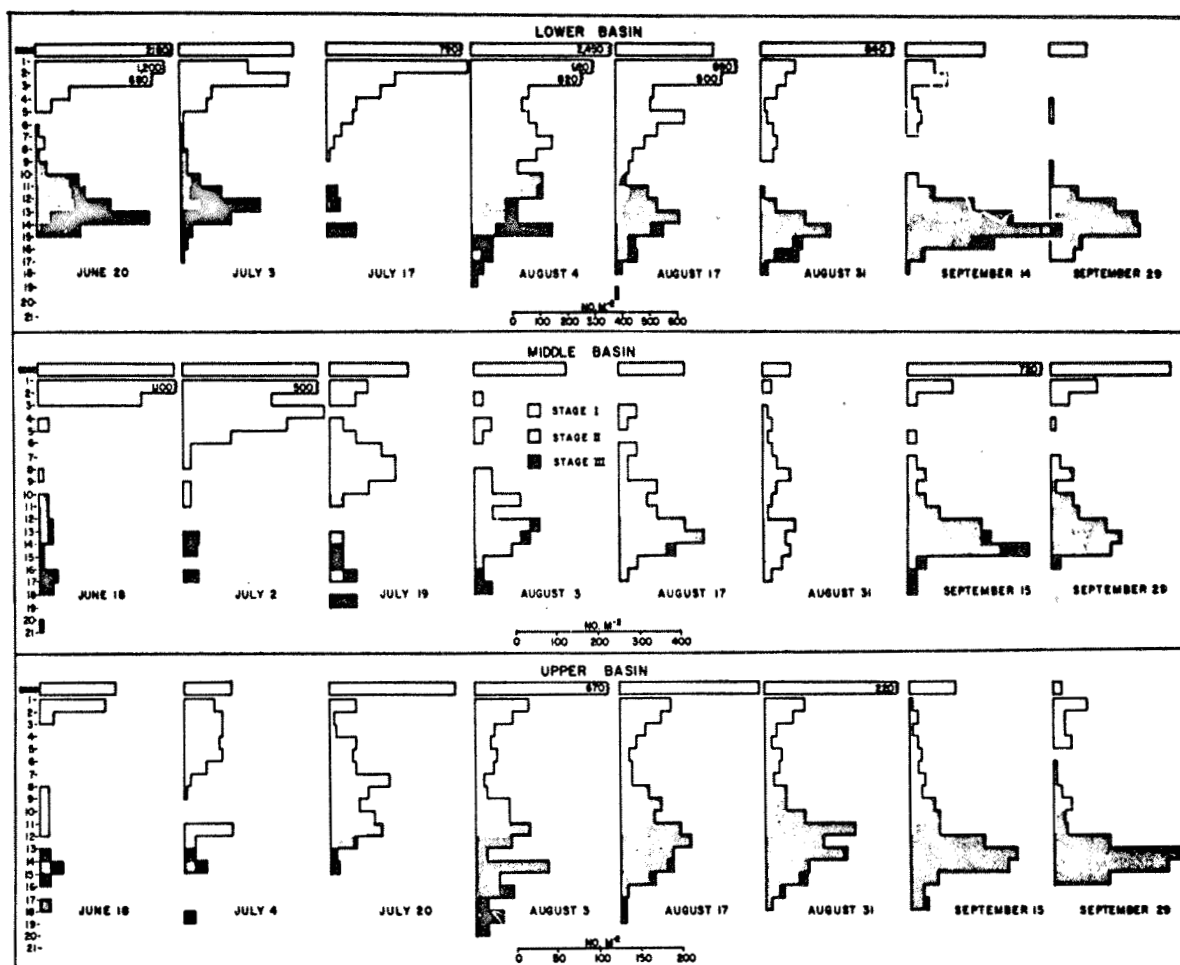


Figure 33. Numbers of *Sagittia elegans* in 1-mm. size groups through the season. Stages explained in text. Note the different scales, being as 1:1/2:1/3 for the upper, middle and lower basins respectively.

Chaetoceros (Figs. 23, 25). Regardless of the timing of egg production and the numbers of eggs produced by the adult S. elegans (which could presumably feed on large copepods), little growth of the new generations was permitted until small nauplii of P. minutus were available in each basin.

Although the very young S. elegans were thus apparently dependent on small nauplii for their sustenance, those individuals which had achieved sufficient growth in the middle and upper basins continued to grow rapidly after the reproduction of P. minutus had virtually ceased. In the lower basin, both broods of P. minutus were nurtured (see p. 88) and made available as food, and O. similis nauplii appeared in early August. In this basin, not only did the older members of the new generation grow phenomenally, but there was a considerable support for even the youngest individuals through early August. It seems that very young S. elegans required small prey, but that beyond a certain size, this predator was able to grow with and capture the increasingly larger nauplii or copepodites.

The young produced in early August in the lower and upper basins seem to represent a second generation, which developed for quite different reasons in these two basins. The cycle in the upper basin was most advanced of the three and adulthood was probably reached because of this advantage of timing. On the other hand, the well-fed new generation in the lower basin grew with unparalleled rapidity, and some members reached maturity by early August. The second generation

produced by these adults seems to have been frustrated by shortages of young nauplii in mid and late August. Although some of the older members of this second generation appear to have "caught up" with the parent generation in the upper basin, there was a severe dying out of the initially much larger second generation in the lower basin. This difference can be attributed to the presence of a distinct second generation of P. minutus in late August and mid September in the upper, but not the lower basin.

Finally, there was a further reproductive period in the middle and upper basins. S. elegans in the middle basin was somewhat retarded, and had not been able to produce an effective second generation in August, but a substantial number of eggs appeared in mid September. At least some of the young produced in the upper basin in August developed rapidly to join their parent generation after the end of August (see above), but the discrete group of young found in late September most likely represented more immediate reproduction, as in the middle basin. Young nauplii of P. minutus were available to sustain these small broods. It seems reasonable to suppose that the discrete groups of stage I individuals lying in size between the old and new generations in mid June and mid July were the vestiges of second-generation broods produced in this fashion in the preceding September.

In summary, the cycles of S. elegans are essentially annual in all three basins. A second summer generation was almost to no avail in the lower basin. In the upper basin,

young of the second generation produced in August grew to become indistinguishable from smaller members of the parent generation, but some of the young produced in September in both upper and middle basins were maintained as small, discrete groups through the winter. Adult reproduction was not necessarily synchronized with the presence of food for the ensuing young, whose survival and growth was dependent on small prey, especially nauplii of P. minutus.

In southern waters, S. elegans may have as many as five generations annually (Russell, 1932). In the subarctic waters of West Greenland, the cycle appeared to Kramp (1939) to be annual. This was confirmed by Dunbar (1941), who found that the cycle could be biennial in the Canadian arctic. His collections from the pure-arctic waters of east Baffin Island were particularly striking, with three very distinct size modes (the breeding generation, the immatures produced in the previous summer, and the contemporary young) apparent in September.

Vertical distribution. The vertical distribution of the population in the middle basin is outlined on Figure 34. Interpreted dynamically it seems obvious that eggs were produced by the adults at depth, that the young sought the surface waters, and that the older stages moved downwards from the surface. There was perhaps some avoidance of the warm water at 15 m., but the pattern suggests that the tendency was to go as deeply as possible with increasing size or age. The largest animals thus came to have their center of abundance

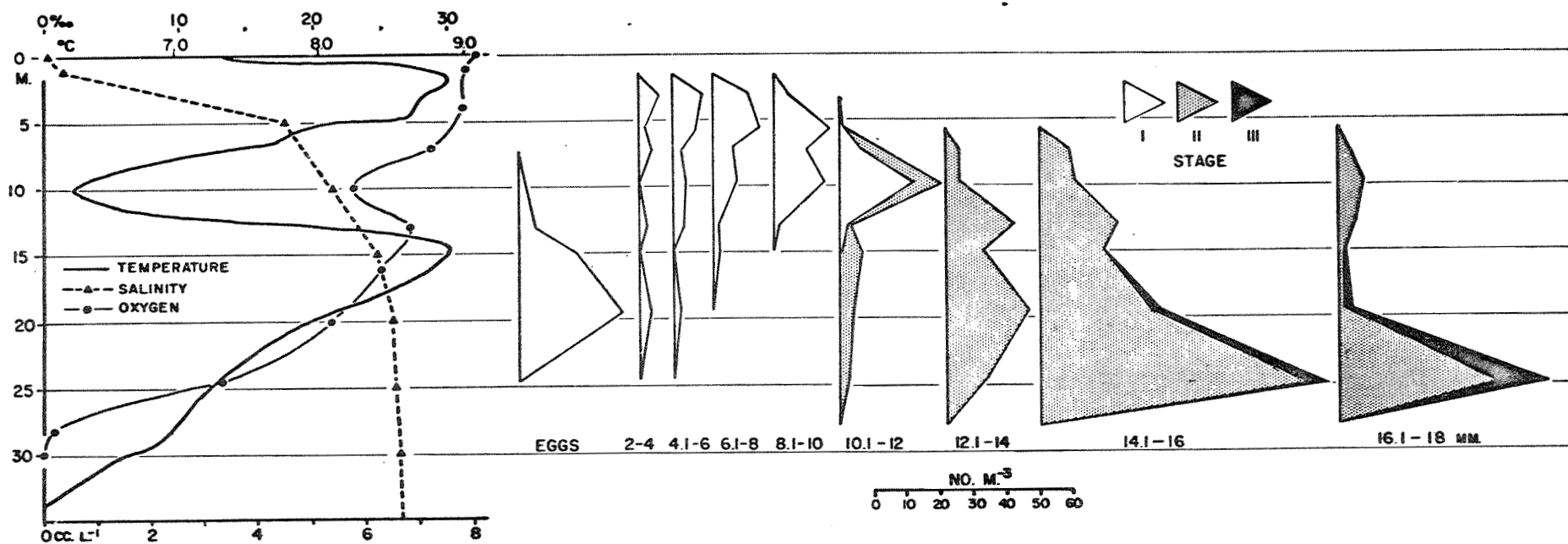


Figure 34. Vertical distribution of *S. elegans* on August 21.

deeper than that of any other animal dealt with in this study. Perhaps they are more tolerant of low oxygen concentrations.

This distribution matches very well the findings of Huntsman (1919). Young S. elegans off eastern Canada were in the warm surface waters, but older animals were found to occupy deeper and colder water, stopping their descent at levels of high salinity. The adults tended to come to the surface at night, but were dissuaded by high temperatures. Russell (1932a) also found that the adults were inclined to go deep (the young were poorly sampled), but that the summer generations were nearer the surface, and indulged in vertical movements. The overwintering generation was non-migratory and persistently deep, which appears to have been true in Ogac Lake.

Size and maturity. Three races of S. elegans were defined by Ritter-Zahony (1911), from arctic, Baltic, and Atlantic waters. Huntsman (1919) believed that the "races" were a result of temperature at development, and other authors have found a complete sequence of types in different environments.

The adults in Ogac Lake were much smaller than so-called S. elegans arctica of arctic marine waters. Dunbar (1941) gave the modal size of mature animals as around 30-32 mm. in northern Canada and West Greenland. In Ogac Lake the adult mode at 13-15 mm. was comparable with that of summer but not winter adults in southern waters (Deevey, 1960; Russell, 1932).

The larger size and two-year cycle of S. elegans in outside waters seem certainly attributable to lower temperatures. The whole question of temperature, growth and maturation of the

northern marine macroplankton has been reviewed recently by Dunbar (1957). To his argument might be added the observation of Russell (1932a) that in S. elegans, too, the number of eggs produced increases with size of adult. Perhaps an adaptive advantage is gained by animals of large size which outweighs the dangers of a long life. And perhaps also diurnal and annual vertical migrations are connected with temperature, size, and maturity in the manner suggested for P. minutus (see p.109).

The cause of excessive overwinter mortality in the middle and upper basins. In the discussion of annual cycles of this species, no account was given of one of the more striking features of Figure 33. There was no great numerical difference between the populations in the lower basin in late September and mid June, but a reduction of the order of 85% is implied in the upper and 70% in the middle basin.

It appears that the habit of older animals to descend deeply does not serve them well in Ogac Lake. In the discussion of vertical distribution it was pointed out that the maximum of large-sized S. elegans on August 21 was found at about 25 m., deeper than the concentrations of any of the prey species. Vertical hauls from 20 m. in early June suggested even greater paucity of older S. elegans in the upper and middle basins than revealed by hauls from 35 m. two weeks later. For this reason the first series was considered unrepresentative (see above), but it does imply that the overwintering populations maintained the same depth habits

revealed by the horizontal collections in August. Thus Figure 35 is constructed to clarify further the hypothetical vertical distribution of the four major species at the end of winter in the middle basin. The obviously detrimental vertical position of the bulk of S. elegans seems an adequate reason for the excessive overwinter mortality in the middle basin.

In the lower basin, 80% of the bottom is above 20 m. (see Fig. 4), and oxygen concentration was probably sufficiently low at that depth to prevent further descent by S. elegans in the small deeper area. If we can presume that the same depth habits are exhibited by the prey species in this basin, then S. elegans would be "forced" to its own advantage to live amidst a much more substantial supply of food. Since there is no known predation on larger S. elegans in the lake, the virtually complete survival of the overwintering generation in this basin, implied by the populations of June and September, is perhaps not surprising.

The mortality in the upper basin, which might have been greatest of the three, can be explained in like fashion. The thermal maximum at depth (see Fig. 12) was even more extensive than in the middle basin; temperatures were fairly uniform between 18-25 m. in summer and there was no falling off of temperature until below 25 m. at anytime between early June and late September. It seems quite possible that P. minutus found the thermal maximum in the upper basin an even stronger barrier to descent than that of the middle basin (see p.101).

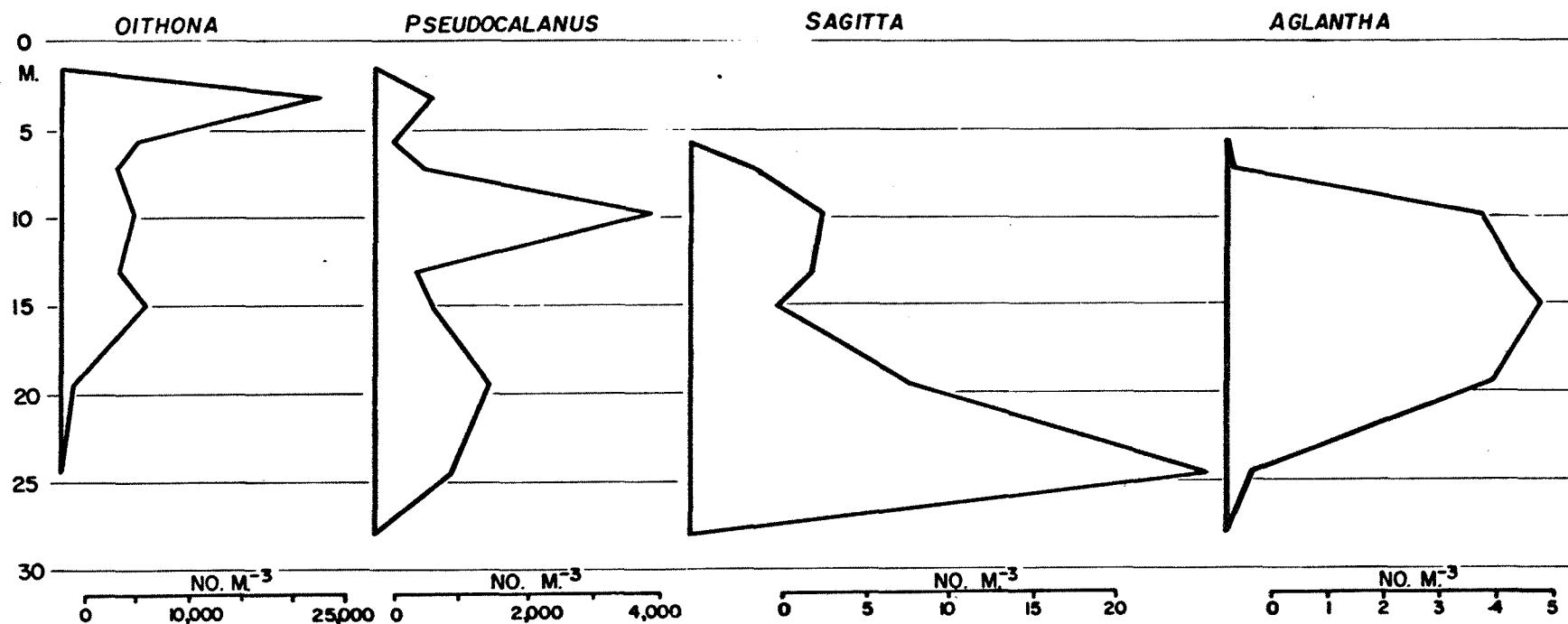


Figure 35. Hypothetical vertical distribution of the four dominant plankton species in the middle basin at the end of winter. Explanation in text.

This might be the explanation of the apparently greater mortality of S. elegans in the upper basin.

The Biology of Aglantha digitale (Müller)

This species is a widespread trachymedusan of the Northern Hemisphere. Development is direct, and the species is thus truly holoplanktonic. Its biomass in Ogac Lake averages somewhat less than that of S. elegans, with which it makes up almost the entire predacious macroplankton.

Annual cycle. The annual cycle of A. digitale is outlined in Figure 36. The three arbitrary maturity stages are defined in the Figure caption. It is evident that differences between the three basins were more extreme in this medusa than in any of the other species dealt with in this study. The animal was virtually absent from the lower basin. Only a single adult specimen was taken there in the regular series of plankton hauls (two adults were also captured by vertical hauls with a 0-mesh, $\frac{1}{2}$ -m. net in late June, compared with dozens in the other basins). Young medusae appeared in good numbers at the end of August, but since A. digitale occurred in the waters outside and was taken in the tidal inflow in late June it seems quite possible that these young were either themselves brought in on the late August tides or produced by allochthonous adults. This curious deficiency of the lower basin will be discussed separately below (p.143).

A. digitale in the middle and upper basins were

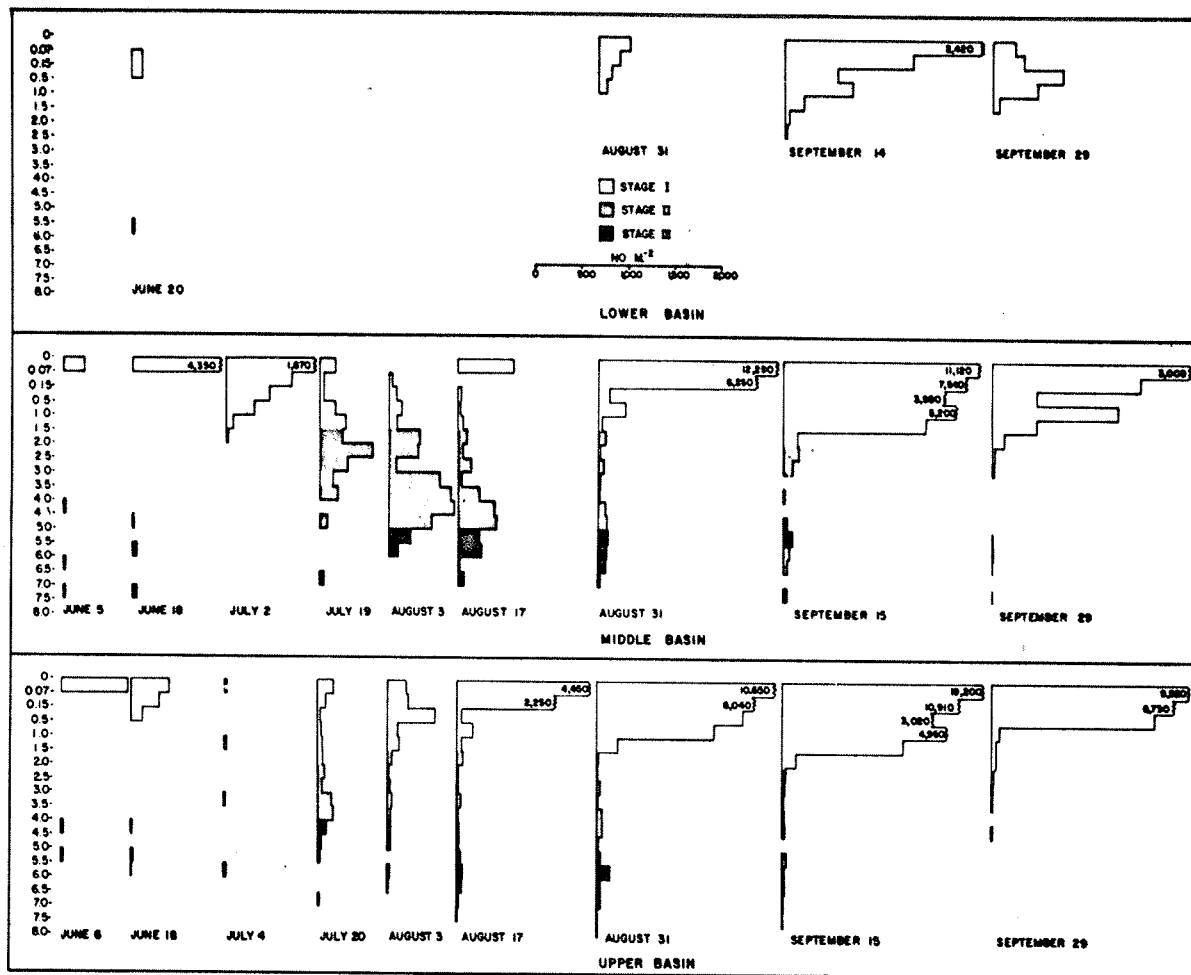


Figure 36. Numbers of *Aglantha digitale* in size groups (bell height) through the season. Gonads were not visible in stage I, averaged less than 10% of bell height in stage II, and more than 10% in stage III, all animals within the size group being grouped to determine the stage.

alike in having two generations during the summer, but differed in the timing and size of these generations.

Only a few large medusae remained at the end of winter in the middle basin, and even fewer in the upper basin. Reproduction of these overwintered individuals took place in June, somewhat earlier in the upper basin. The source of food for the tiny medusae of these initial reproductive bursts is problematical. After early July, there is no difficulty in attributing the rapid growth of the young A. digitale to the large populations of P. minutus nauplii which appeared then (see Fig. 23). But before this, the earlier increase and decline of young medusae in the upper basin and their later increase and maintenance in the middle basin seem to be correlated with the presence of Chaetoceros in the respective basins. It is possible that the smallest medusae noted, which were mere disks about 0.1 mm. across, found even the youngest nauplii of P. minutus rather difficult to capture, but were able to utilize larger phytoplankters directly. At any rate, the decline of young medusae in the upper basin (the extremely low count on July 4 might be partly due to sampling error or patchiness) was perpetuated as a consistently smaller population in this generation through the summer.

The earlier reproduction by the overwintering generation in the upper basin was in its turn reflected in the earlier achievement of adulthood and breeding in the upper basin. It is probable that some or even all of the young,

stage I, medusae on August 3 were the beginning of a second generation in the upper basin. Most of the older medusae of the upper basin had reached stage III by mid August and young appeared abundantly, but the middle basin did not show this until two weeks later. Small nauplii of O. similis were available in mid August, but these grew larger quite rapidly (Fig. 31) and might have been unavailable as food for the smallest medusae. This may explain why the enormous numbers of young medusae produced in both basins failed to achieve much growth through August and September.

By late September the early-summer generation was not represented in the upper basin and was very nearly extinct in the middle basin. The smaller members of the generation destined to overwinter had already begun to suffer much reduction by late September, and presumably only the larger individuals would have survived to produce the summer generation of the following year.

This alternation of a more copious summer generation with a smaller overwintering one is unique among the four chief plankton species. It resembles somewhat the cycle of P. minutus in the middle basin, but this cycle is at least partly "imposed" on the copepod by the hydrographic accident of the late-August tides, which killed off the older copepodites (p. 92).

A. digitale passes through several generations, differing in adult size, during summer around the British Isles (Russell, 1953), but is supposed to be annual around Denmark and in West Greenland (Kramp, 1942). Kramp did not

deal with very small medusae which were the direct evidence of reproduction in Ogac Lake. He believed that smallish medusae at the beginning of the season in south Greenland had overwintered, but there is a distinct hint in his material (his Table VII) that an early spring reproduction is involved. Farther north he found large, mature individuals predominating in August, and presumed that these too were produced the previous year. There is no assurance, however, that these had not been spawned by the overwintering generation earlier in summer. Grainger (1959) found slight size increase during the winter in northern Foxe Basin, but maximum gonad size was recorded in February. Specimens were too few for firm conclusions (none taken between February and July), but it appears quite probable that A. digitale would have been capable of breeding in spring, before the time suggested by Kramp on the assumption of an annual cycle.

It seems unsafe to make conclusions about the number of generations in waters of uniform temperature (where the generations are not distinguishable on adult size) unless sufficiently fine-mesh nets are used to capture the youngest stages, and unless the seasonal coverage is reasonably thorough. The extremely rapid development of the summer generation in Ogac Lake underlines the necessity for such systematic collections.

Vertical distribution. Several authors (e.g. Østvedt, 1955) have noted that young A. digitale frequent the warmer surface waters, while the adults are almost always

found deeper.

Figure 37 depicts the vertical distribution of the various size groups in the middle basin on August 21. At that time medusae smaller than 0.5 mm. must have represented the beginning of the new, overwintering generation. Although these medusae were distributed mainly in the thermal maxima, there was a distinct avoidance of the near-surface waters, perhaps because of intolerance of low salinities. Regardless of the proximal cause of this behaviour, it resulted in very few of the youngest medusae being found at around 3m., where the nauplii of both O. similis and P. minutus predominated. The deeper maximum of young medusae on the contrary coincided with the naupliar maximum. Slightly larger A. digitale were more common near the surface, but animals greater than 2-3 mm. in bell height occupied depths centered around 15 m. Although the center of distribution thus coincided with the thermal maximum, there is no suggestion that temperature was an important control of distribution in the larger medusae, which were almost as common in the cold water at 10 m.

Size, gonad development and races. In Ogac Lake A. digitale were much smaller as adults than those recorded from arctic marine waters (e.g. Kramp 1942, Grainger 1959) and more comparable with those in the summer generations of more southern waters (e.g. Russell, 1953). An example of the more typical arctic A. digitale was collected from the tidal inflow of June 30: it was over 19 mm. in bell height and had gonads almost 6 mm. long. This may be compared with the maximum bell height of 7.9 mm. and gonad length of 2.8 mm.

recorded in Ogac Lake.

Much discussion is found in the literature on the variability of size and gonad development which, along with color and certain rather variable meristic characters, have been used to define varieties, races and even species. Kramp (1942), who had accepted the existence of races in Danish waters, failed to find any distinct groups in the seasonally more uniform waters of West Greenland. To Russell (1953), "it seems reasonable to suppose that we have here a single species which, owing to its very wide distribution, shows considerable variation in the size to which it grows under different environmental conditions".

Certainly it seems unnecessary to invoke genetic explanations for the much smaller size of mature A. digitale in the warm waters of Ogac Lake than in the sea outside when comparable differences are exhibited seasonally around the British Isles (Russell, 1953). There is further a striking demonstration of the effect of temperature on gonad development in the lake (Fig. 37). Gonads averaged consistently larger in animals taken in the colder water around 10 and 25 m.

Presumably temperature has a differential effect on growth and maturation, permitting maturation at a smaller size in warm waters, without increasing gonad size proportionately. For this reason the absolute or relative size of gonads is not a safe indication of the reproductive state of an individual medusa.

The apparent competitive exclusion of A. digitale

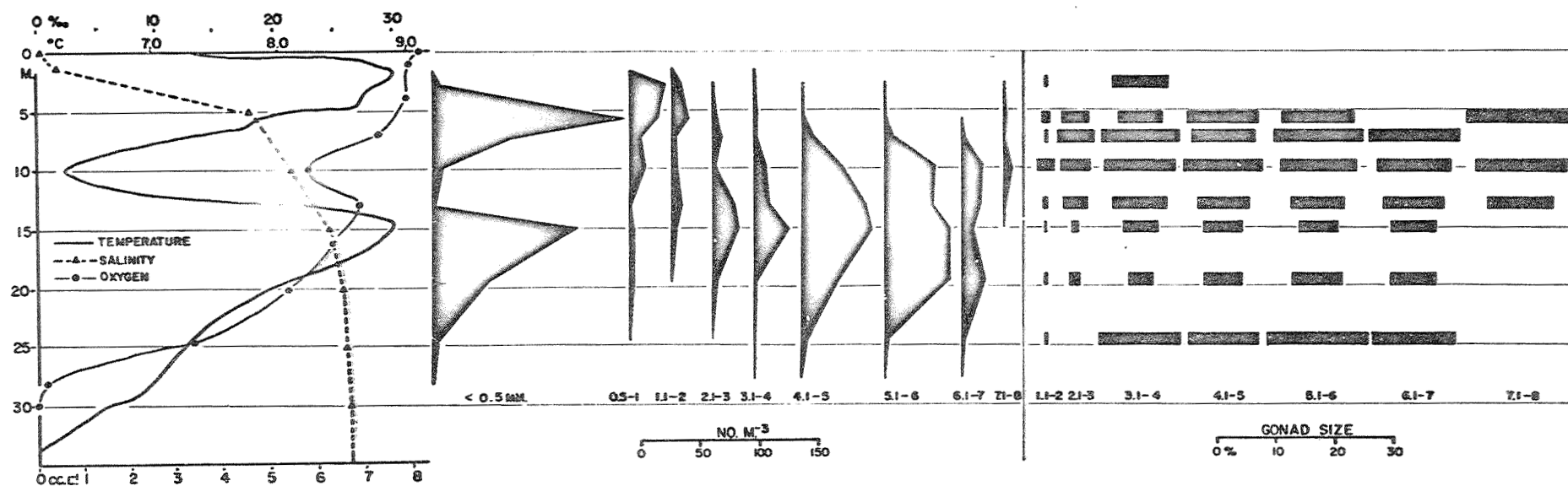


Figure 37. The vertical distribution of *A. digitale* in the middle basin on August 21, and the development of gonads (as a % of bell height) at different depths.

from the lower basin. As pointed out earlier (p. 135), a single adult taken on June 20 was the sole representative in the lower basin of the overwintering generation of A. digitale, and the few young medusae taken at that time were not the forerunners of a flourishing summer generation, as found in the other basins.

It might be argued that the summer generation was thwarted by a lack of food at a critical time. The Chaetoceros flowering of the lower basin and the ensuing development of P. minutus were two weeks later in the lower basin, and young medusae produced in June might have experienced lean times until mid July.

The large numbers of young which appeared after the late-August tides might have been produced by a tenuous and unsampled summer generation, but were more likely brought in by the tides or produced by allochthonous adults. Whatever their source, they indicate that there is no general suppression of reproduction and early growth in the lower basin; yet the medusa was virtually absent at the end of the previous winter.

The argument to be developed here is that large A. digitale were prevented from developing in the lower basin through competition with S. elegans, the only other predaceous plankter of significance in the lake.

It has been indicated (p. 132) that the much greater overwinter mortality of S. elegans in the upper and middle basins was due to the descent of the larger animals to depths (maximum at 25 m.) below the available food supply--particularly

P. minutus (maxima at 10 and 20 m.) and O. similis (maximum near surface). It was suggested that S. elegans was "forced" to its own advantage to occupy shallower depths in the lower basin, in the midst of a plentiful supply of prey.

A. digitale occupied intermediate depths, between 10-20 m., in the middle basin on August 21 (above). Figure 35 outlined the hypothetical depth distributions of the two predators and their prey at the end of winter in the middle basin, based on the population structures in early June and the vertical distributions of the same sizes and stages on August 21. The advantage for A. digitale and disadvantage for S. elegans are obvious. In the lower basin A. digitale would be thrown into coexistence with S. elegans above 20 m. It is tempting to trace the elimination of A. digitale to this coexistence. The effect of the flourishing population of S. elegans may be simply to reduce the food supply in the lower basin below the level tolerated by A. digitale. Although the estimates on Table XII are obviously only approximate, P. minutus appears to have been decidedly scarcer in the lower basin at the end of winter, although the reverse was true of O. similis, whose depth distribution (Fig. 35) may have placed it above much predation by either predator, and whose standing crop might reflect more closely the primary productivity of the three basins.

Full-grown A. digitale in the lake were much smaller than adult S. elegans, and their reproductive cycles were semiannual and annual respectively. When food is sufficient,

Table XII. Estimated numbers of overwintering generation of P. minutus and O. similis remaining at the end of winter in the three basins, before post-reproductive mortality can be presumed to have operated.

<u>Basin</u>	<u>P. minutus</u> Number per m ²			<u>O. similis</u> Number per m ²		
	<u>Early June</u>	<u>Mid June</u>	<u>Average</u>	<u>Early June</u>	<u>Mid June</u>	<u>Average</u>
Lower	17,700	15,400	16,600	133,000	197,400	165,200
Middle	34,000	39,700	36,900	149,600	82,800	116,200
Upper	18,100	21,400	19,800	82,800	63,500	73,200

small size and fast growth might be thought competitively advantageous, but it is possible that metabolic demands would not be satisfied when food was scarce.

S. elegans is also a much more highly organized predator than A. digitale. Hardy (1956) describes how S. elegans hangs motionless in the water, then darts out, aided by well-developed sight, to seize its prey. A. digitale probably performs something more akin to random sweepings, which must be energetically expensive and less efficient when food is scarce.

In conclusion, the evidence for the competitive suppression of A. digitale is circumstantial and indirect; but it seems quite as sound as is usual in suspected cases of competition in nature.

Discussion: Niches and Competition in Ogac Lake, and the Diversity of the Arctic Zooplankton

Only a few species make up the zooplankton of Ogac Lake. In the first place, the unusual hydrographic conditions must be physiologically intolerable for some species (e.g. Calanus). Yet there are a number of common arctic-subarctic forms which are quite euryhaline and eurythermal, but unrepresented in the lake--for example the calanoid Acartia longiremis, abundant in Ungava Bay (Fontaine, 1955), and several widespread medusae. It may be that some species are excluded by the established residents, which certainly demonstrate the importance of competitive interaction among

themselves. Thus the two chief copepods differ markedly in size, food, and vertical distribution, and must exhibit little or no overlap of niches. The status of the rare Cyclopina in the lake is unknown, but Metridia is at least partly carnivorous (Lebour 1922, Ussing 1938) and may thus avoid competition with the other copepods. Little opportunity is given the two larger predators in the lake for separation of niches trophically, and when they are forced to occupy the same physical space, A. digitale is eliminated. Conceivably there is an "empty" niche for a predator which could carry out its life cycle in the surface waters and feed on O. similis.

Such niche diversification and delimitation is not surprising in the confined biotope of Ogac Lake. Hutchinson (1951) amassed information which indicates the necessity for niche separation among freshwater copepods, often by means of much more subtle differences of size and food selectivity. However, it can also be argued that the paucity of zooplankton in the lake is a result of the same sorts of circumstances which limit the diversity of the zooplankton in the arctic seas outside.

Although it is often generalized that the marked environmental fluctuations in the arctic inhibit the evolution of a diverse fauna, it should be borne in mind that temperatures are quite uniformly low through the season in the seas. The evidence from Ogac Lake suggests that some arctic marine species are markedly influenced by small temperature differences and adapted to a surprisingly narrow range. The more important physical variables for the zooplankton appear to be those which limit almost all the primary production to a rather small

portion of the year. Although there is a considerable metabolic adaptation (Dunbar, 1957), low temperature seems to have the almost inescapable consequence of slowing down growth and maturation of the arctic zooplankton, and hence increasing the generation length. Fischer (1960), in a detailed consideration of latitudinal variation in organic diversity, decided that "the evolutionary advantage of tropical over high-latitude organisms due to different generation length is at best a minor factor", but he appears to have overlooked a most important effect of long generations. Hutchinson (1953) has clarified the relationship between generation length and fluctuations of the environment, and it is this relationship which seems important in considering the diversity of the arctic zooplankton.

The herbivorous zooplankton must depend on a very short season of primary production in which to reproduce and gain as much growth as possible, after which it continues to compete for the diminished food through the year. In more southern waters, several generations may be supported during the year or, most important, the entire life history of a species may occupy only a small segment of the year through competitive advantages at that time, removing itself from the necessity for competition through storage of the adequate food or formation of resting stages at other times of year. The seasonal alternation of Acartia clausi and A. tonsa in Long Island Sound (Conover, 1956) is an excellent example of the advantages in southern waters. Thus a list of 52 copepods from Delaware Bay (Deevey, 1960) consists almost entirely of species which were captured

only at certain times of year, while one from Northern Foxe Basin (Grainger, 1959) consists of 9 species which were taken at all times of year.

While the carnivorous zooplankton is assured of a variety of prey through the year in the arctic, it too is subject to the limitation of slow development and the necessity of sustained competition for resources. Reproduction may occur at any time of the year (Grainger 1959, Dunbar 1960) and there may be opportunities for diversification through depth preferences. But it is clear from conditions in Ogac Lake that competition may operate between full-grown animals of very different systematic position, forced to coexist for long periods of time.

Dunbar (1960) and Fischer (1960) conclude that the limited diversity of the polar biota, including the zooplankton, is due chiefly to their short history of evolutionary elaboration. In more southern waters an important source of diversity is the gradient from brackish to neritic to oceanic conditions. It is therefore interesting to note that the chief inhabitants of Ogac Lake are abundant forms of the open ocean as well, although the populations in the lake may show some incipient adaptation to the warm, brackish conditions. It is true that even offshore zooplankton in the arctic might have to be adaptable to considerable seasonal freshening, but it seems that a specialized zooplankton, dependent on a certain permanence of brackish conditions, has not had much opportunity to develop in northern seas since glacial times. An older

brackish fauna, elements of which are best represented in the Palearctic, may have suffered greater extinction in the American arctic, where glaciation was much more extensive.

In conclusion, there appear to be certain evolutionary opportunities in inshore arctic waters, but the slow growth of the zooplankton and the compressed season of primary production, both of which seem unavoidable consequences of physical conditions, severely limit the number of niches available to the arctic marine zooplankton.

SUMMARY

1. Ogac Lake ($62^{\circ}52'N$, $67^{\circ}21'W$) is the landlocked head of an inlet of Frobisher Bay, Baffin Island, whose salinity is replenished by the highest tides in the open-water season. Two specimens of Atlantic cod (Gadus morhua L.), not known in the sea outside, were collected by an expedition in 1927. The lake was not further examined until a brief visit in 1951 and a five-week expedition in 1952 provided information on the general nature of the lake. A longer expedition was clearly desirable, and the material presented here is a part of that collected by the author between early June and early October, 1957.

2. The lake is L-shaped, and has an area of some 148 ha. and volume of $34,360,000 \text{ m}^3$. It is divided into three basins by shallow sills. The lower basin is smallest and shallowest and the upper and middle basins have about the same areas and maximum depths. The development of volume is

similar in the lower and middle basins, but considerably greater in the upper basin. These morphometric features have important hydrological and biological consequences.

3. The tides in Frobisher Bay are among the world's highest and the largest of them may reach about a meter above the level of the lake. There is excellent agreement between the hypothetical tidal cycle, determined from three other localities in Frobisher Bay, and the entry of water into the lake through the narrow gap of the outlet stream. In 1957, 40 tides entered in the four spring-tide series at the ends of June, July, August and September, and another 11 probably entered in late October.

4. The relationship between the predicted height of the inflowing tide and the rise of the lake was determined empirically, and the contribution of freshwater drainage into the lake shown to be negligible. Thus the volume of tidal inflow, all of which stays in the lake and displaces surface water, can be calculated from the area of the lake and the rise of level. About 8,400,000 m.³, or one-quarter the lake's volume, entered in 1957, mostly in late August and late September.

5. The temperature and salinity of the inflowing water varied seasonally. During early summer, when the fiord outside was stratified, smaller tides brought in warmer and less saline water. In September, tides of all sizes brought in water of about the same high salinity and low temperature.

6. Ogac Lake is strongly stratified. Densities (σ_t)

increased persistently with depth at all times during the season and, except for an upper meter or two of fresh water in summer, no holomictic layer was found. Since tidal inflows sought their own density level, they did not tend to cause vertical mixing.

7. The loss of salt during the freshening period up to early August amounted to some 61,500,000 kg., or about 18.4 kg. m.⁻² in the lower, 44.2 kg. m.⁻² in the middle and 45.8 kg. m.⁻² in the upper basin. The loss per unit area was thus about the same in the upper and middle basins, where the reach of the wind gives comparable opportunity for downward mixing, but less in the more sheltered lower basin. Freshening occurred deeper in the middle basin, possibly due to morphometric advantages for downward mixing.

8. The concentration of salt in the tidal inflows as well as the amount of fresher water they displace from the surface are important in restoring salinity. There was still a deficit in the salt budget after the late-September tides of some 8.1 kg. m.⁻² in the lower, 2.2 kg. m.⁻² in the middle and 14.9 kg. m.⁻² in the upper basin. It can be calculated that the late-October tides, if evenly distributed over the lake, would leave the lake with some 19,400,000 kg. or 13.1 kg. m.⁻² more salt than present at the end of the previous winter. Actually, it is likely that most of the tidal water would flow over the levels in the lower and middle basins already made denser by the previous tides, and restore more salt to the upper basin, where the deficit was greatest at the

end of September. The balance doubtless varies from year to year, but no trend is shown between 1951 and 1957.

9. An apparent freshening at depth in the upper basin following the late-September tides is tentatively attributed to turbidity currents.

10. Rough estimates of total energy delivered are derived from available figures of clear-day insolation corrected from records of clear and overcast days or portions of days.

11. Gross annual heat budgets have been calculated as 7,900 cal. cm.⁻² in the lower, 9,350 cal. cm.⁻² in the middle and 8,700 cal. cm.⁻² in the upper basin of the lake. The heat budget of a nearby freshwater lake of comparable size and form to the lower basin was about 4,800 cal. cm.⁻², which points out the advantage that the meromictic Ogac Lake has in retaining heat.

12. Ogac Lake is much warmer at all seasons than the sea outside, due to its small size and landlocked nature, but also to the conservation of radiant heating by the highly stable waters. Considerable warming at depths to about 30 m. appears due to radiation.

13. Marked temperature inversions result from the penetration of cold tidal waters at intermediate depths. Smaller inversions from tides early in the season were slowly obliterated, but persistent inversions at about 10 m. in the middle and 12 m. in the upper basin apparently resulted from the penetration of large cold tides late in the previous season. A similar major inversion pattern might be expected from year to year.

14. Oxygen was absent and H_2S present below 25 m. in the lower, 30 m. in the middle and 32.5 m. in the upper basin. The rate of decrease of oxygen with depth was greatest in the lower, intermediate in the middle and smallest in the upper basin; the differences are attributable to morphometry of the basins.

15. Oxygen changes in the stable water must be almost entirely biogenic. After maintenance or increase of oxygen concentrations in June through mid July, the seasonal low was reached in early August. Thereafter there was a slow recovery. The changes can be ascribed in a qualitative way to the plankton cycles.

16. Pronounced oxygen minima occurred in early and mid August in the middle and upper basins. These were found at the depths of temperature minima, and resulted from the concentration of older copepodite stages of Pseudocalanus minutus at these depths.

17. The zooplankton consists of a depauperated selection of marine forms common outside. The uncommon hydro-medusan Melicertum octocostatum may be a boreal brackish element, but no specialized brackish fauna dominates the zooplankton. The four common species in the lake are the copepods Pseudocalanus minutus and Oithona similis, the trachymedusan Aglantha digitale and the chaetognath Sagitta elegans. The residents of the lake may be genetically or ontogenetically adapted to conditions of the lake, for the allochthonous zooplankton brought in by the tides is soon eliminated.

18. The phytoplankton cycle is outlined to the extent necessary as background to the zooplankton. Chlorophyll values are insufficient to give a quantitative picture of primary production through the season, but showed a decline after early July in the middle and upper basin, and a maintenance in the lower basin through the summer. Values were high just within the anaerobic level, where they probably reflect dead chlorophyll, sinking from the biogenic depths.

19. The diatoms Nitzschia and Fragillaria flowered in June and early July in the lower basin, and were followed by a production of Chaetoceros through the summer. The cycle was initiated by Chaetoceros in the middle and upper basins, and it declined soon after. The sustained Chaetoceros production in the lower basin is probably due to morphometric advantages for recirculation of nutrients in this basin. For other morphometric reasons the tidal inflows would pick up most bottom material when entering the middle basin. This appears to explain why Chaetoceros flowered briefly in this basin alone after the late-August tides, and why it was more abundant in the same basin following the tides in late September. Other diatoms, mostly undersampled and nanoplanktonic, showed distinct recoveries after mid August, and dinoflagellates were common in August. Although the copepod cycles were markedly influenced by the phytoplankton, grazing does not in its turn appear to have been the effective control on diatom populations.

20. In Pseudocalanus minutus the development of the

overwintered generation, the production of eggs, and the maintenance and growth of the nauplii are all dependent on the production of Chaetoceros. Two broods of some 30 eggs each were produced by the females. The nauplii of both broods were sustained through the summer in the lower basin, but only the first continued to develop through copepodite stages in the middle and upper basins. The old generation died out in August after reproducing, but older copepodites and adults of the new generation suffered severe mortality before significant reproduction in the lower and middle basins, apparently as a result of temperature effects of the late-August tides. The adults in the upper basin were spared this mortality and produced the largest second summer generation, but the development of their young was thwarted by lack of food. Fewer eggs were hatched by the remaining adults of the middle basin, but the nauplii grew rapidly on the timely Chaetoceros flowering, and the first summer generation was apparently supplanted by the second. Very few adults remained in the lower basin, and their young were not well sustained. The reproductive cycle was thus essentially annual in the lower and upper basins, but two generations were produced in the year in the middle basin.

21. The vertical distribution of P. minutus in the middle basin was strongly affected by temperature. Young nauplii were born at depth and concentrated at the thermal maximum, while older nauplii moved surfacewards and developed through copepodite II there. A descent to depth was initiated in copepodite III, but a positive thermal gradient of only

about 3°C. between 10 and 15 m. was sufficient to balk downward movement, at least temporarily.

22. The size of copepodites and adults of P. minutus was shown to depend on food supply, and the effect of the rather narrow range of temperature was not discernible. Vertical differences in the size of copepodites support the view that there was little exchange between populations living at different depths in the middle basin.

23. Allochthonous P. minutus were common immediately after the tides, but rare two weeks later. Evidence suggests that Ogac Lake did not satisfy the depth and/or temperature requirements of these outside animals.

24. The seasonal (ontogenetic) descent of P. minutus over its wide geographical range seems to remove it from the dangers of prematurity and untimely reproduction in warm surface waters when diatoms are scarce. A strong correlation between female size and number of eggs per ovisac has been demonstrated elsewhere, and it is suggested that only two broods (ovisacs) are produced by this species. Thus larger size, which may result from lower temperatures, may confer a selective advantage, and one of the adaptive values of diurnal vertical migration might be the increase of fecundity through the assimilation in deeper waters of food captured near the surface, which is almost always warmer.

25. The growth, reproduction and development of Oithona similis in the lake seem unrelated to Chaetoceros, which was the food of P. minutus. Regardless of the amount of

egg production which took place earlier, the successful development of nauplii in each basin first occurred when the recovery of small diatoms was noted in the net samples. It is possible that the old generation could feed on the detrital residue of the major diatom flowerings in spring, but the nauplii at least seemed dependent on the nannoplanktonic diatoms. The average number of eggs per ovisac ranged seasonally between about 4 and 8, but the number of broods (ovisac pairs) produced by a female could not be determined. The nauplii were sustained through mid September, and, although there was some egg production by females of the new generation at least in the lower basin, no significant second generation of nauplii appeared, and the reproductive cycle seemed strictly annual.

26. All copepodite stages of O. similis were commonest near the surface, although the nauplii were more abundant in deeper water, centered at the thermal maximum. Their distribution is in accord with the non-migratory, surface-living behavior of the species elsewhere.

27. Reproduction by adult Sagitta elegans, which could feed on larger copepods, was not necessarily synchronized with the presence of food for the ensuing young, whose survival and growth in all three basins was dependent on small prey, especially nauplii of P. minutus. The cycles were essentially annual in all basins. A second summer generation was attenuated in the lower basin. The cycle was most advanced in the upper basin, and some of the second-generation young produced there

in August grew to become indistinguishable from smaller members of the first summer generation. Some of the second-generation young produced in September in both upper and middle basins were maintained as small, discrete groups through the winter.

28. Adult S. elegans from Ogac Lake averaged 13-15 mm. long, less than half the size of marine arctic S. elegans and about the same length as S. elegans of southern waters in summer. The differences appear due to temperature effects on growth and maturation, and cast further doubt on the validity of described races of this species.

29. Young S. elegans were found in the surface waters, with their naupliar prey, but the largest animals had their center of abundance in the middle basin at about 25 m., deeper than that of any other animal dealt with in this study. Most of the populations at the end of September were large animals, which could be expected to overwinter at depths below the concentration of prey in the middle and upper basins, which seems to account for the excessive overwinter mortality in these basins. Since 80% of the lower basin is shallower than 20 m., and oxygen concentrations low at that depth, S. elegans would be "forced" to live amidst a plentiful supply of food, and the virtually complete survival of the overwintering population in this basin can be traced to this advantage.

30. Aglantha digitale was almost absent from the lower basin, but important in the rest of the lake. Small numbers of adults in June represented the overwintering population. The tiny medusae produced by direct development from this

population may have subsisted at first on phytoplankton, but further growth depended on the presence of young copepods. After mid August the large summer generation produced enormous numbers of young medusae, which were not well supported by available prey. The summer generation was almost extinct at the end of September, and only the larger of their offspring are presumed to have survived as the small overwintering generation.

31. Young A. digitale may have been intolerant of the low salinities and avoided the near-surface waters where other young forms were concentrated, but were common in warm water just a little deeper and at 15 m. in the middle basin. The older animals occupied intermediate depths centered around 15 m., but seemed uninfluenced by temperature.

32. Adult A. digitale in Ogac Lake were much smaller than those of the sea outside, and were comparable with adults in summer in southern waters. Marked differences in gonad size were noted in animals living at different depths, which seem to result from differential effects of temperature on growth and maturation. This lends support to the view that "races" of A. digitale are ecophenotypic.

33. Evidence is given that the virtual exclusion of A. digitale from the lower basin results from competition with older Sagitta elegans, which are "forced" to occupy shallower depths at which A. digitale is abundant in the other basins. There is an indication that prey species are reduced by S. elegans in the lower basin to levels below those tolerated by the less efficient predator A. digitale.

34. Although there appear to be evolutionary opportunities for the development of a specialized brackish zooplankton, slow growth and the compressed season of primary production, both of which seem unavoidable consequences of physical conditions, severely limit the number of niches available to the arctic marine zooplankton.

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