SOME RELATIONSHIPS BETWEEN PHYTOPLANKTON POPULATIONS AND PHYSICAL-CHEMICAL FACTORS IN LADYSMITH HARBOUR, BRITISH COLUMBIA

by

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ABSTRACT

The physical characteristics and distributions in space and time of salinity, temperature and phytoplankton in Ladysmith Harbour are described. It is shown that water exchange in Inner Ladysmith Harbour is the result of horizontal mixing and a two-layered circulation. The mean rate of water renewal in the Inner Harbour is calculated to be 32.2 percent of the mean volume per day. It is shown that four blooms of phytoplankton may occur in Ladysmith Harbour during the growing season, each having characteristic distributions. The distributions of phytoplankton during the first three blooms are discussed in relation to the physical characteristics and processes in and near Ladysmith Harbour. It is stated that the generic composition of the phytoplankton in Ladysmith Harbour varies in time and space. The rate of water exchange is shown to be such that endemic species of diatoms may develop in the Inner Harbour and that under certain conditions apparent endemism may occur. It is shown that both population succession and local sequence may be responsible for changes in the generic composition of the phytoplankton with time. Using the mean rate of water exchange and the assumption that renewal of water results entirely from the two-layer circulation, the net rates of advection of phytoplankton into Inner Ladysmith Harbour are calculated. It is shown that variations in the standing crop appear to be more closely related to changes in the rate of advection of phytoplankton than to changes in the rate of removal of cells by zooplankton. The rate of recruitment of phytoplankton by growth is calculated. It is computed that recruitment of cells by advection exceeds the recruitment by growth in Inner Ladysmith Harbour.

ACKNOWLEDGMENTS

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He also expresses his gratitude to Pacific Oceanographic Group and its members for advice and use of equipment, the Department of Transport, Air Services Division for the issuance of unpublished meteorological data, and the Dominion Bureau of Power and Water for freshwater discharge data.

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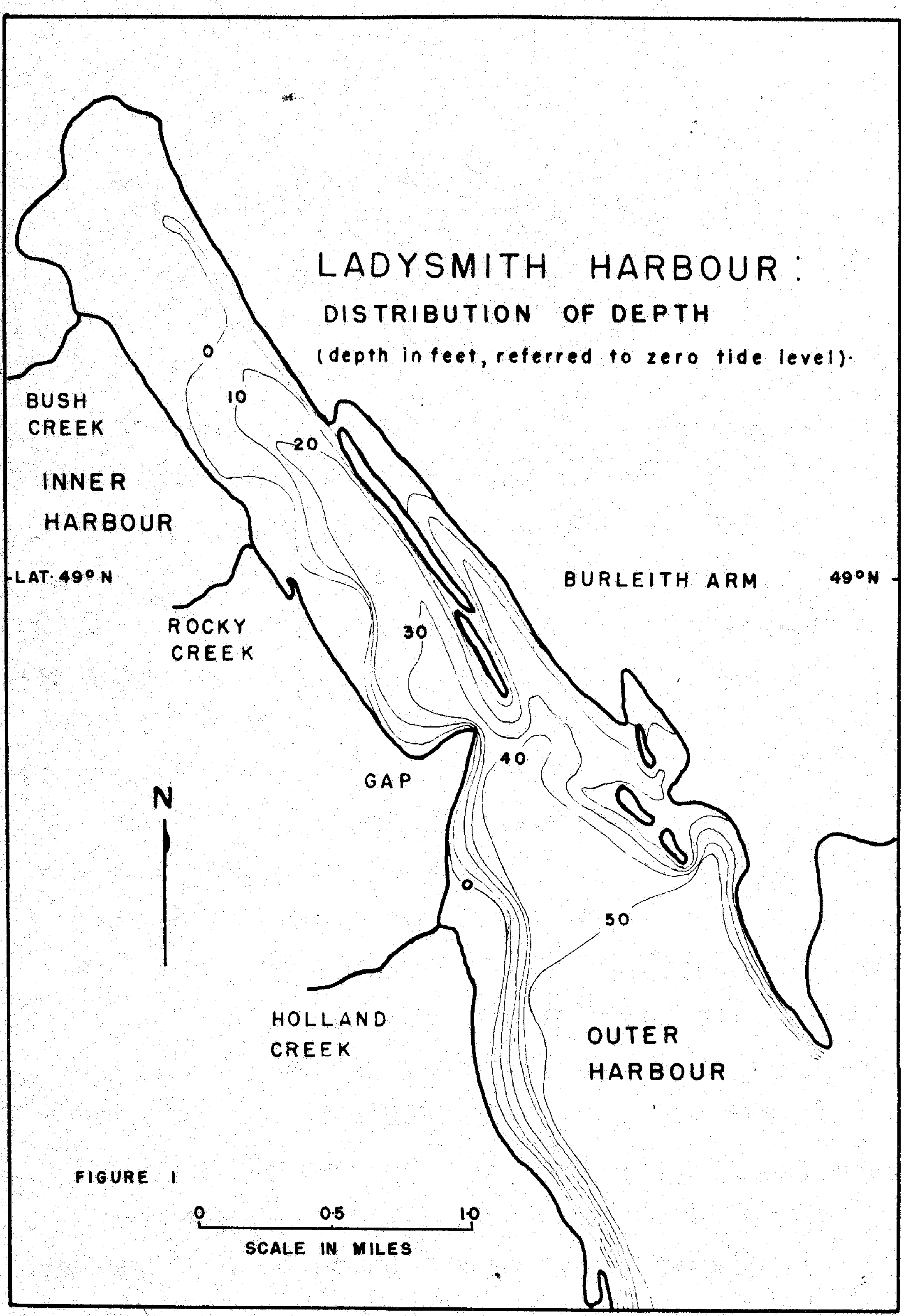

LADYSMITH HARBOUR:
DISTRIBUTION OF DEPTH
(depth in feet, referred to zero tide level)·
0
10
20
30
40
50
0
BUSH CREEK
INNER HARBOUR
LAT· 49° N
49° N
BURLEITH ARM
ROCKY CREEK
GAP
N
HOLLAND CREEK
OUTER HARBOUR
0
0·5
1·0
SCALE IN MILES

FIGURE I

SOME RELATIONSHIPS BETWEEN PLANKTON POPULATIONS AND PHYSICAL-CHEMICAL FACTORS IN LADYSMITH HARBOUR, BRITISH COLUMBIA

I. INTRODUCTION

Two types of agents may control the abundance, composition and distribution of plankton in a local area. First, local processes, such as grazing, nutrient depletion and regeneration, mixing and heating may act on local plankton populations. Secondly, renewal of the water in the area through circulation or mixing may act on populations directly by adding and removing organisms and indirectly by influencing the properties of the water in the area.

Many of the qualitative effects of different types of water movements on the production and distribution of plankton are well known and have been used to account for and predict various marine biological phenomena. An indication of success attained in this field is the fact that the converse is also true: distributions of marine organisms have been used in deducing physical processes in the sea.

However, the possibility of defining quantitative relationships between water movements in an area and its plankton has received little attention. Ketchum (1954) extended his estuarine circulation theorem to express the relationship between rates of circulation and distributions of endemic plankton populations and summarizes the other two attempts at work of this nature (Barlow, 1952, Ketchum et al, 1952).

In this thesis oceanographic data from Ladysmith Harbour have been used in an attempt to assess the effects of local factors and water exchange on the distribution and total crop of phytoplankton in Ladysmith Harbour. Ladysmith Harbour is a small, narrow bay situated on Latitude 49°N. on the east coast of Vancouver Island. In contrast to the typical British Columbia Inlet, it is short, about four and one half miles long, shallow, with extensive intertidal flats and apparently less dominated by fresh water inflow. A constriction, approximately at the middle, divides the harbour into a shallow inner portion and a wider and deeper outer bay (fig. 1). The harbour opens into Stuart Channel, a typical coastal passage separated from Georgia Strait by two chains of islands (fig. 2).

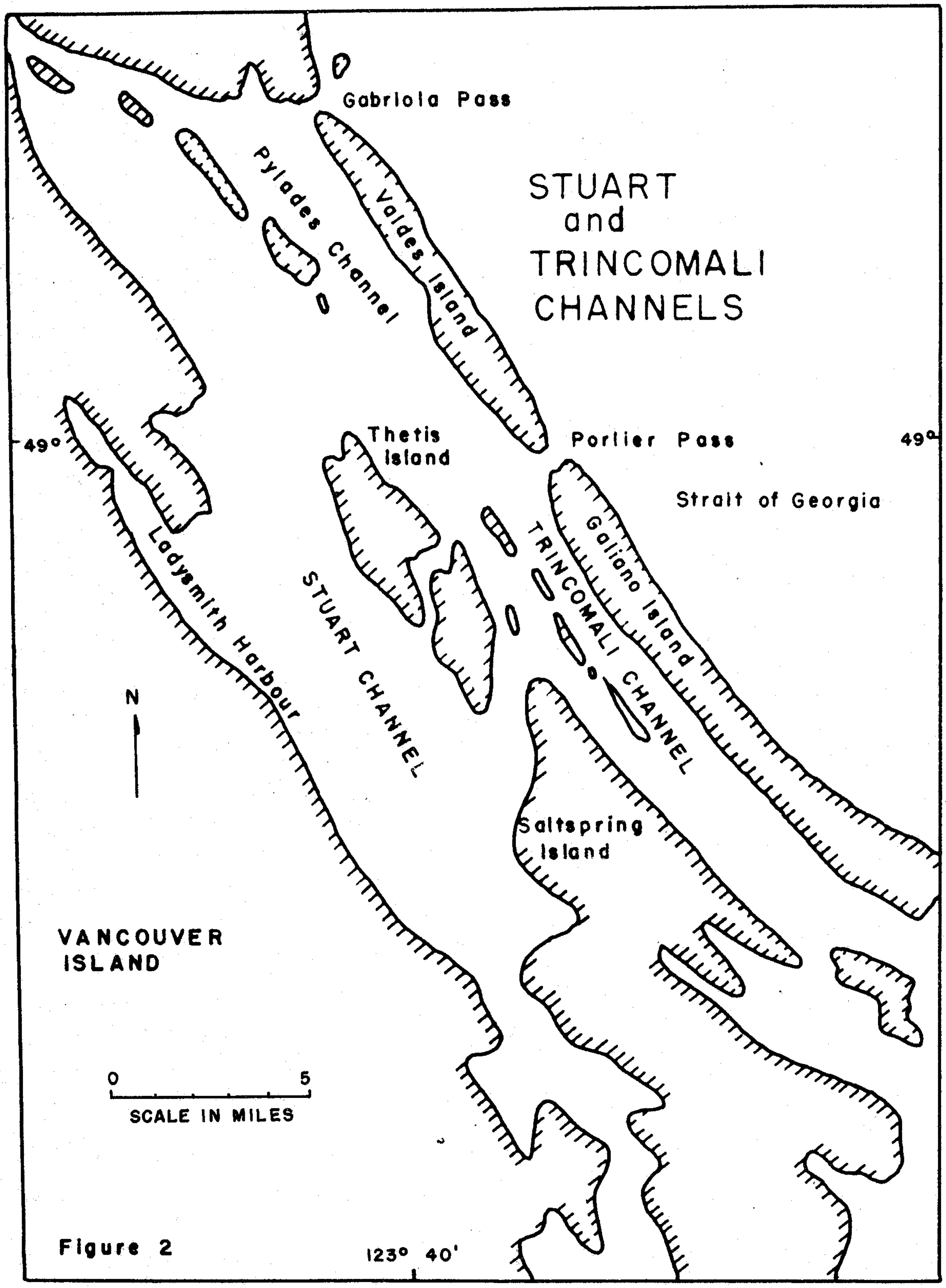

Gabriola Pass
STUART
and
TRINCOMALI
CHANNELS
Pylades Channel
Valdes Island
Thetis
Island
Porlier Pass
49°
49°
Strait of Georgia
Galiano Island
TRINCOMALI CHANNEL
Ladysmith Harbour
STUART CHANNEL
N
Saltspring
Island
VANCOUVER
ISLAND
0
5
SCALE IN MILES
123° 40'

Figure 2

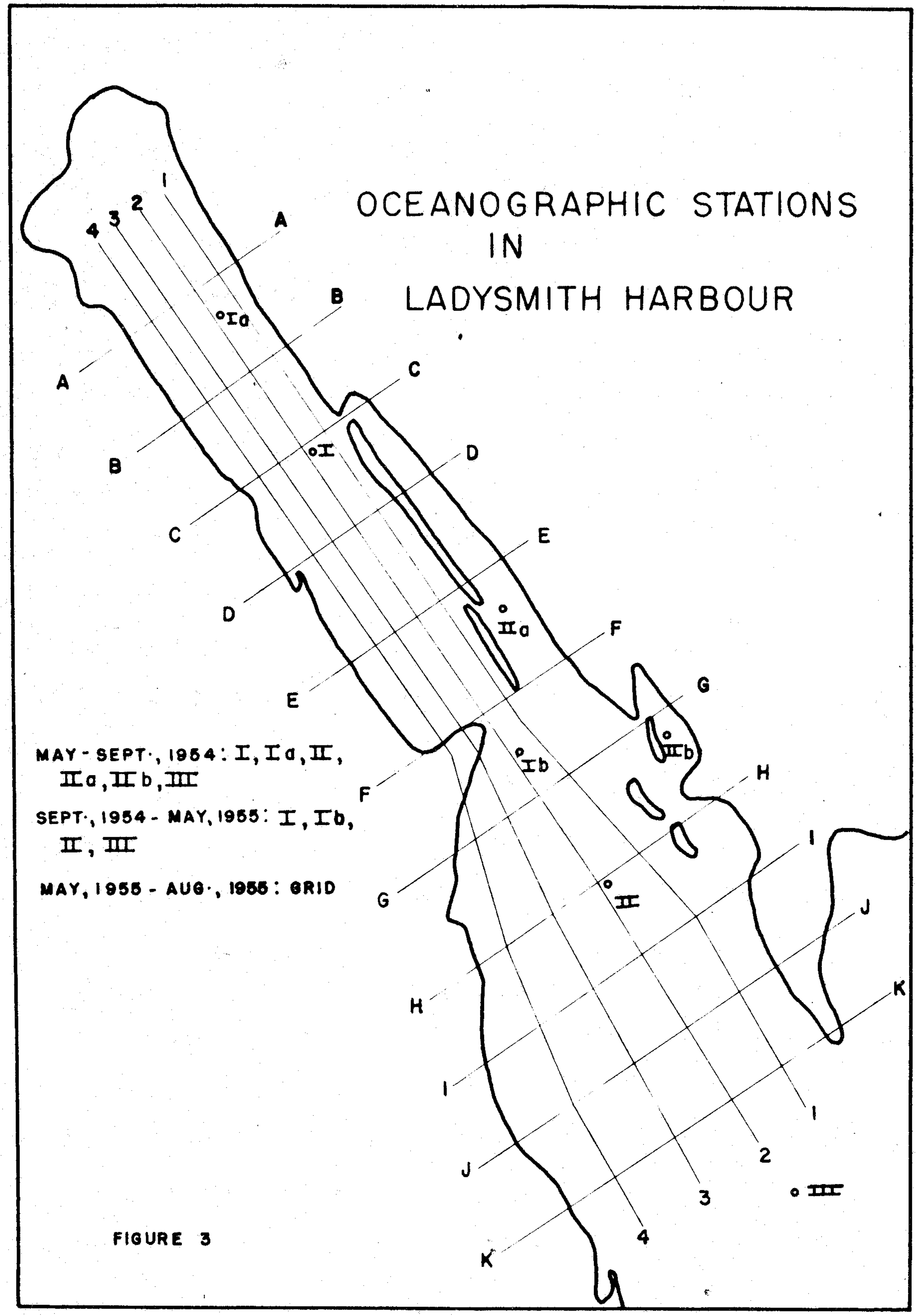
II. COLLECTION AND TREATMENT OF DATA

Sixty-seven cruises were completed in and near Ladysmith Harbour between May, 1954 and August, 1955. Six permanent stations were established in the Harbour (fig. 3) and were sampled for salinity, temperature and plankton at intervals ranging from three to ten days in the summer of 1954. Between September, 1954 and May, 1955 four stations (three of the original permanent stations and one additional) distributed along the length of the harbour were occupied at intervals of about a month.

In May, 1955 emphasis was shifted from longitudinal sampling of the harbour as a whole to a more intensive study of the Inner Harbour. A grid of stations (fig. 3) covering the Harbour was established. Periodically the whole grid or selected lateral sections were sampled for plankton, salinity and temperature. It was found that the length of time necessary to secure all three of these types of data on a single cruise was such that changes in distribution due to tidal action could be significant. For this reason after May, 1955 each cruise was restricted to securing one or two types of information.

Most of the data were collected from a small open inboard-powered boat equipped with a hand windlass and a plankton pump. A thirty-six foot launch similarly equipped was used for the more extended cruises into Stuart and Trincomali Channels.

An Atlas hydrographic bottle, a reversing thermometer and a 200 foot bathythermograph were operated from the hand


OCEANOGRAPHIC STATIONS
IN
LADYSMITH HARBOUR
MAY - SEPT., 1954: I, Ia, II, IIa, IIb, III
SEPT., 1954 - MAY, 1955: I, Ib, II, III
MAY, 1955 - AUG., 1955: GRID
Ia
I
IIa
Ib
IIb
II
III
A
B
C
D
E
F
G
H
I
J
K
1
2
3
4
FIGURE 3

windlass to obtain water samples and temperatures. Plankton samples were taken from subsurface depths through hose one inch in diameter by a rotary pump driven by a power take-off from the inboard engine. In most cases three cubic feet of water measured by a meter were filtered through #20 or #25 silk or monel netting.

The types of pumps and size of hose generally used in plankton sampling are inefficient in capturing most zooplankton, although excellent for quantitative studies of phytoplankton and some of the smaller and less active zooplankters (Gibbons and Fraser, 1937). The pump used in this study was of low capacity, delivering water at a rate of about one cubic foot per minute. While this does not affect the phytoplankton values, zooplankton concentrations derived from the samples are low.

A Chesapeake Bay Institute confined current drag was used to obtain velocity profiles (Pritchard and Burt, 1951). Surface flow patterns were observed with wooden floats as described by Tully and Waldichuk (1953).

Salinities were determined by Mohr titration.

The concentrations of predominant genera of phytoplankton were obtained by identifying and counting the cells in a fraction of each sample in a ruled chamber of known volume and converting these counts to numbers of cells per liter. The volume of the samples analysed ranged from $\frac{1}{60,000}$ to $\frac{1}{4000}$ of the original sample. It was found necessary to dilute samples with heavy concentrations of cells in order to facilitate counting.

Between 1/20 and 1/5 of the volume of each sample taken at Station I in the summer of 1954 was analysed for the concentration of the dominant zooplankton. Included in this category were copepods, copepodids, zoea of crab, polychaete larvae, and nauplii of copepods and barnacles. Since the adults of the species of copepods observed were similar in size to the copepodids they were included in the counts of copepodids.

Since the distributions of variables in Ladysmith Harbour fluctuate continuously with tide, stations sampled over a period of twenty-four hours were occupied on three occasions. The fact that cruises were made at various stages of the tide also allows conclusions to be drawn concerning the mean distributions of variables.

In addition to data taken during the above program, data secured by other workers and agencies have been used and are listed as follows:

(a) Salinity, temperature and plankton from Station I taken at weekly intervals in 1951 and 1952 (D.B. Quayle, unpub.).

(b) Data from a series of stations occupied by C.N.A.V. Ehkoli in Stuart Channel and Ladysmith Harbour in May, 1955 (Scagel, 1955).

(c) Discharge data for Haslam Creek (Canada Dept. Northern Affairs and National Resources No. 114, 1951-1952, and unpub.).

(d) Meteorological data from Cassidy Airport (Can. Dept. Transport, unpublished).

(e) Waldichuk M., 1954. unpublished data.

III. RESULTS AND DISCUSSION

A. Morphometry

The distribution of depths in the Harbour is indicated in Figure 1. About one third of the area of the Inner Harbour lies above the zero tide line. Most of this intertidal zone lies at the head of the harbour. Two mud flats lie on the west side of the harbour.

Along the east side of the Inner Harbour the rocky shore drops sharply. From the west, the bottom slopes gradually, changing from a mixture of mud and gravel to a soft organic ooze at the zero tide level. The deepest part of the Inner Bay lies along the eastern shore.

Mean depths in the Inner Harbour range from three to 35 feet in the channel and in the Outer Bay from 35 to about 130 feet.

The constriction between the two parts of the bay is about 800 feet across. The narrow channel formed by this constriction is deepest at the western side and shallows rapidly toward the east shore forming a modified sill.

The difference in depth between the two parts of the harbour may have effects on the distribution of plankton due to restriction of the depth of the euphotic zone, lack of a deep reservoir of nutrients and the greater ratio of surface area to volume in the Inner Harbour. The latter suggests that the relative concentrations of sessile and bottom filter feeders and fixed plants will be higher in the Inner Bay.

Unless the increased concentration of filter feeders is offset by the effect of the shallow depths in excluding such planktonic grazers as the more abundant copepods, phytoplankton in this harbour may experience a gradient of grazing. The greater relative concentration of plants per unit volume in the Inner Harbour suggests that phytoplankton will meet increased competition for nutrients there. However, the difference in the ratio of surface area to volume may result in higher relative concentrations of bacteria in the Inner Harbour. If this is the case, the rate of regeneration of nutrients there could be higher, perhaps offsetting the effect on phytoplankton of competition for nutrients. The fact that such regeneration would occur within the euphotic zone would add to the importance of the nutrient turnover.

B. Freshwater Drainage

The drainage area of the whole harbour is 39.6 square miles and that of the Inner Harbour is 20.4 square miles. The average annual rainfall is about 37 inches, giving a mean annual discharge of fresh water into the Inner Bay of about 5.5×10^6 cubic meters. This would form a layer 1.5 meters thick on the Inner Bay. No single stream dominates the drainage. Three major streams, two in the Inner Bay and one larger one in the Outer Harbour discharge from the west shore. Small creeks, seepage and direct runoff contribute the rest of the freshwater drainage.

While none of the streams entering Ladysmith Harbour are metered, discharge figures are available for Haslam Creek in an adjacent watershed about five miles northwest of Ladysmith (Water Resources Pub. 114). The drainage area of Haslam Creek is about 27 square miles, comparable to that of the Inner Harbour. These discharge figures indicate peaks of flow in November, February and April-May. The November and February maxima occur during periods of heavy rainfall and may be separated by a time when precipitation is being stored as snow in the watershed. The melting of this stored runoff may result in the spring peak discharge.

C. Distribution of Salinity

Surface salinities ranging from 13 o/oo to 29 o/oo have been observed at Station I in Ladysmith Harbour (Quayle, unpublished data). Subsurface salinities may exceed 29.5 o/oo, but are not known to reach 30 o/oo. Typically three major salinity minima occur each year. Two are associated with the autumn and winter peaks of freshwater discharge. The third occurs in midsummer when drainage has an almost negligible effect on salinity.

Cruises into Stuart, Trincomali and Northumberland Channels indicate that the summer salinity minima result from intrusions of Georgia Strait water, diluted by the Fraser River spring freshet, into the Stuart-Trincomali Channels system. Several such intrusions may occur in a summer, with increases in salinity between them (fig. 4).

In late fall and early summer salinities above the halo-

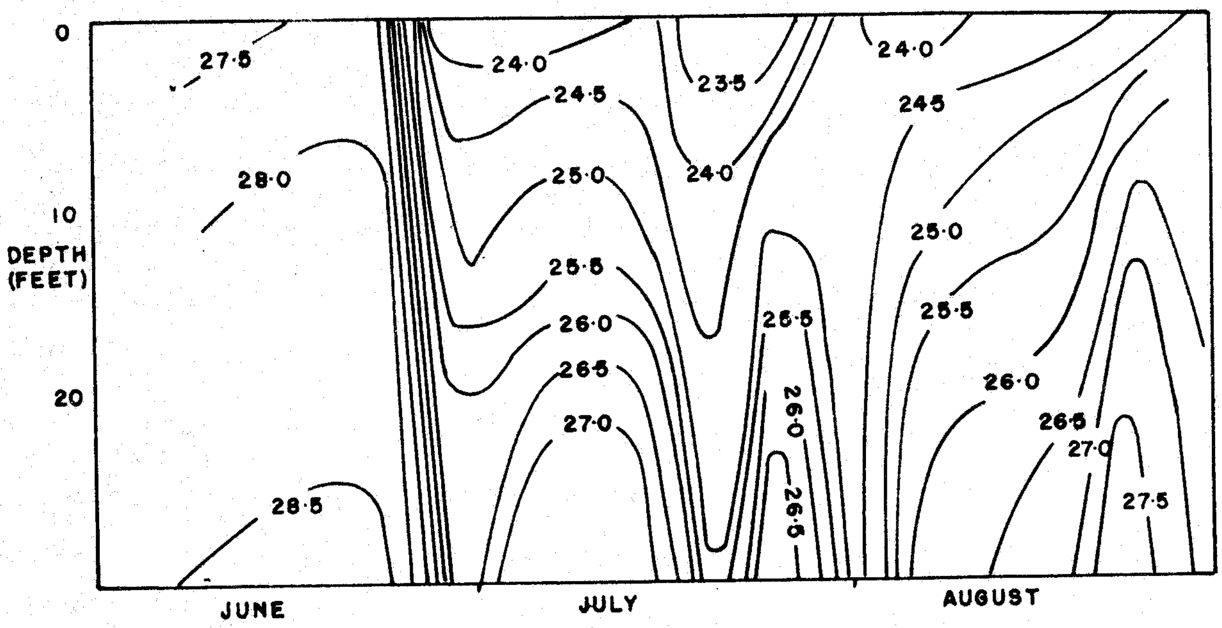


FIGURE 4 DEPTHS OF ISOHALINES (S ‰), STN. I, LADYSMITH HARBOUR, SUMMER, 1954.

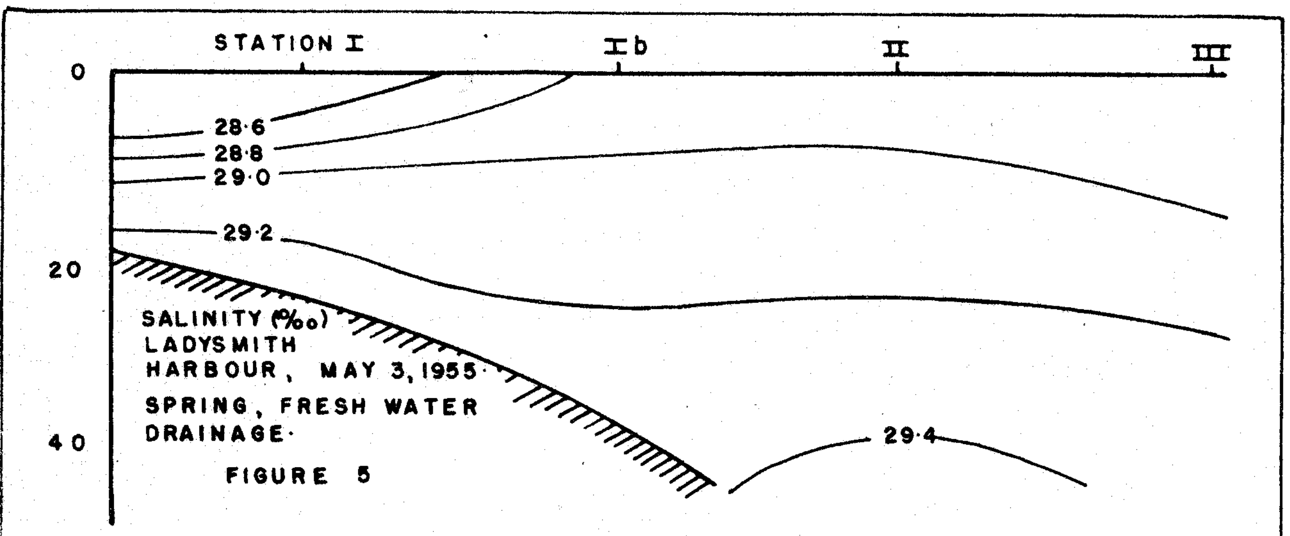
cline tend to increase to seaward. In midsummer when dilution is occuring this gradient is reversed and salinities decrease to seaward. In late summer and early fall the gradients above the halocline may be variable. At the latter times change in salinity along the harbour may be negligible, or salinities at Station II in the Outer Harbour may be either higher or lower than at Station I or Station III.

Longitudinal salinity gradients below the halocline are usually smaller than those above. At times the gradient below the halocline is the same as the upper gradient and at times it is opposite in direction.

The longitudinal gradients are typically small - less than one part per thousand along the length of the harbour. However, salinity data from Station I in the winter of 1951 reveal very strong vertical gradients of salinity in the upper three feet. If wind mixing in the more exposed Outer Harbour could break down this structure, then large horizontal gradients might develop in winter. Such gradients were not observed in this study since surface salinities were not observed during the first year. However, the winter cruises do indicate that the vertical gradients of salinity are much stronger in the Inner Harbour than just off the harbour, suggesting that wind mixing may act as suggested.

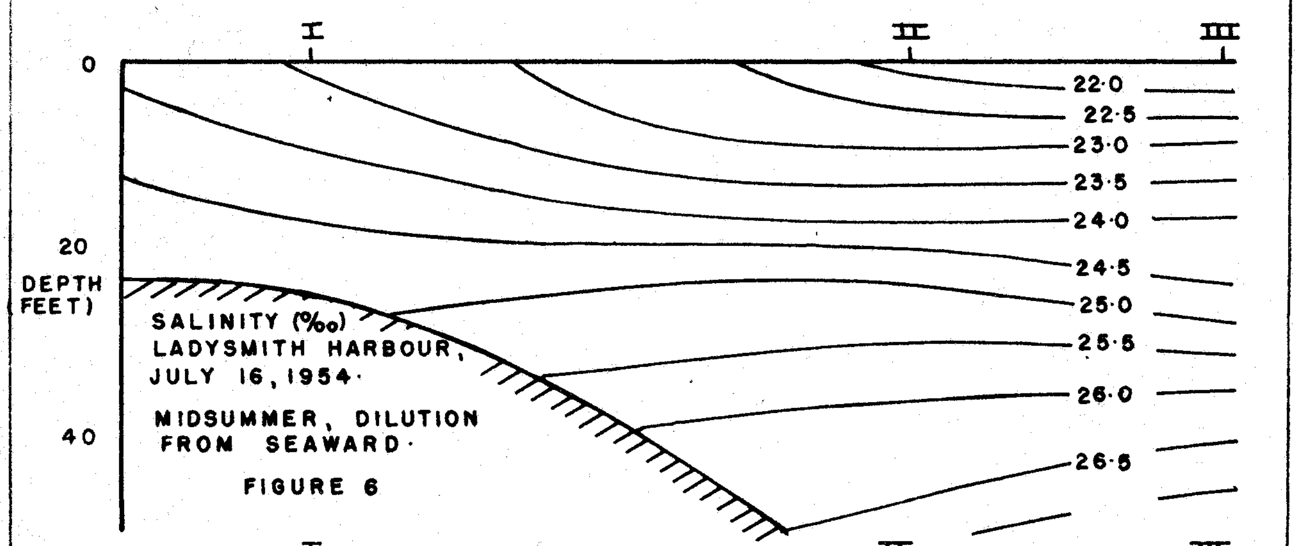
Typical longitudinal salinity sections in the harbour are shown in Figures 5, 6 and 7.

Transverse salinity gradients in both Inner and Outer



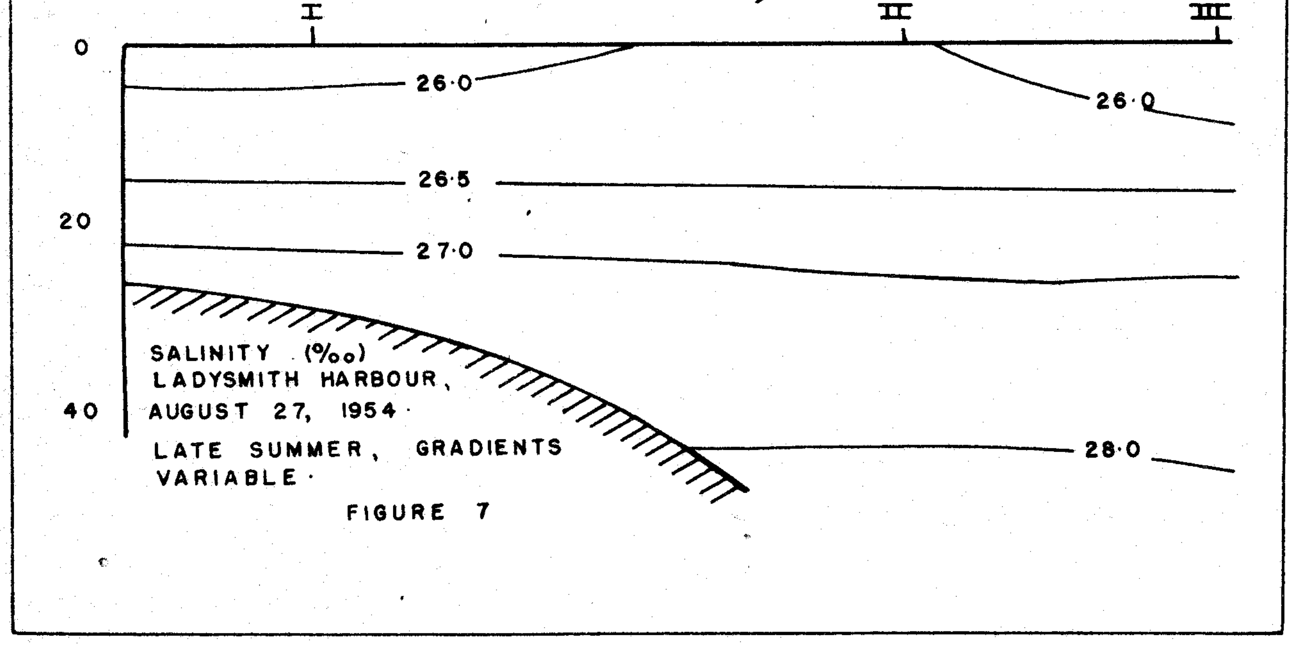
SALINITY (‰) LADYSMITH HARBOUR, MAY 3, 1955.
SPRING, FRESH WATER DRAINAGE.

FIGURE 5



SALINITY (‰) LADYSMITH HARBOUR, JULY 16, 1954.
MIDSUMMER, DILUTION FROM SEAWARD.

FIGURE 6



SALINITY (‰) LADYSMITH HARBOUR, AUGUST 27, 1954.
LATE SUMMER, GRADIENTS VARIABLE.

FIGURE 7

Harbours are usually of the order of 0.1 - 0.2 o/oo across the width and are always less than 0.5 o/oo in the spring and summer, the only periods when lateral salinity gradients were observed. The lateral gradients are variable but a tendency to lower salinities on the west side is observed, except when dilution from seaward is occuring. Sometimes the lateral gradients reverse below the halocline.

Observations made at six stations (ED 1.5, ED 3.5, H 4, H 1, K 1, K 4) occupied by three vessels over a period of twenty-four hours on May 18-19, 1955 indicate that salinities above and below the halocline tend to vary with tidal height. Salinities in the Outer Harbour tended to increase on flood tides and decrease on ebb tides. The fact that the reverse was true at the pair of stations in the Inner Harbour could be due to the movement of relatively dilute water off the mouth of Holland Creek (fig. 1) into the Inner Bay on the flood tide. The halocline in the Outer Harbour showed a tendency to a steady decrease in depth rather than any marked tidal fluctuations. The range of variation of salinity with tide was about 0.1 - 0.6 o/oo.

The average excursion of the intersection of isohalines with the surface on ebb or flood tides was about one half a mile. Since cruises in the first two patterns of stations required a maximum of about three hours, the maximum distortion in longitudinal plots of salinity due to tidal variation during the cruise should be about one quarter of a mile. Since the maximum distortion amounts to less than one eighth of the length of the harbour, it is neglected.

Observations made at a station occupied for twenty-four hours on May 29-30, 1954 in the constriction forming the entrance to the Inner Harbour indicate that the extremes of salinity at this location occur at times of maximum tidal current rather than at the extremes of tidal height. This could result from the bottom configuration in the Gap which may impede water flow except at maximum current speeds. However, lateral temperature sections across the constriction indicate strong and characteristic distortion in the configuration of isotherms for both ebb and flood tides (fig. 13). Since the twenty-four hour station was situated to the east of the middle of the Gap, the change in salinity may be an effect of the distortion rather than a true indication of the average salinity of the water moving through the constriction.

D. Distribution of Temperature

Maximum surface temperatures of about 75° F occur in August and minima of about 39° F in February. Temperature maxima and minima generally coincide with salinity minima. This may result partly from the coincidence of radiation and salinity cycles and partly from the stability at salinity minima which usually occur with strong vertical gradients.

Inner Ladysmith Harbour has a source and sink of heat in addition to the usual ones of oceanographic and meteorological origin in the extensive area of intertidal flats. The large intertidal zone will gain or lose heat during low tide periods according to the conditions prevailing. When the flats are submerged during high tides the gain or loss of heat will be passed on to the water. This phenomenon, coupled with the effect of the shore configuration in restricting water exchange and wind mixing, may be reflected in the temperature distributions. In addition, the shallow depths eliminate the possibility of modification of temperatures resulting from mixing with deep water.

In spring, summer and early fall temperatures above the thermocline tend to decrease, sometimes irregularly, toward the mouth of the harbour (figs. 8, 9, 10, 11, 12). Temperature gradients in the thermocline are sometimes strong. Below the thermocline the gradients may be similar or opposite to those above the thermocline.

Temperatures in the Inner Harbour tend to decrease from head to mouth and from west to east in spring and summer. This may result from the fact that the intertidal flats, sources of heat in spring and summer, lie at the end and side opposite to the source of colder water. At times the distributions of temperature as indicated by extensive use of the bathythermograph are quite irregular within the net gradient (fig. 12). This irregularity may result partly from the effect of the constriction mentioned on page 16. In longitudinal plots of the distribution of temperature taken by bathythermograph on the flood tide, isotherms rise sharply

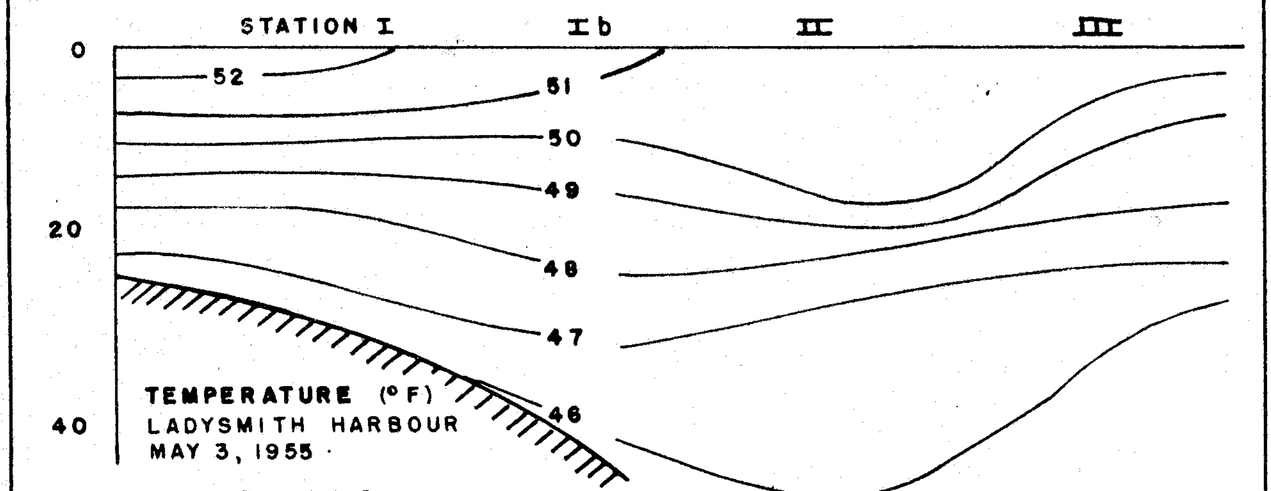


FIGURE 8

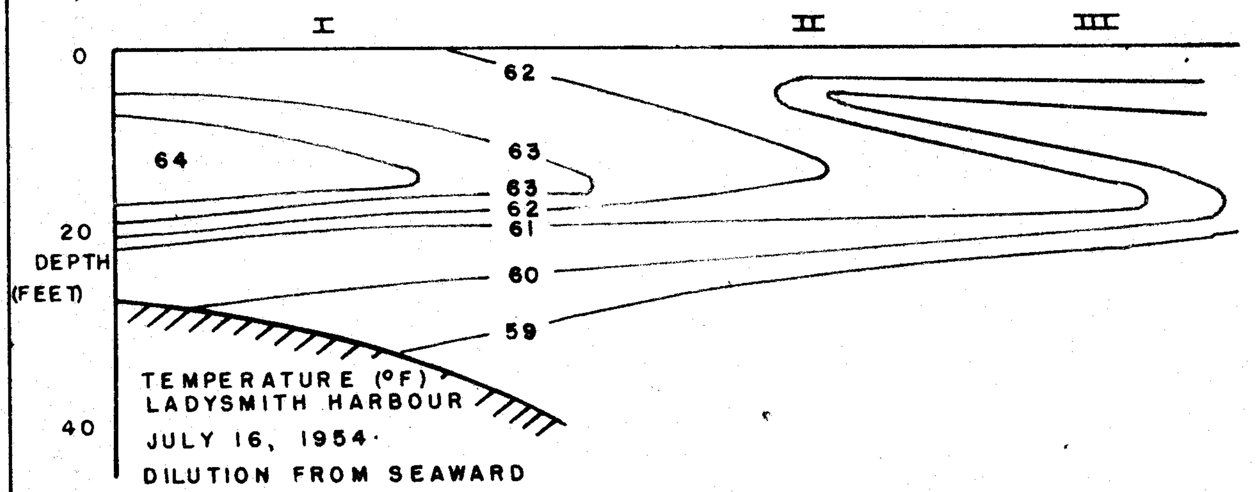


FIGURE 9

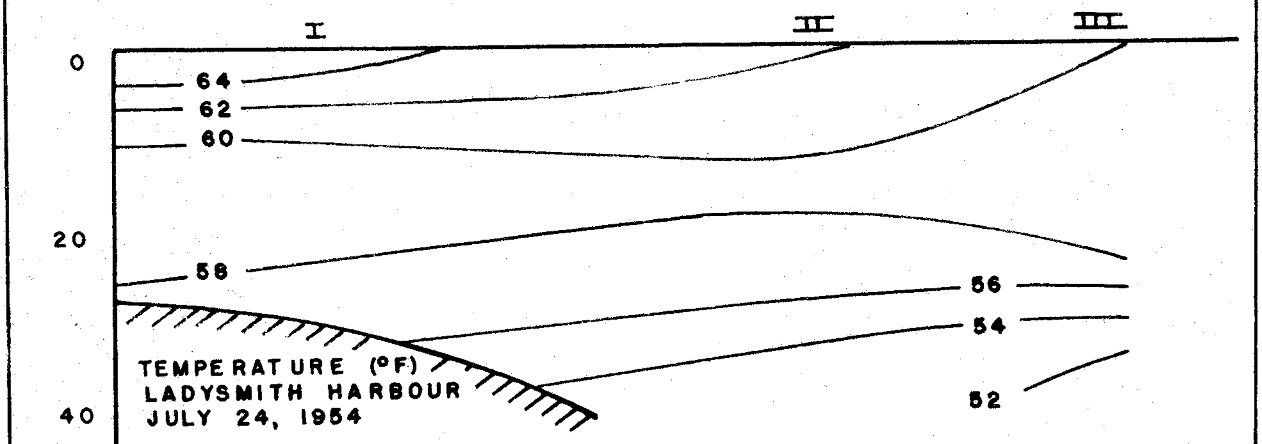


FIGURE 10

over the "semi-sill" in the constriction and follow the bottom down closely inside the sill (fig. 12). During large tidal rises relatively cold water from the greater depths of the Outer Harbour may be forced in over the sill, and be unable to move out on the following ebb tide. This effect may be enhanced by the existence of a two-layer system of circulation in which cold water tends to flow inward along the bottom. The distribution of the intertidal sources of heat and mixing resulting from a jet stream through the Gap on flood tides may also contribute to the sometimes irregular distribution of temperature.

Characteristic transverse distributions of temperature for both flood and ebb tides were observed in the Gap (fig. 13). The transverse gradients are typically strong with temperatures in the upper zone decreasing from west to east on the flood tide and from east to west on the ebb. Toward the bottom the gradients tend to reverse. These characteristic distributions may be a combined result of the constriction and a two-layer system of circulation.

Variations in temperatures at the six stations occupied for twenty-four hours on May 18-19, 1955 were more irregular than variations in salinity. The temperature changes differed at each of the three sections and, except for stations H_1 and H_4, the stations in each pair exhibited differences in the change of temperature with tide.

Of the six stations only $ED_{3.5}$ and K_4, the inner and outermost on the west side of the Harbour revealed regular

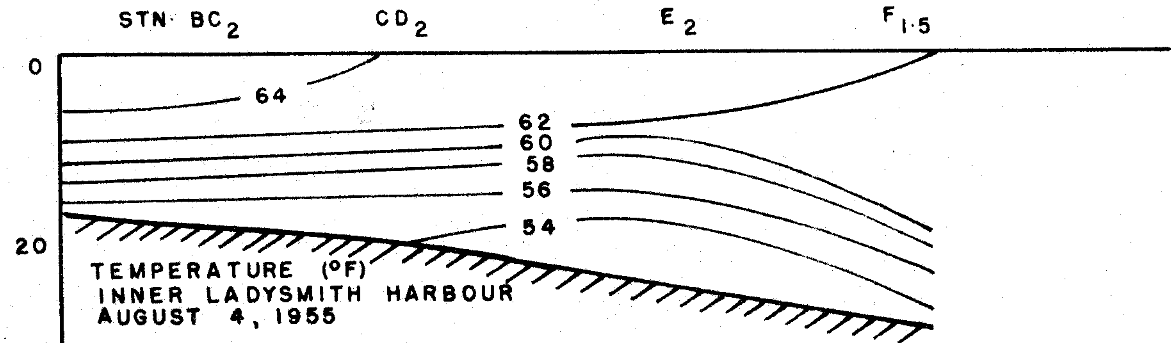


FIGURE 11

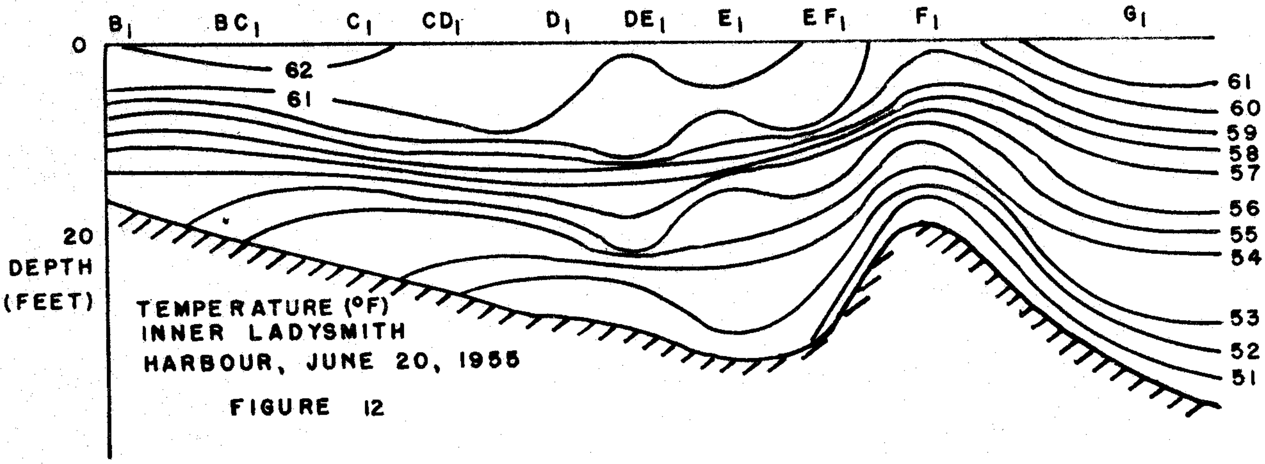
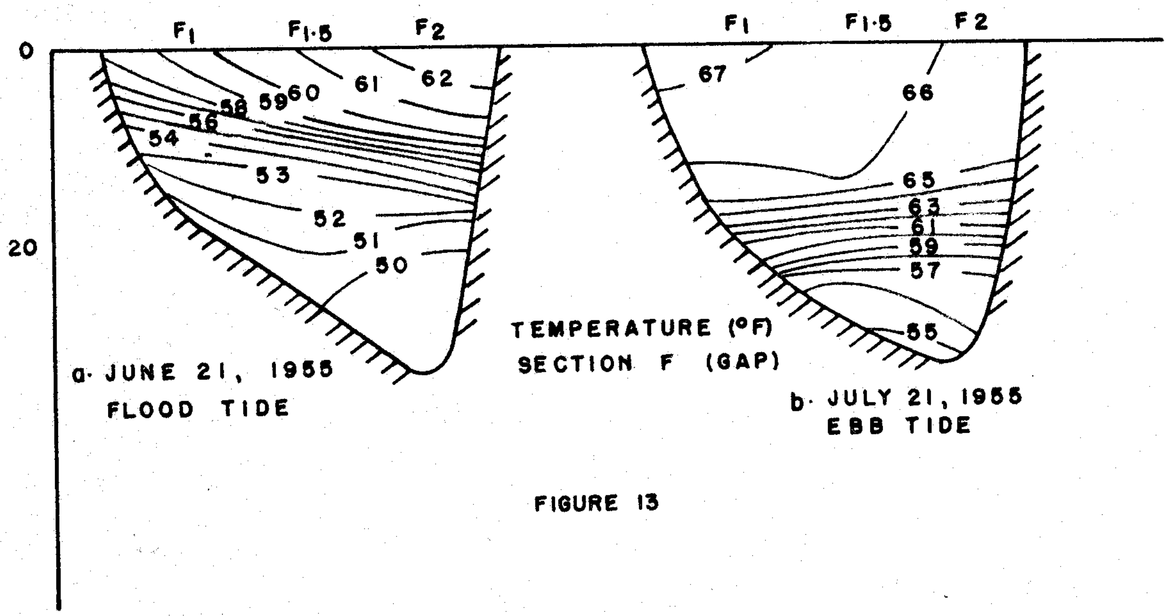


FIGURE 12



a· JUNE 21, 1955
FLOOD TIDE

b· JULY 21, 1955
EBB TIDE

FIGURE 13

variation in temperature with tidal height. At station $ED_{1.5}$ paired with $ED_{3.5}$ but on the east side of the inner Bay, shallow layers of warm water were observed at both lower low water periods, as might be expected. However, isotherms below a depth of ten feet showed little change in depth, other than to appear slightly shallower at low water after the small ebb tide. This effect could be attributed to the movement of the upper water out over the relatively immobile deeper water on this small tide.

At Stations H_1 and H_4 in the Outer Harbour surface temperatures tended to vary directly with tidal height. Below a depth of about twenty feet the changes in temperature at these two stations were similar, showing an increase on the small ebb, a marked decrease on the small flood and virtually no change on the large flood and large tides. The temperatures at intermediate depths showed a steady decrease at Station H_1, the eastern station, and paralleled the deeper temperature changes at Station H_4.

As already mentioned, temperatures at Station K_4, the western station at the mouth of the Outer Harbour, varied directly with tidal height. Temperatures below a depth of about ten feet at Station K_1, across the Harbour from K_4, varied inversely with tidal height. Above ten feet, at Station K_1 a decrease in temperature occured on the first flood tide and a slow increase in temperature continued from the first high water period until occupation of the stations was terminated.

The complexity of these variations of temperature with tide could be due to simple distributions of temperature and complicated patterns of flow, to complicated distributions of temperature and simple flow patterns or to intermediates between these two alternatives. The relative regularity of the variation in salinities suggests that the distribution of temperature rather than flow patterns may be responsible for the complex variation of temperature with tide. Some temperature sections from the Outer Harbour reveal complex distributions indicating that this may be the case.

The station occupied for twenty-four hours in the Gap indicates that temperatures varied in much the same way as salinities. Extremes occurred at times of maximum current speed rather than at high and low-tide periods.

On August 10-11, 1955 a station was occupied for twenty-four hours at position CD.5 in the grid of stations covering the Inner Harbour (fig. 3). Bathythermograph casts and observations of velocities at eight depths were made at intervals of one hour for the twenty-four hour period. At high and low tides and halfway between high and low tides bathythermograph casts were made at four stations across Section CD.

In general maximum temperatures occurred at low tides and minimum temperatures at high tides. The maximum change in temperature of about 4°F took place at a depth of 12 feet on the large flood tide between lower low water and high water. The depths of the isotherms did not change smoothly, but with many small irregular fluctuations which were greatest in the lower region of the thermocline. These fluctuations may indicate turbulence or be an effect of the constriction.

Each of the eight observations on the transverse distribution of temperature indicated that temperatures above the thermocline increased toward the west side of the harbour. No distinctive variations in the lateral distributions of temperature with tide were observed other than a general increase and decrease of temperature.

Longitudinal temperature gradients in the Inner Harbour vary from 2F° to about 7F° along its length. For the whole harbour, the longitudinal gradient may exceed 10F°.

Vertical temperature gradients from less than 2F° to over 18F° in 25 feet have been observed in the Inner Bay.

Transverse gradients of up to 2 F° across the width of the Inner Harbour may occur.

E. Water Exchange in the Inner Harbour

1. Tide

The volumes of water and percent changes in the volume of the Inner Harbour due to tidal action are discussed since they may give an indication of the rate of water exchange and the magnitude of the role that tide plays in water renewal in the Inner Bay.

The volume of water contained by the Inner Bay was obtained by taking the areas enclosed by successive depth contours (U.S. Hydrographic Office Chart No. 2564), multiplying by the appropriate depth increment and summing the volumes so obtained. The intertidal area, being of little interest to mariners is not contoured on the hydrographic charts. Since it was necessary to know the distribution of intertidal depth contours in order to calculate changes in volume due to tide a rise of six feet was assumed between the zero tide level and intersection of the mudflats with the approximately vertical shoreline. The slope between the zero and six foot levels was assumed to be such that the three foot contour divided the area between them in half. The volume of water beneath different depths is presented in Figure 14. Table I indicates the percent changes in volume occuring on various ranges of ebb tide.

Mean tide level in Ladysmith Harbour is about 8 feet and the mean tidal range is about 7 feet giving a mean volume of about 16.4×10^6 cubic meters with a range of $+ 4.2 \times 10^6 m^3$, $- 3.5 \times 10^6 m^3$. Thus about 37 percent of the mean high tide volume of the Inner Bay is involved in each tide or about 70 percent/day.

The sum of mean area of the two small passes into Burleith Arm is about 5 percent of the cross-sectional area of the Gap. This suggests that at least 90 percent of tidal exchange occurs directly with the Outer Harbour through the Gap.

The magnitude of the tidal volume changes and the effect

TABLE I

Percent Changes in Volume of Inner Ladysmith Harbour on Various Tidal Ranges

Tidal Range	% Change in Vol.	Tidal Range	% Change in Vol.
15-12 ft.	13.7 %	12-3 ft.	59%
15-9	27.4	12-0	69
15-6	41.1	9-6	19.3
15-3	53.3	9-3	35.6
15-0	62.0	9-0	47.6
12-9	16.0	6-3	20.4
12-6	32.0	6-0	35.4

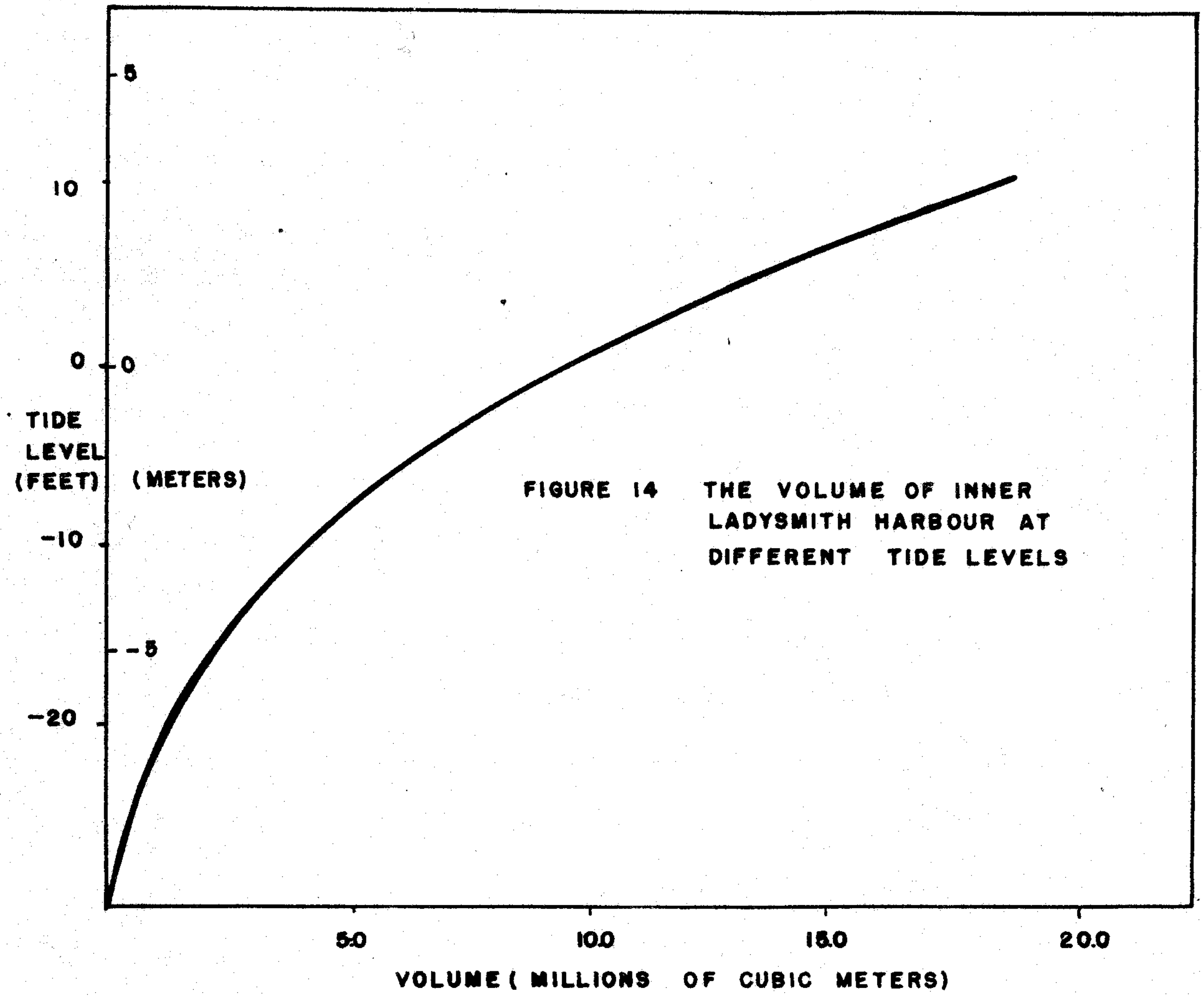


FIGURE 14 THE VOLUME OF INNER LADYSMITH HARBOUR AT DIFFERENT TIDE LEVELS

of the constriction at the Gap in producing a jet stream which should enhance horizontal mixing suggests that tidal exchange may be an important factor in the renewal of water in the Inner Bay.

It seems unlikely that all the water entering on flood tides would be the same as that which left on the preceding ebb or that it is all new water. This suggests that 70 per-cent of the mean high tide volume per day is an approximate upper limit to the rate of water renewal.

2. Renewal Rates from Changes in Salinity

If known changes in salinity in the Inner Harbour occur as a result of horizontal exchange and if the salinity of the water causing these changes is known, the volumes of water exchanged can be calculated if volume continuity is assumed.

The amount of salt in a body of water of constant volume after a change in salinity resulting from volume exchange can be expressed as:

$VS_2 = VS_1 - \Delta VS_1 + \Delta VS_2$, where V = volume of the body of water; ΔV = volume of water replaced; S_1 = mean salinity of the body of water at t_1 before the change; S_2 = mean salinity of the body of water at t_2, after the change; and S_D = the salinity of the water causing the change in salinity.

The volume replaced is:

$$\Delta V = \frac{V(S_2 - S_1)}{(S_D - S_1)}$$

Expressed as P , percent of the volume of the body of water replaced per day, this becomes:

$$P = \frac{(S_2 - S_1)}{(S_D - S_1)} \times \frac{100}{(t_2 - t_1)}$$

The data required are the average salinity of the body of water before and after the change in salinity, the salinity of the dilutant (replacement water) and the time interval.

Salinity data from the summer of 1954 indicate that three periods of dilution from seaward occured in the Inner Bay. Between the periods of dilution, salinities in the Inner Harbour increased (fig. 4). The pertinent data are from Stations I, II and III.

In order to calculate exchange rates for the Inner Harbour from this data the following assumptions must be made:

a. It is assumed that salinities from Station I represent the average for the Inner Harbour. Data from the grid of stations in the Inner Bay in 1955 suggest that this tends to be the case.

b. It is assumed that salinity changes in the Inner Harbour result from exchange with water having the salinities observed at Station II in the Outer Harbour.

It has been stated that these salinity changes result from exchange with water to seaward of the Inner Bay. The movement each day of 70 percent of the mean high tide volume of the Inner Bay into the Outer Harbour through the jet stream affords ample opportunity for horizontal mixing to occur. Calculations indicate that the mean volume of water moving out of the Inner Harbour on an ebb tide would cover the area in the Outer Harbour, the center of which is approximately the position of Station II. While few observations of the distribution of salinity were made within this area, those available suggest that salinity gradients within the area are small. Station II salinities will therefore be accepted as an approximation to the mean values for S_D.

c. Freshwater discharge is assumed to cause negligible changes in salinity. Discharge rates into the Inner Bay range between 0.3 and 3 cubic meters per second and average about one cubic meter per second for the period being considered.

d. It is assumed that exchange between the Inner Harbour and Burleith Arm is negligible. Since it is suggested that at least 90 percent of the tidal volume changes in the Inner Harbour occur directly with the outer harbour, error from this assumption may be small.

If the use of Station II salinities as values for S_D is accepted two problems concerned with averaging must be considered. First, the question of whether the salinity, S_D, should be a time average must be dealt with. Secondly, since the depth at Station II is about three times that at Station I, a depth to which salinities at Station II should be averaged must be chosen.

As used here the expression for obtaining renewal rates represents an integration of salinity changes over several days. Better results would be obtained if calculations could be made for each tide or each day, since Station II salinities will change continuously between cruises. The data are insufficient for this. In order to take into account the fact that Station I salinities at t_2 will be the result of exchange with waters of the full range of Station II salinities between t_1 and t_2 , S_D should consist of the average of Station II salinities at t_1 and t_2. Whether or not this average is valid depends on the way salinities varied between cruises. Such time averages appear to work for some periods during which salinities increased but not for periods of dilution.

Dilution occurs suddenly, suggesting that discrete clouds or fronts of fresh water move into the Ladysmith area mixing with and replacing water of high salinity. This is supported by the fact that S_D 's for periods of dilution based on time averages are higher than Station I salinities at t_2. The time average gave good results for all but one period of salinity increase.

The average depth of the Inner Harbour is about 24 feet. If no vertical mixing occurs with water from below this depth and only horizontal mixing need be considered , averages of Station II salinities to a depth of 24 feet should be satisfactory for S_D. It could be argued that the strong vertical gradients of salinity and temperature with resulting stability would tend to dampen vertical mixing and reduce error from this source. This appears tenable for periods of salinity decrease but not for increases in salinity.

S_D's for the first two periods of dilution, based on 24 foot t_2 averages give renewal rates of 19.3 and 16.0 percent per day. The magnitudes appear reasonable and agreement is close. S_D for the third period of dilution (July 24-August 2), averaged in the same way, cannot be used since this S_D is greater than the salinity supposedly resulting from its influence. The configuration of isohalines in the longitudinal section for August 2 suggests that an inflow of dilute water above a depth of 15 feet occurred. S_D averaged to this depth gave a renewal rate of 19.5 percent per day which agrees well with the above two rates.

The fact that vertical mixing has been assumed negligible does not mean that it has been inoperative. The 24-and 15-foot averages used here may be more saline than the corresponding averages for the true dilutant, but the added concentration due to time increase in salinity could correct for possible effects of vertical mixing.

There seems to be no clear cut approach to averaging salinities to obtain S_D for periods during which Inner Harbour salinities increased. During the middle of August Inner Harbour salinities increased in spite of an apparent decrease in salinity toward the mouth of the harbour above the twenty-four-foot level. Due to lack of data it can only be assumed that the increase was a result of upward intrusion of more saline water from beneath the 24 foot level.

To take the effect of upward intrusion or vertical mixing into account the depths to which salinities were averaged were increased, thereby increasing the value of S_D. No one depth gave satisfactory results. Averages to a depth of 30 feet in two calculations and to 40 feet in two others were necessary to produce salinity changes in the observed direction.

Although this method of averaging is arbitrary, longitudinal sections of temperature indicate that at times water from these and greater depths may move up the sloping bottom and through the constriction into the Inner Harbour.

The rate of renewal for July 16-20, a period of increase in salinity, was obtained in two ways. The first used an S_D consisting of t_2 salinities averaged to a depth of 24 feet and the second used ~~of~~ the mean of Station II salinities at the two dates averaged to a depth of 40 feet as S_D. The respective rates are 27 percent and 21 percent of the mean volume per day, and are in good agreement with the other values (Table 2).

TABLE 2

Renewal Rates from Salinity Changes

Summer 1954

Date	S_D	S_1	S_2	P
June 22-27	25.10 o/oo	28.18 o/oo	25.21 o/oo	19.3 o/o
July 12-16	23.35	25.57	24.15	16.0
July 16-20	25.16	24.15	25.07	27.0
	25.21			21.7
July 24-Aug 2	23.74	25.06	24.22	19.5
Aug 2-Aug 5	25.11	24.22	25.07	32.0
Aug 5-Aug 12	25.72	25.07	25.62	12.0
Aug 12-20	26.74	25.62	26.63	13.0

The mean of the seven rates calculated by this method is 20.1 percent of the mean volume per day with a standard deviation of 6.5 percent. All values are within the 70 percent upper limit obtained from a consideration of changes of volume with tide. According to the mean value, about one third of the water moving to the Outer Harbour on an ebb tide is exchanged.

The results for periods of dilution agree well and were obtained with a minimum of manipulation. The agreement among rates from periods of increase in salinity may be apparent rather than real because of the arbitrary way in which averages were adjusted in order to produce salinity changes in the observed direction.

It may be inferred from the necessity to manipulate averages that:

a. the data on the distribution of salinity in both space and time was inadequate.

b. the assumptions discussed above are not valid.

c. the variability in small inshore bodies of water is such that even cruises separated by intervals of a few days may miss significant changes in properties and distributions.

d. velocity gradients or net circulations exist and should have been taken into account in choosing salinities for S_D.

3. Circulation

Velocity observations and distributions of salinity, temperature and density suggest that net circulations do exist. Longitudinal distributions of salinity, temperature and sigma-t, the density anomaly (figs. 15, 17, 18, 19), suggest that during most of the year a two layer system of circulation with outflow in the upper layers and inflow in the deeper layers exists. During periods of dilution from seaward in summer this circulation reverses and inflow occurs in the upper layers (fig. 16).

The mean distribution of velocity with depth at a Station occupied for twenty-four hours in the Gap indicated a net flow outward of about 10 centimeters per second above a depth of about nine feet and a net flow inward of about the same speed below this level. Taking into account the mean cross-sectional areas above and below the depth of no net motion transports of 54 cubic meters per second outward and 89 cubic meters per second inward were calculated. According to these transports a net flow inward of 35 cubic meters per second occurred during the course of these observations. Predicted tidal heights at the start and termination of this station were approximately equal. No appreciable change in the volume of the harbour was observed. Fresh water drainage rates for this period suggest that transport out should have exceeded the flow in by about 3 cubic meters per second if continuity of volume was to be maintained.

It may be concluded that the velocities from this station did not represent the mean for the cross-section, that a lateral circulation existed or that a net outflow

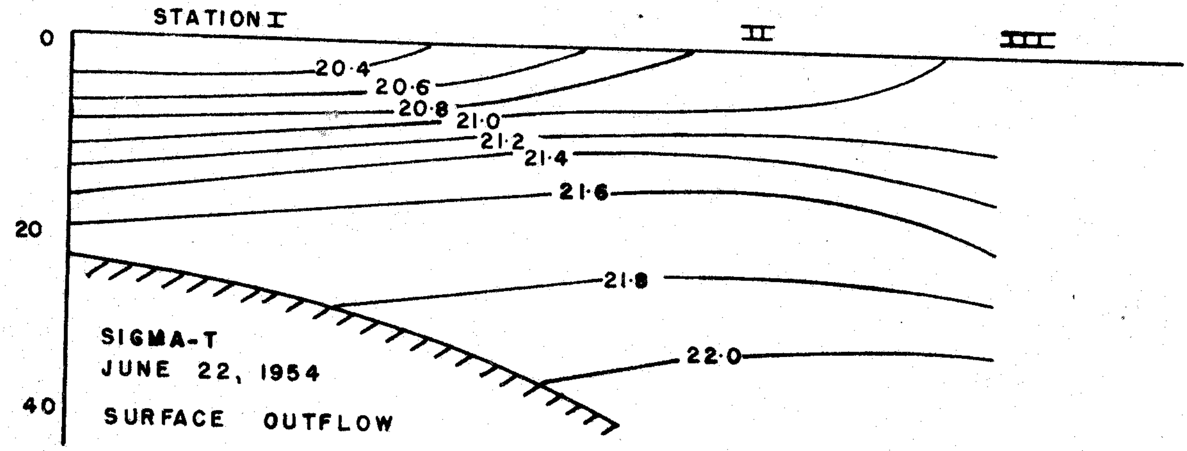


FIGURE 15

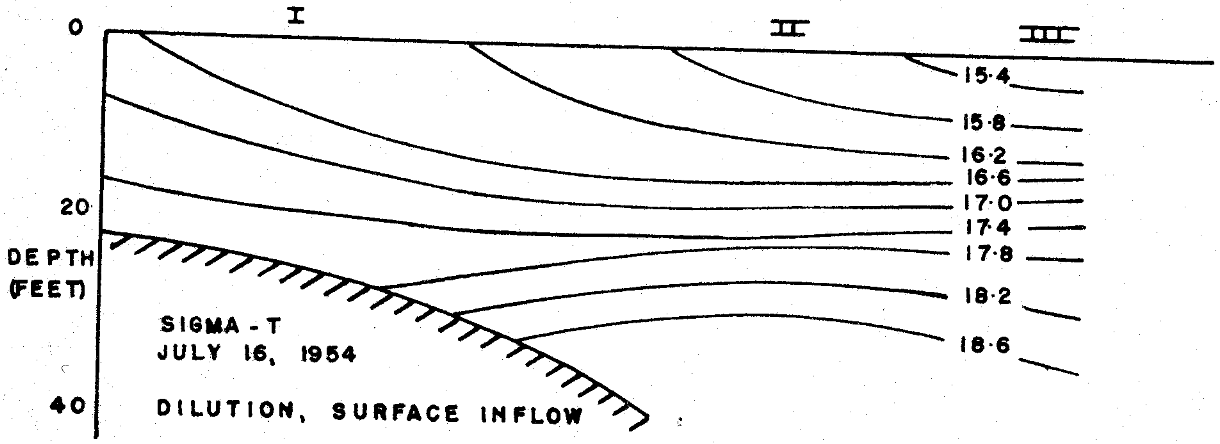


FIGURE 16

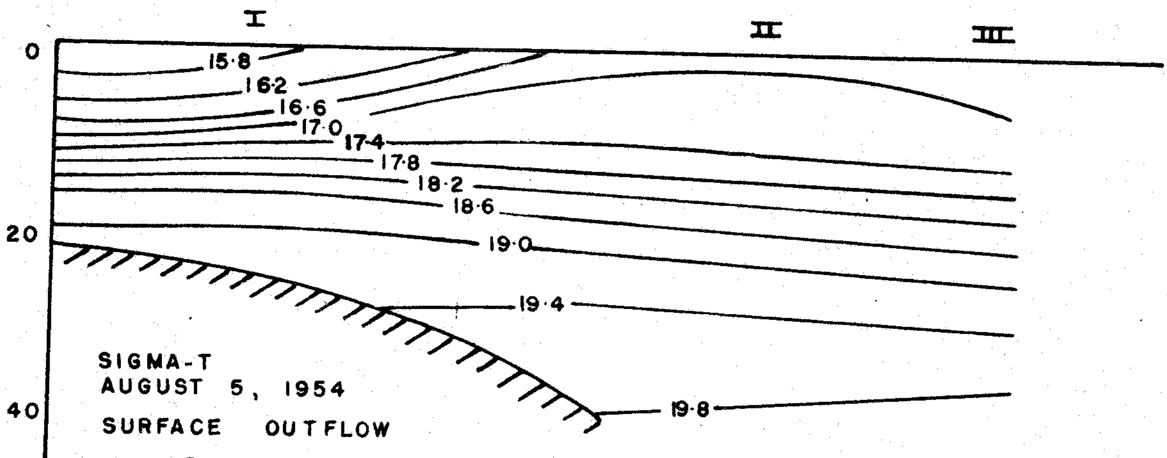


FIGURE 17

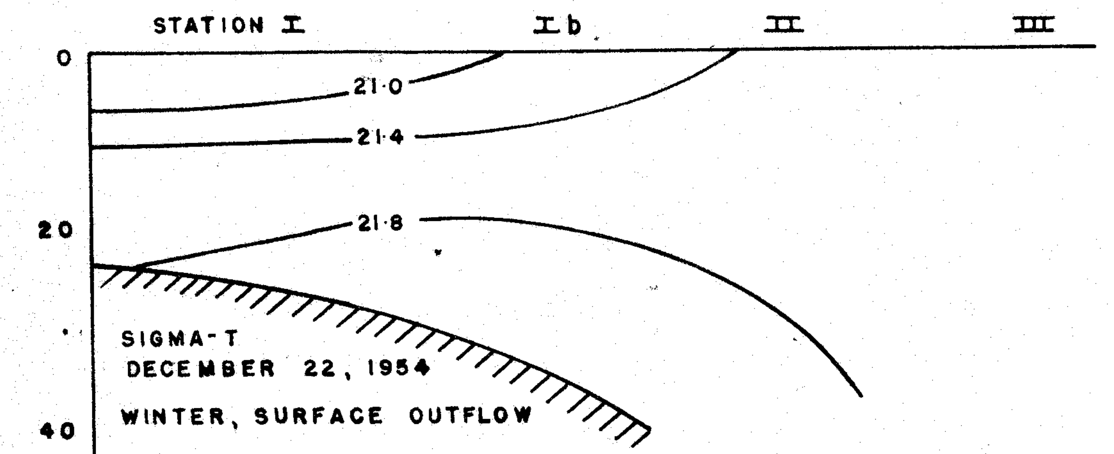


FIGURE 18

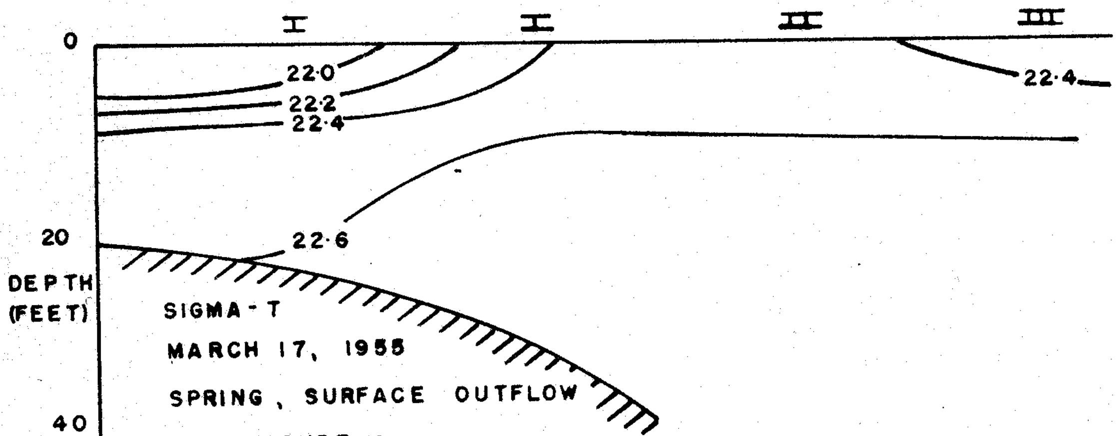


FIGURE 19

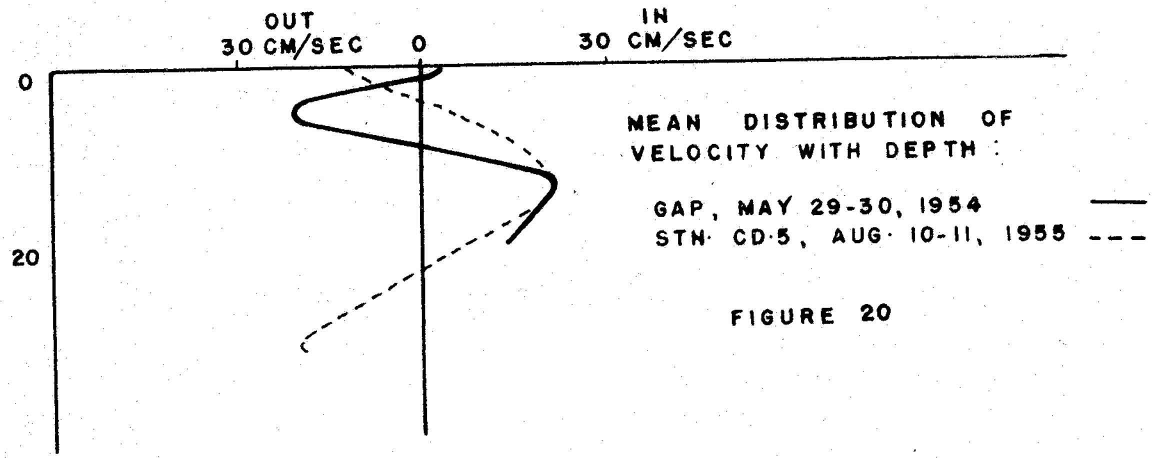


FIGURE 20

through the two small passes into Burleith Arm occurred (fig. 1).

At the August 10-11 anchor station the mean velocity profile for the 24 hours (fig. 20) suggests that a three-layer circulation with outflow near the surface and bottom and inflow in the mid-depths existed. Marked ebb currents near bottom occurring near the end of the two flood tides gave rise to the net outward velocities near the bottom. Again, since a net inflow was observed it can be suggested that the velocities did not represent the mean for the cross-section, that a lateral circulation existed or that a net outflow into Burleith Arm occurred

The significance of the ebb currents near the bottom while flood currents were observed in the rest of the water column is not known.

Observations of the movements of free drags suspended at different depths from surface floats indicate that on the flood tide velocities at mid depths (10-15 ft.) are greater than those near the surface in spite of the prevailing up-harbour wind. No such observations are available during ebb tides.

While the water transports calculated from velocities observed at the stations occupied for 24 hours do not indicate continuity of volume they can be used to support the existence of the two-layered system of circulation inferred from the longitudinal distributions of salinity, temperature and density.

The pressure forces maintaining the outward flow in the surface layers of water appear to result from fresh-water drainage in winter, drainage and heating in spring and fall and from differential heating in the summer.

Observations on the movements of dettritus and foam-lines on calm evenings at and just before high tide periods indicated that surface currents may ebb on the west side of the Inner Harbour while the surface water on the east side is stationary or moving inward. The few observations on the lateral distribution of velocity indicate that the flood tide currents are stronger on the east side of the harbour. The one set of observations of velocities at several depths at a station on the west side of the harbour just after the turn of the tide to the ebb indicates that ebb currents along the west shore may be about the same speed as flood currents along the east shore. These scattered observations suggest that an anticlockwise lateral circulation exists. Some distributions of surface temperatures are compatible with such a circulation.

On the other hand some studies of the surface flow patterns using wooden floats suggest that the flood tide may be stronger along the western shore in the inner half of the Inner Bay.

Some surface distributions of surface properties, the existence of semi-permanent tide-lines extending diagonally across the harbour and the movements of surface floats suggest that water of low density originating near the head of the harbour tends to move seaward against and over denser water moving inward on the flood tide.

Other observations on distributions of flow patterns and properties at the surface suggest that slight upwelling of relatively cold and saline water may occur at times in the inner half of the Inner Harbour.

Thus lateral water movements in the Inner Harbour appear to be confused and variable. Some appear to be related to tidal factors and others to distributions of density. However, the number and quality of current observations allow no definite conclusions to be drawn concerning lateral circulations in the Inner Harbour.

4. Two Layered Circulation and Exchange Rates

a. Continuity of Salt and Volume

The relationship between transports of water and salt for a body of water receiving freshwater drainage and in which continuity of salt and volume are maintained by a two layer circulation may be expressed as:

(1) $Si\ Ti = Su\ Tu$, where Si = salinity of the inflowing layer; Ti = the rate of transport of water inward; Su = salinity of the outflowing layer; and Tu = the rate of transport of water outward.

Since continuity of volume has been assumed,

(2) $Tu = Ti + D$, where D = the rate of freshwater discharge.

(3) $\because$ (1) and (2), $Ti = \frac{SuD}{(Si-Su)}$.

Thus, if the rate of freshwater discharge and the mean salinities of the inflowing and outflowing layers are known, water transports and hence renewal rates can be calculated. As already indicated, although no drainage data are available for Ladysmith Harbour, a stream in a neighbouring watershed similar in size to that of the Inner Harbour is metered. The products of the ratio of the drainage area of the Inner Harbour to that of Haslam Creek and discharge rates from Haslam Creek are assumed to represent the rates of freshwater discharge into Inner Ladysmith Harbour. Distributions of salinity, temperature, and density indicate that the required two layered system of circulation obtains for most of the year. The depth of no net motion, necessary to obtain Si and Su, was taken to be the inflection point of the sigma-t profile.

On the basis of salinity data taken in the Inner Harbour in the spring and summer of 1955, Station I salinities were accepted as approximations to the mean salinities of the upper and lower layers. The mean salinity above the depth of no net motion was used as Su and that below as Si.

The salinity data indicate that while the mean annual salinity of the Inner Harbour remains relatively constant salinities within any year fluctuate continuously. However, at periods of salinity maxima and minima the change of salinity with time is zero and continuity of salt may be considered satisfied.

The volume of the Inner Harbour was assumed to be constant.

The data used and the results are presented in Table 3.

The results may be summarized as follows:

(1) 1951: the mean of the 15 rates calculated is 29.5 percent of the mean volume renewed per day.

(2) 1952: nine values were computed the mean of which was 35 percent of the mean volume per day.

(3) 1954: the mean of the six renewal rates calculated is 27 percent per day.

(4) 1955: three rates were calculated, their mean is 35 percent per day.

(5) The mean of all renewal rates calculated by this method is 32 percent of the mean volume of the Inner Harbour per day.

The 1951 rates are more closely clustered around their mean than are those for the other years. It may be significant that 1951 was the only period during which surface salinities were observed.

Several sources of error may exist:

(1) Since observations were not continuous the observed maxima and minima may be apparent rather than real.

(2) The freshwater discharge rates used may not represent the true rates for Inner Ladysmith Harbour.

(3) The salinities used for Si and Su may not represent the true values. This would be the case if Station I salinities were not the mean values for the Inner Harbour or if the choice of the depth of no motion was in error.

(4) Occasionally freshwater drainage into the Outer Harbour may

TABLE 3

Water Transports and Renewal Rates from Continuity of Salt and Volume

Date		Depth of no motion	D	Su	Si	Ti	P
1951 Feb.	9	5 ft.	13.9 m^3/s	20.5 0/oo	27.7 0/oo	40 m^3/s	2%/day
	19	11	2.8	24.2	27.3	22	11
Mar	19	2	3.3	22.8	27.3	17	9
April	12	5	5.5	27.6	28.3	217	110
	23	6	3.0	26.3	28.1	44	23
May	20	7	2.2	26.1	27.5	41	22
	29	8	1.5	27.1	27.7	68	36
June	7	14	0.8	25.5	26.3	26	13
	13	7	0.6	25.6	27.1	10	5
	20	10	0.4	25.7	26.2	21	11
	26	10	0.2	26.1	26.8	7	4
Oct	8	5	2.8	27.2	29.0	42	22
	18	14	2.9	28.2	29.0	104	55
	25	6	6.4	27.5	28.6	160	84
							30
Nov	29	5	6.9	23.1	28.1	32	17
1952 Jan	31	6	12.9	24.1	29.2	64	34
Feb	7	6	10.1	27.8	29.1	216	114
	14	6	4.8	22.9	27.9	18	9
	26	6	4.8	27.7	28.7	131	69
Mar	21	3	2.1	27.6	29.1	39	20
April	2	11	2.8	28.0	28.9	41	22
May	1	10	11.8	27.5	29.0	216	114
	17	7	5.4	28.2	28.8	252	133
							30
Sept	12	10	0.25	27.3	28.3	7	4
1954 June	6	8	2.6	27.6	28.1	133	70
	22	11	2.0	27.9	28.4	114	60
July	12	14	2.1	24.6	26.5	38	20
	20	12	0.8	23.9	25.9	9	5
Aug	20	8	0.3	25.1	27.2	4	2
	27	12	0.3	26.0	26.7	12	7
1955 May	30	8	2.9	28.5	28.9	109	57
June	15	12	1.2	26.8	27.3	67	35
	29	8	0.7	26.8	27.4	24	13

influence Inner Harbour salinities. If sources of freshwater in addition to local drainage are present renewal rates based on local drainage only will be in error.

(5) If the lateral circulation mentioned earlier became important, freshwater discharge from a stream emptying down-harbour from Station I might not influence salinities at that station. In such a case renewal rates based on Station I salinities would be in error. Although the lateral circulation is not known to be significant in spring and summer it could be important in fall and winter.

(6) In some longitudinal distributions of salinity, temperature and density the two layered circulation is not well defined. This may result from small longitudinal gradients or from almost neutral stability. At such times renewal rates calculated on the assumption of a two layer circulation will be in error.

The fact that exchange rates do not appear to vary seasonally with freshwater drainage may be due to several reasons. The fact that rates close to the mean are distributed around the year suggests that tidal action, which is relatively constant, may control the rate of exchange. The lack of variation of the rate with freshwater drainage could indicate that the influence of differential heating takes over as the influence of drainage decreases. It is also possible that exchange is related to the rate of freshwater discharge but that the inadequacies of the date obscure the relationship.

b. Continuity of Heat and Volume.

A method of obtaining renewal rates analogous to the method used above exists if continuity of heat and volume can be assumed.

The following expression equates the factors in the heat budget of a body of water if continuity of heat and volume are maintained:

$Qs + Qr + Qe + Qh + Qv = 0$, where Qs = incident solar radiation; Qr = solar radiation reflected from the surface of the water; Qe = heat used for evaporation; Qh = heat gained or lost by conduction; and Qv = the net transport of heat by water movements. All these factors are measured in gram calories per square centimeter per minute.

If continuity of heat is maintained and the appropriate meteorological and oceanographic data are available, $(-Qv)$ can be calculated. Then if the circulation and the distribution of temperature are known the water transports necessary to supply or remove $(-Qv)$ can be calculated.

1. $(-Qv)A = \rho C \theta_u T_u - \rho C \theta_i T_i$ where $(-Qv)$ = the amount of heat passing through a square centimeter of upper water surface per unit time; A = the area of the upper water surface; C = the specific heat of the water; ρ = the density of the water; θ_u = the temperature of the upper layer; Tu = the rate of water transport out; θ_i = the temperature of the lower layer; and Ti = the rate of transport of water inward.

2. If it is assumed that Tu and Ti are approximately equal,

$$(-Qv)A = \rho C \, Ti(\theta_u - \theta_i)$$

and $$Ti = \frac{(-Q_v)A}{\rho C(\theta_u - \theta_u)}$$

and $$P = \frac{1440 \, T_i}{V} = \left|\frac{1440(-Q_v)A}{V \rho C(\theta_u - \theta_i)}\right|$$, where P = percent of the mean volume replaced per day; V = the mean volume of the body of water; and 1440 = the number of minutes in a day.

The product, ρc, was neglected in the calculations since its value is close to unity.

Data required are air temperatures, relative humidities, wind speed, cloud cover, incident solar radiation, sea surface temperatures and the distribution of temperature in the body of water. The two layer circulation in Ladysmith Harbour has been indicated previously.

Meteorological data from Cassidy Airport, about four miles north of Ladysmith Harbour were used. Values of solar radiation were taken from tables prepared by Kimball (1928). Water temperatures from Station I and from lateral section C (fig. 3) were assumed to be the mean for the Inner Harbour. Data from the summer of 1955 suggest that this tends to be the case. For the methods of calculating the factors in the heat budget the reader is referred to Sverdrup et al (1942).

The transports and renewal rates calculated by the heat budget method are presented in Table 4. The mean of the 15 rates computed using the heat budget is 32.2 percent of the mean volume of the Inner Harbour per day.

This method is subject to most of the sources of error discussed in the calculation of renewal rates from considering continuity of salt. Two additional sources of error may exist in the heat budget method. First, there may be a difference in the meteorological conditions at Cassidy Airport and Inner Ladysmith Harbour. Secondly,

TABLE 4

Water Transports and Renewal Rates From Heat Budget Calculations

Date	(-Qr)	Depth of No Net Motion	Vi	m	u	i	P	Ti
June 6, 1954	0.054 (gm.cal. per cm^2 per min.)	8 ft.	$9.4 \times 10^6 m^3$	426 gm.	13.5°C	12.3°C	15%/day	$28m^3/s$
July 12	0.090	14	6.1	244	16.0	13.5	21	39
20	0.012	12	6.8	304	16.9	14.8	3	5
Aug. 27	0.123	12	6.8	304	14.8	13.2	34	65
Jan. 15, 1955	-0.087	15	5.7	213	6.9	7.2	164	130
Feb. 10	-0.056	8	9.4	426	6.2	7.2	19	35
June 15	-0.025	10	7.8	365	17.6	14.8	4	7
July 2	0.049	7	9.9	213	15.3	11.9	11	20
3	0.095	8	9.4	426	14.1	12.1	16	30
12	0.246	13	6.5	274	19.6	13.8	20	38
20	0.297	13	6.5	274	19.4	13.8	25	47
21	0.316	15	5.7	213	19.3	16.5	63	121
22	0.399	11.5	7.2	320	19.8	16.4	52	99
Aug. 4	0.162	12	6.8	304	16.9	13.4	11	21
9	0.134	13	6.5	274	18.4	16.0	26	49

the source and sink of heat present in the large area of intertidal flats was not taken into account.

Agreement between the rates calculated for the few dates on which both heat and salt budget methods could be used is poor and the range of values is large. This may result from the many assumptions made and the fact that they may not have been justified in each calculation. However, since the mean of the heat budget rates (32 %) agrees with the mean of those computed from the salt budget (32 %) it is felt that the mean can be used with more confidence than the individual rates.

The mean of all rates calculated is 32.2 percent of the mean volume of the Inner Harbour per day with a standard deviation of 18.2 percent.

How much of this deviation can be attributed to real variations in the exchange rate and how much to the inadequacies of the data is not known. Values between about 15 and 50 percent per day do not appear unreasonable as rates of exchange. However, the values near the limits of the range, those below 10 and above 100 percent, seem likely to be the result of faulty assumptions. Variations in the gradients of density do occur and could result in fluctuations in the renewal rate if longitudinal density gradients and exchange rates are related. As a result of wind, tide or other factors such as density distributions and Coriolis force, water from the Inner Harbour could ebb out along one side of the Outer Harbour and be replaced by water flooding in along the other side. Variations in such a tendency would result in a fluctuating renewal rate whether exchange was dominated by two layer circulation or by horizontal mixing.

Velocity observations and distributions of salinity, temperature and density indicate that a two layer circulation does operate in Ladysmith Harbour. The effect of the constriction at the Gap in producing a jet stream from tidal currents suggests that horizontal mixing may contribute significantly to renewal of the water in the Inner Harbour. The relative magnitude of these two processes is not known and probably varies. However, in subsequent sections it is assumed that water exchange results entirely from the two layer circulations.

F. Distribution of Phytoplankton

1. Abundance

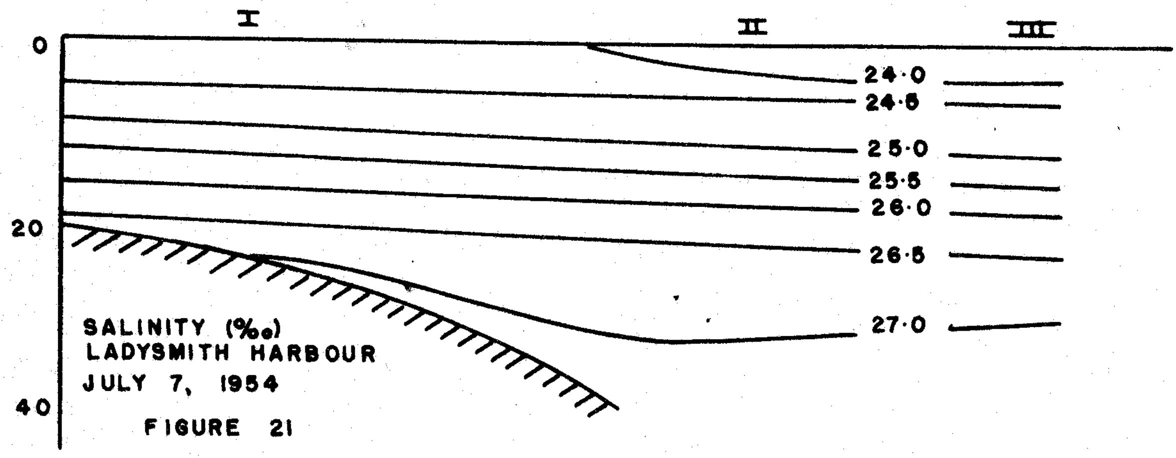
Four phytoplankton blooms may occur in Ladysmith Harbour during the growing season. The spring bloom in Ladysmith Harbour may start early in May and last from three to six weeks. During this time, although patchiness is evident and concentrations vary with time, the gradients of concentration along the length of the Harbour are generally small. A second bloom or series of blooms may occur in midsummer. Concentrations during the midsummer blooms generally increase toward the mouth of the Harbour and may be low in t he Inner Harbour. Observations in late August and early September of 1954 indicate that a third bloom, confined to the Inner Harbour, occurred. Concentrations of plankton from the only cruise made during the fall bloom increased toward the mouth of the Harbour.

The maintenance of the concentrations of phytoplankton in the shallow Inner Harbour during the spring blooms suggests that water exchange may be important in supplying either organisms or nutrients or both. Since concentrations of plankton and nutrients are usually higher in the lower layers, the two-layer circulation during this period would tend to advect both plankton and nutrients into the Inner Harbour.

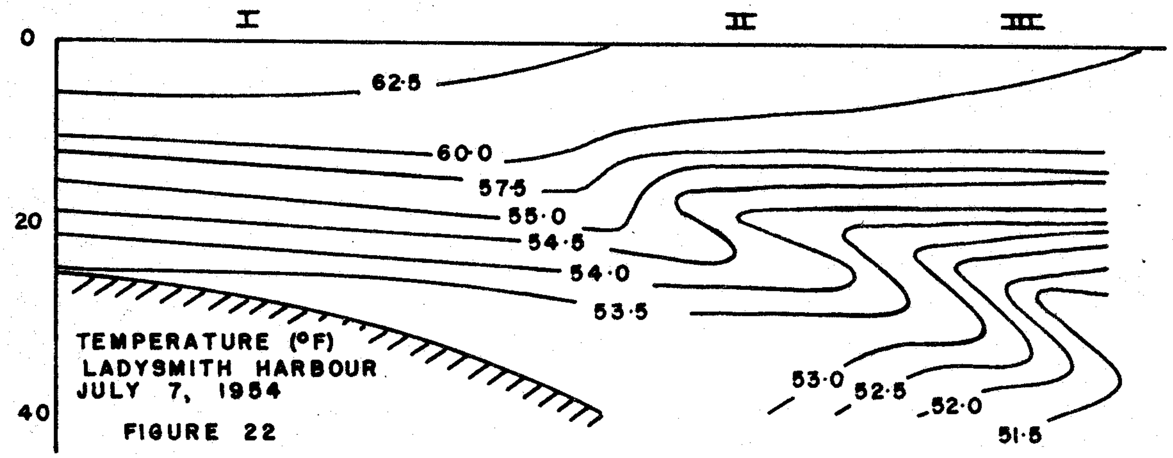
The fact that the establishment of a gradient with concentrations of phytoplankton decreasing to seaward coincided with the reversal of circulation during the first dilution in the summer of 1954 may further indicate the importance of the spring circulation in maintaining phytoplankton populations in the Inner Harbour. The surface inflow associated with dilution would tend to replace water in the Inner Harbour with water from the plankton-poor and nutrient-depleted upper layers to seaward.

Another factor could operate if the sporadic reversal of the circulation during dilution proved to be unimportant. When depletion of nutrients to seaward of the Inner Harbour reached a certain depth, the inflow in the lower layer might fail to advect sufficient nutrients into the Inner Harbour to maintain production at the level prevailing during the spring bloom.

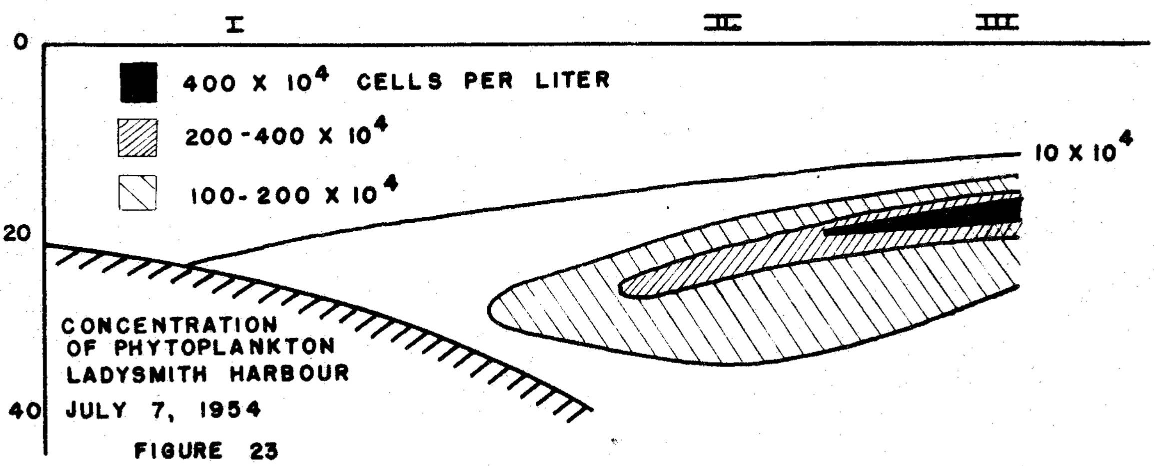
Two mechanisms may be responsible for the occurrence of blooms of phytoplankton in midsummer at a time when plankton concentrations have frequently been observed to be low in other geographical areas. Temperature and salinity sections for July 7, 1954 suggest that relatively dilute water was moving into Ladysmith Harbour over the more saline deep layers. (fig. 21). The vertical gradient of salinity was strong. Tongues of temperature suggest that strong velocity gradients existed between the two layers (fig. 22). Between the two layers and associated with a tongue of low temperature was a narrow band of very high concentrations of diatoms (fig. 23). This may indicate that entrainment of nutrients into the upper layer gives rise to production, or that mixtures of the two layers are fertile.



SALINITY (‰)
LADYSMITH HARBOUR
JULY 7, 1954
FIGURE 21



TEMPERATURE (°F)
LADYSMITH HARBOUR
JULY 7, 1954
FIGURE 22



CONCENTRATION
OF PHYTOPLANKTON
LADYSMITH HARBOUR
JULY 7, 1954
FIGURE 23

This phenomenon of high standing crops in the interface between low salinity Georgia Strait water and the deeper layers is not always evident. However, such entrainment or mixing could result in conditions suitable for production which could persist after the structures revealing the processes had deteriorated. Also plankton so produced might persist after the processes had ceased.

Some data (fig.24) suggest that the area in Trincomali Channel between Porlier Pass and the north end of Thetis Island is a highly productive one. This area is adjacent to a region of intense tidal mixing which could supply the nutrients necessary to maintain a large standing crop of phytoplankton. The distribution of salinity on July 2, 1954 (fig. 25) suggests that the water causing the summer dilutions in Ladysmith Harbour enters the Stuart-Trincomali Channel system through Porlier Pass. If this is the case, then movement of plankton-bearing water from Trincomali Channel into the Ladysmith Harbour area is also possible. Sporadic intrusions of water from Trincomali Channel into Stuart Channel could result in small clouds or masses of water rich in phytoplankton which could occasionally pass by or enter Ladysmith Harbour.

Probably both advection of plankton originating in Trincomali Channel and entrainment are at least partly responsible for the midsummer blooms in Ladysmith Harbour.

The third bloom, confined to the Inner Harbour, follows the decomposition of large amounts of eelgrass and sessile algae which appear floating in the late summer. Since the

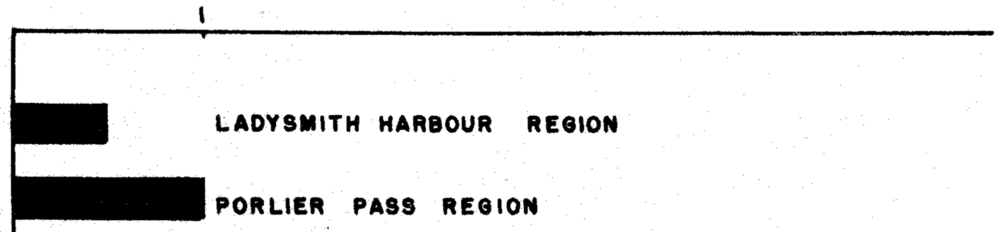


FIGURE 24. MEAN RELATIVE MAGNITUDES OF STANDING CROPS OF PHYTOPLANKTON IN THE LADYSMITH HARBOUR AND PORLIER PASS REGIONS FOR THE DATES:

JUNE 4, 1954
JULY 2
SEPT. 9
MAY 17, 1955
JULY 11.

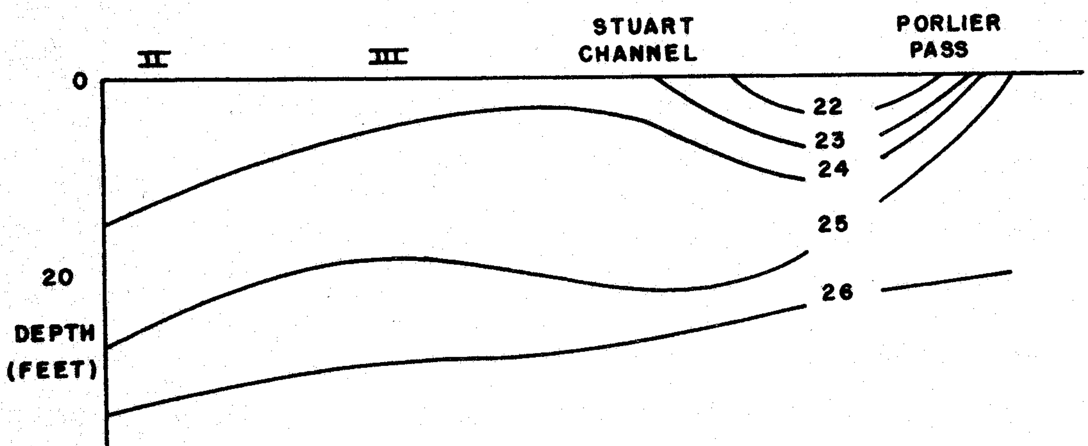


FIGURE 25. SALINITY (‰)
LADYSMITH HARBOUR - PORLIER PASS
JULY 2, 1954.

relative concentration of these forms is higher in the Inner Harbour than to seaward plankton blooms resulting from the release of nutrients through decay of sessile plants would be more intense in the Inner Harbour.

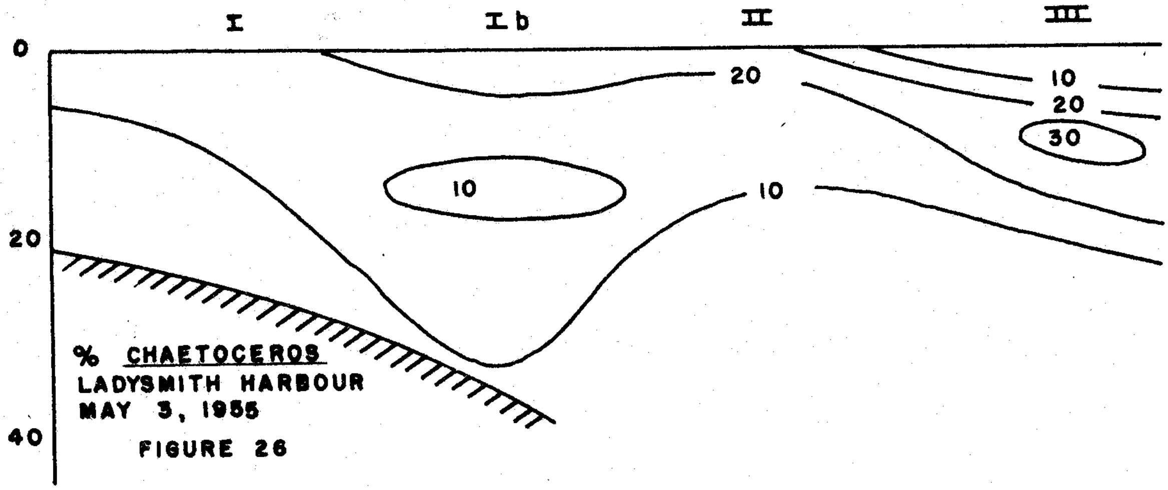
Data taken from the Inner Harbour during May, June and July of 1955 indicate that distributions of phytoplankton there may reveal either even gradients or at times patchiness. Patchiness in the distribution of phytoplankton may result from small areas of productivity or from localized grazing. Both factors probably operate in the Inner Harbour. Intermittent flow of fertile water in through the Gap on strong flood tides could result in small masses of water which could produce localized blooms. Lateral water movements in the Inner Harbour have been described previously as complicated and variable. If masses of water were retained in intermittent or temporary eddies in regions of the Inner Harbour where concentrations of sessile and bottom grazers were high, an otherwise even distribution of phytoplankton could become patchy through grazing. Flow patterns suggest that this may sometimes occur. The occurrence of copepods and larval decapods in swarms could also result in patchiness due to uneven grazing.

2. Distribution of Genera of Phytoplankton

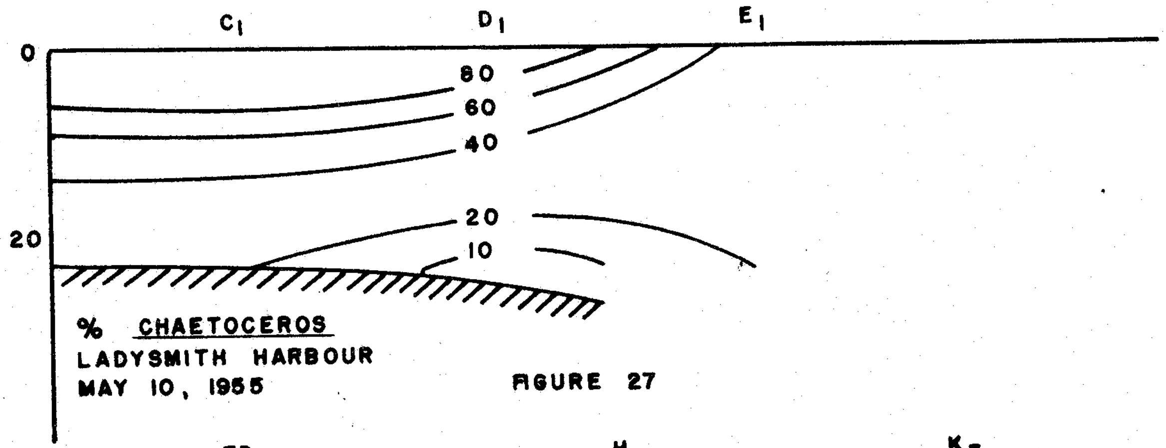
The generic composition of phytoplankton in Ladysmith Harbour varies in both time and space. Results from 1954 and 1955 suggest that the sequence of genera in time is as follows: *Thalassiosira*, *Chaetoceros*, *Skeletonema*, *Chaetoceros*, and in late summer a complex of dominant genera. No one type of distribution of genera along the Harbour appears common. It can only be said that the generic composition of the phytoplankton in the Inner Harbour tends to differ from that to seaward.

Ketchum (1954) shows that exchange rates may be important in determining the types and distributions of plankton in estuaries. After considering known division rates of phytoplankton he concludes that endemic phytoplankton populations should be able to maintain themselves in estuaries having exchange ratios of 0.5 or less. The exchange ratio is defined as the proportion of water moving seaward from the estuary on the ebb tide and not returning on the following flood tide. Inner Ladysmith Harbour, with a daily renewal rate of about thirty percent of the mean volume per day (exchange ratio less than 0.15), should thus be able to maintain endemic phytoplankton populations. That is, the rates of division of plytoplankters are such that they could maintain or increase their numbers in the Inner Harbour in spite of depletion to seaward by the circulation. However, if the rate of reproduction of the plankton fell below a critical level due to grazing or nutrient depletion the endemic population would be unable to maintain itself. In this case the composition of the plankton in the Inner Harbour would resemble that to seaward providing that the composition to seaward remained constant. If the composition to seaward varied the time lag between the changes in the composition of the phytoplankton in the two parts of the Harbour would give rise to apparent endemism.

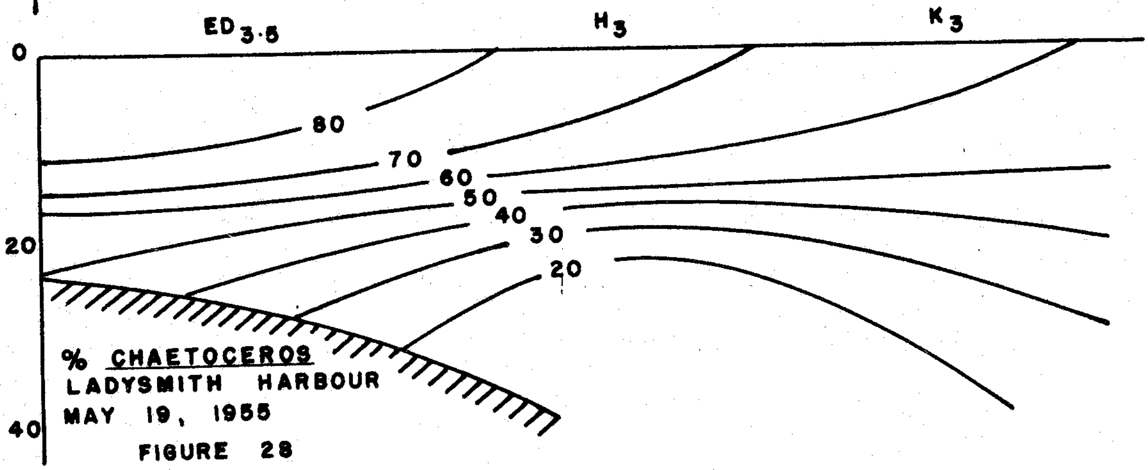
The increase in the proportion of the total population of phytoplankton formed by *Chaetoceros* between May 3, 1955 and May 18-19 appears to have been a form of population succession. On May 3, *Thallassiosira* was the dominant genus at all depths in Ladysmith Harbour. The composition varied little longitudinally (fig. 26). By May 10, *Chaetoceros* had become dominant in the upper layers on the east side of the Inner Harbour. The proportion of the population formed by this genus decreased markedly to seaward (fig. 27). The observations taken at the six stations sampled over a 24 hour period on May 18-19 indicated that *Chaetoceros* had extended its distribution farther to seaward in the upper layer of the Harbour by this date (fig. 28). At each of these stations except H_1, the proportion formed by *Chaetoceros* varied inversely with tidal height (fig. 29), suggesting that the genus was dispersing from the Inner Harbour. In the Inner Harbour the greatest concentrations of phytoplankton during the 24 hour period were associated with increases in the proportion of *Chaetoceros*. This would be expected if *Chaetoceros* was endemic to the Inner Harbour. During the same period, the highest concentrations in the Outer Harbour were associated with high proportions of *Thalassiosira*. A cruise into Stuart and Trincomali Channels on May 17 indicated that *Thalassiosira* was dominant throughout these bodies of water. Thus, between



% CHAETOCEROS
LADYSMITH HARBOUR
MAY 3, 1955
FIGURE 26



% CHAETOCEROS
LADYSMITH HARBOUR
MAY 10, 1955
FIGURE 27



% CHAETOCEROS
LADYSMITH HARBOUR
MAY 19, 1955
FIGURE 28

May 3 and May 18-19 Chaetoceros had increased from a relatively minor form to a dominant one in spite of depletion to seaward by circulation in the upper layers and the advection of other forms into the Harbour in the lower layer. Through population succession Chaetoceros had become endemic to the Inner Harbour. The change appeared to have been associated with an increase in temperature and a slight drop in salinity.

The change in the composition of the plankton between June 12 and June 22, 1954 may have been brought about by the circulation. On June 12 Chaetoceros was the dominant genus in the Harbour. Skeletonema formed less than 50 percent of the phytoplankton but the proportion it formed increased with depth and to seaward (fig. 30). By June 22 Skeletonema had increased until it had formed the major constituent of the phytoplankton (fig. 31). The proportion of the population it formed was greatest in the Inner Harbour. This change in distribution could be interpreted to mean that the inflow of water in the deeper layers had carried Skeletonema into the Harbour where it largely replaced the formerly dominant Chaetoceros. The fact that Chaetoceros formed a higher fraction of the population in the Outer Harbour than in the Inner Harbour on June 22 could have resulted from its advection out of the Inner Harbour or from changes beginning in the population after Skeletonema had attained dominance.

If Skeletonema had attained dominance in the Inner Harbour through advection followed by population changes in the Outer

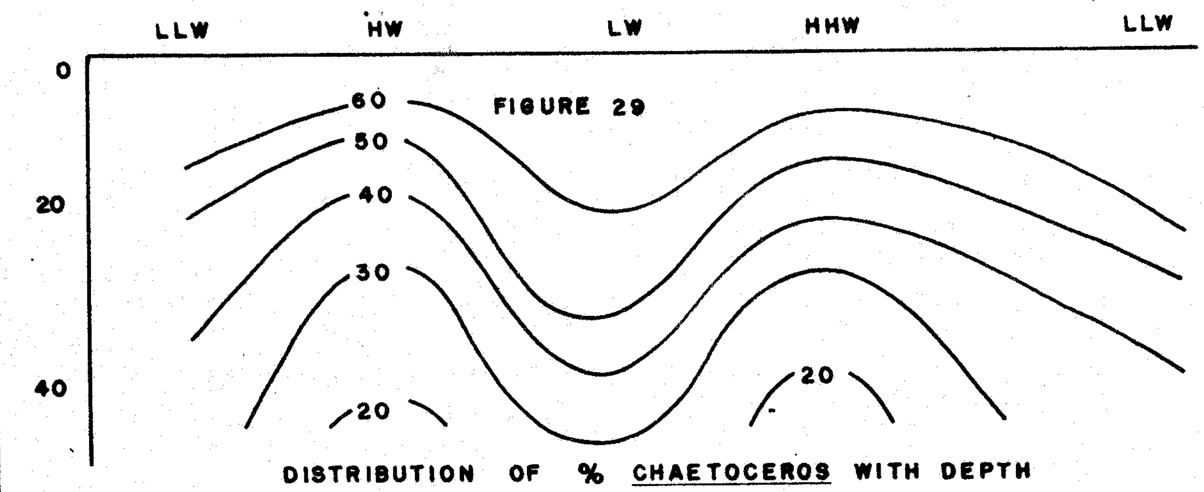
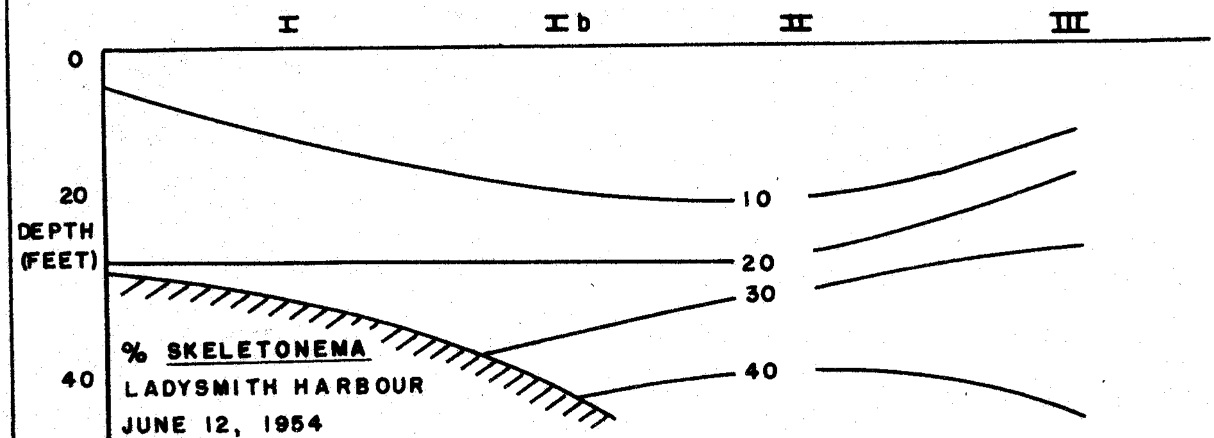


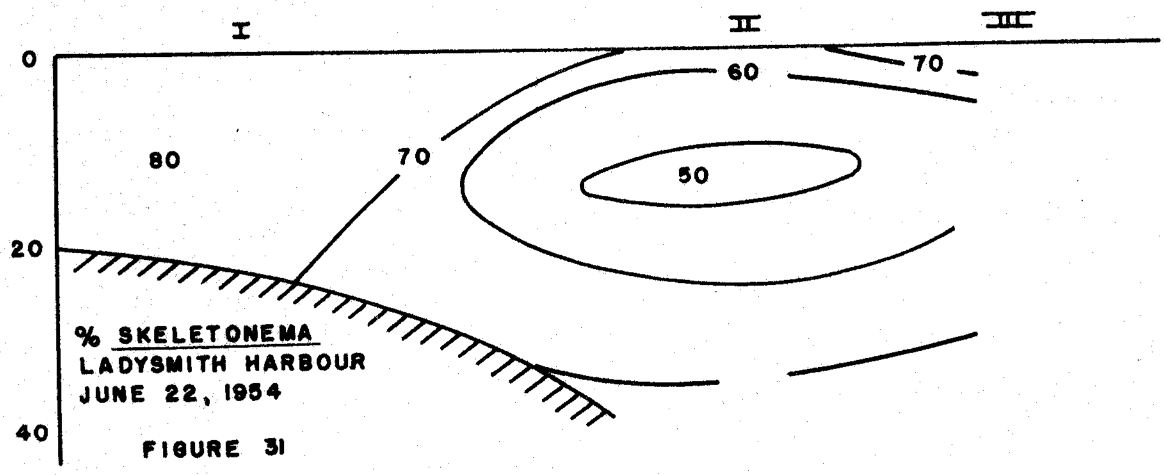
FIGURE 29

DISTRIBUTION OF % CHAETOCEROS WITH DEPTH
STATION K_3 MAY 18-19, 1955



% SKELETONEMA
LADYSMITH HARBOUR
JUNE 12, 1954

FIGURE 30



% SKELETONEMA
LADYSMITH HARBOUR
JUNE 22, 1954

FIGURE 31

Harbour resulting from either succession or sequence the greater proportion of this genus in the Inner Harbour is a case of apparent endemism. However, the time interval between these two cruises, 10 days, is too great to allow definite conclusions to be drawn. The division rate of diatoms, which may be as high as one and a half per day, is such that the change in numbers and proportion of Skeletonema could have resulted from population succession.

The distributions of the genus Chaetoceros cannot be related to any particular conditions of salinity and temperature. This genus contains many species adapted to a wide variety of conditions.

Only one species of the genus Skeletonema, S. costatum, has been observed in British Columbia coastal waters. The occurrence of this species did not appear to be related to particular values of salinity or temperature. On June 12, 1954 it was associated with the deeper and more saline layers. On August 2, 1954 the highest numbers and proportions of this genus were associated with low salinities. In general Skeletonema was most prominent during July, 1954, the period during which dilutions were occurring.

Few generalizations concerning the distribution of genera can be drawn. The increase in the proportions of Skeletonema following the period when Chaetoceros was dominant was associated with dilution. Following this, Chaetoceros again became the most prominent genus, although Skeletonema, Thalassiosira, and Nitzschia at times formed significant proportions of the populations. The generic composition of the phytoplankton tends to vary vertically and longitudinally as do salinity and temperature. The lateral gradients of composition are usually small. Except for the first instance discussed above no clear relationships between distributions of genera and physical-chemical factors or circulation are evident. A statistical study of the relationships between species of phytoplankton occurring in Ladysmith Harbour and the salinity and temperature observations might prove fruitful but is beyond the scope of this study.

G. Advection, Grazing and Growth of Phytoplankton in the Inner Harbour

1. Advection of Phytoplankton

It has been indicated that a two-layer circulation operates in Ladysmith Harbour. The net transport of phytoplankton in a body of water with such a circulation can be expressed as:

$PT = PiTi - PuTu$, where Pi = the mean concentration of phytoplankton in the inward flowing layer; Pu = the mean concentration of phytoplankton in the seaward moving layer; Ti = the rate of transport of water in; and Tu = the rate of transport of water to seaward.

If PT is positive a net gain of phytoplankton results from advection. If PT is negative the reverse is true. The expression applies to phytoplankton only. For zooplankton, which perform diurnal vertical migrations, the amount of time spent in each layer would have to be considered.

In calculating net transports of phytoplankton for Inner Ladysmith Harbour, it is assumed that plankton concentrations at Station I represent the mean for the Inner Harbour and that the mean transport of water inward, 78 cubic meters per second, prevailed throughout the period studied (June 6, 1954 to August 27, 1954). During periods of outflow in the upper layer, Pi and Pu were taken to be the mean concentrations below and above the depth of no net motion respectively. When the circulation reversed during dilution Pi and Pu were taken from the upper and lower layers respectively.

Variations in the mean standing crop in the water column at Station I and in the net rate of transport of phytoplankton are presented in Figures 32 and 33. The products of the mean of the rates for each pair of consecutive cruises and the time interval between each pair of cruises were summed to obtain the total amounts of phytoplankton advected into the Inner Harbour (fig. 34), (Table 5).

2. Grazing

The principal grazers on phytoplankton in the Inner Harbour were assumed to be the zooplankton and the populations of oysters (*Crassostrea gigas*) and clams (principally *Protothaca*). Changes in the mean concentration of zooplankton in the water column at Station I are shown in Figure 32.

The rate of grazing by zooplankton can be expressed as the volume of water cleared of phytoplankton per unit time. It is assumed here that the zooplankton filter phytoplankton from the water continuously and indiscriminately. Although there is some evidence that some zooplankters feed intermittently and are able to select the species of phytoplankton consumed there are also data suggesting the contrary (Marshall and Orr, 1955, Jørgenson, 1955). In a recent summary of filter feeding in invertebrates, _Calanus finmarchicus_, Stage III is quoted to have a filtration capacity of 1.2 mililiters per hour at a temperature of 17°C. _Pseudocalanus minutus_, _Temora longicornis_, and _Centropages hamatus_ are quoted to filter 0.18, 0.35 and 0.54 mililiters per hour respectively at a temperature of 10°C (Jørgenson, 1955). Since these four species of copepods are of about the same size as the organisms counted as zooplankton in this study the mean of their filtration rates, about 14 mililiters per day per organism, is used here.

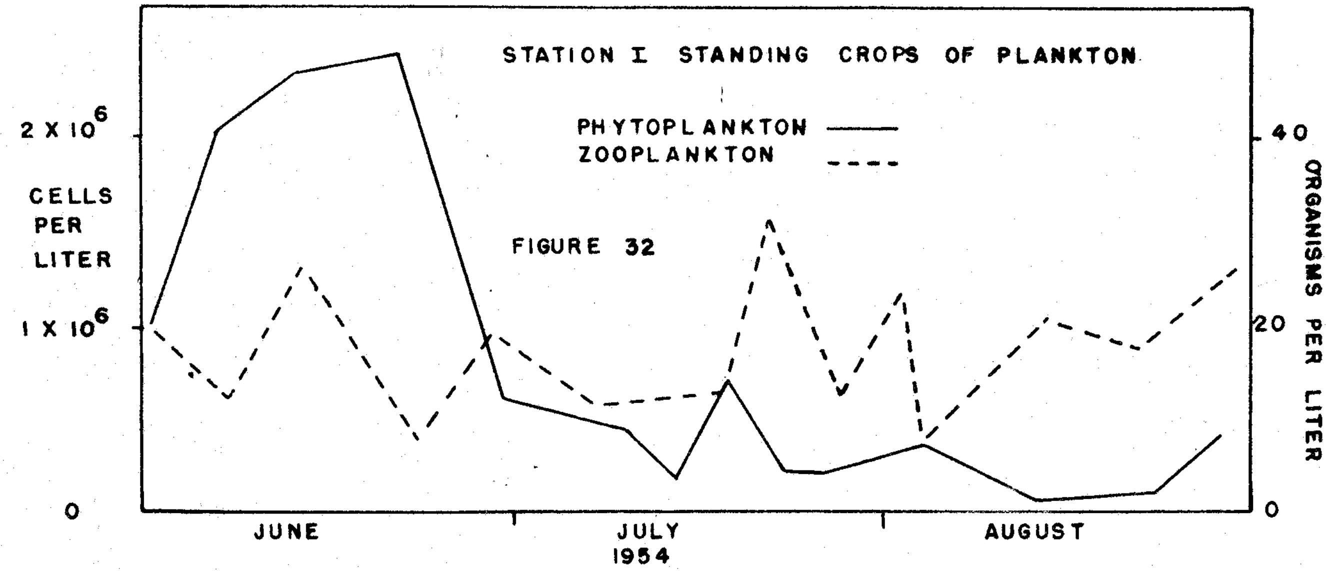
Zooplankton concentrations at Station I are assumed to represent the concentrations for the Inner Harbour.

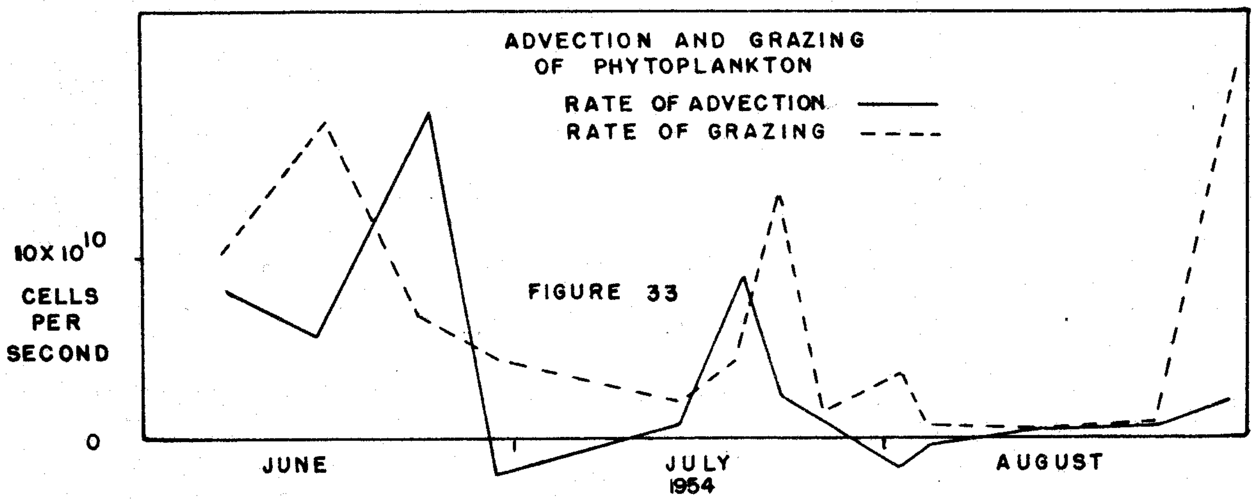
There are about 2 million oysters and 5 million clams in the Inner Harbour (D.B.Quayle, personal communication). The mean rate of filtration of water by the Atlantic oyster (_Ostrea virginica_) having a mean wet weight of soft parts of about 20 grams is about 10 liters per hour per organism at temperatures between 9°C and 32°C (Jørgenson, 1955).

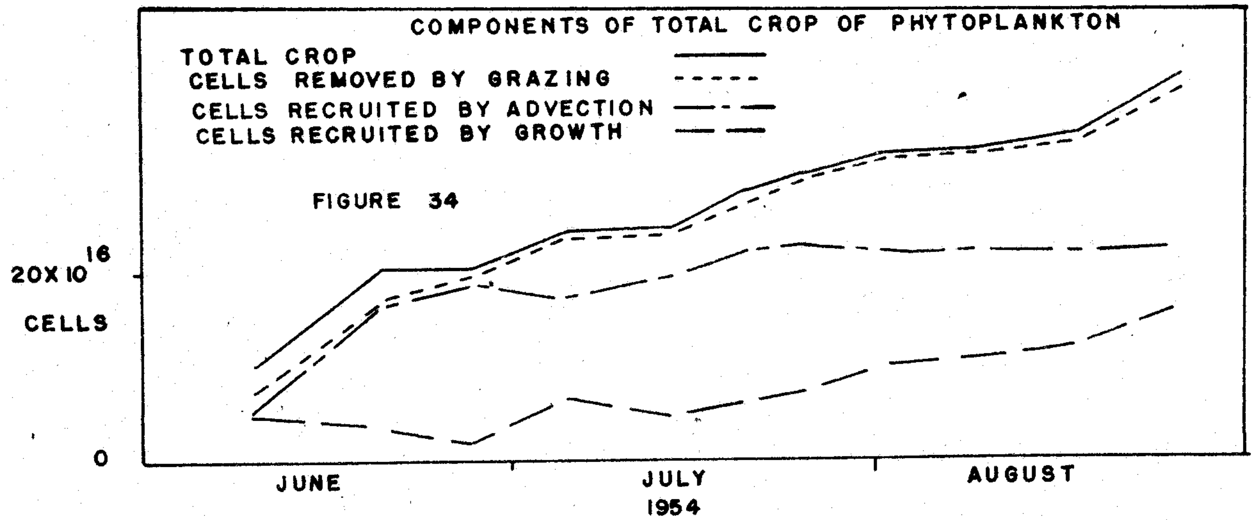
The mean wet weight of soft parts of Crassostrea gigas from the Inner Harbour is about 50 grams (Quayle, unpublished data), more than twice the weight of the C. virginica used to obtain filtration rates. Accordingly, the rate of filtration for oysters in the Inner Harbour is calculated at about 20 liters per hour per oyster. The clams filter about one liter per hour per clam (Quayle, personal communication).

However, the clams and oysters are situated principally in the intertidal zone and therefore spend only part of the time submerged and filtering. The distribution of bivalves with respect to variations in tidal height is assumed to be such that these organisms filter water only one half of the time. Taking this into account the rate of filtration by clams and oysters is calculated to be 5.4×10^8 liters per day. It is further assumed that this rate remains constant over the period considered and that the water filtered by the bivalves has a concentration of phytoplankton equal to the mean for the water column at Station I.

The rate of removal of phytoplankton (fig. 33) by grazing is calculated as the product of the filtration rate of the grazers and the concentration of phytoplankton. The total amounts of phytoplankton removed from the Inner Harbour by grazing are shown in Figure 34. The values were obtained by taking the product of the mean of the grazing rates between pairs of consecutive cruises and the time interval and summing the values obtained.


STATION I STANDING CROPS OF PLANKTON
PHYTOPLANKTON
ZOOPLANKTON
FIGURE 32
2 X 10^6
CELLS PER LITER
1 X 10^6
0
40
20
0
ORGANISMS PER LITER
JUNE
JULY
1954
AUGUST


ADVECTION AND GRAZING OF PHYTOPLANKTON
RATE OF ADVECTION
RATE OF GRAZING
FIGURE 33
10X10^10
CELLS PER SECOND
0
JUNE
JULY
1954
AUGUST


COMPONENTS OF TOTAL CROP OF PHYTOPLANKTON
TOTAL CROP
CELLS REMOVED BY GRAZING
CELLS RECRUITED BY ADVECTION
CELLS RECRUITED BY GROWTH
FIGURE 34
20X10^16
CELLS
0
JUNE
JULY
1954
AUGUST

3. Growth

Figure 31 indicates that the total crop of phytoplankton in Inner Ladysmith Harbour for the period being considered is greater than the amount recruited by advection. The difference must be due to production of phytoplankton by growth in the Inner Harbour. The total production of cells by growth necessary to make up this difference is plotted in Figure 34.

In Table 5 the standing crop, changes in the standing crop, the number of cells recruited by advection, and the number of cells removed by grazing and the recruitment of cells through growth are presented. The rates of production of cells per day are also tabulated.

Four of the 12 rates of growth are negative. Thus, the rates of grazing for these dates must be too low or the rates of advection of phytoplankton are too high. The other rates of cell production are below or only slightly above the approximate upper limit to the rate of reproduction for diatoms of one cell division per day.

According to the calculations about 17×10^{15} cells were produced by growth in the Inner Harbour. Phosphate concentrations observed in Stuart Channel in the winter of 1954 (Waldichuk, unpublished data) suggest that the concentration of PO_4 -P in Ladysmith Harbour before the onset of the spring bloom is about 2.5 micro-gram atoms per liter. Using data recorded by Harvey (1950), Jørgenson (1955), and Scagel (personal communication), one micro-gram atom of phosphate-

TABLE 5

Advection, Grazing and Growth of Phytoplankton in Inner Ladysmith Harbour

Date	Standing Crop in cells	Change in Standing Crop	Recruitment, Advection	Mortality, Grazing	Recruitment, Growth	Rate of Growth
June 6, 1954	34.4×10^{15}					
		5.0×10^{15}	47.2×10^{15} cells	-73.1×10^{15} cells	34.5×10^{15}	5.8×10^{15} cells/day
June 12	39.4					
		1.6	128.0	-103.0	-23.0	-2.3
June 22	41.6					
		-31.2	43.3	-23.0	-10.9	-2.2
June 27	9.8					
		-6.9	-13.3	39.0	34.4	2.3
July 12	2.9					
		10.2	19.2	10.4	1.4	0.4
July 16	13.1					
		-8.2	24.0	29.6	-2.6	-0.7
July 20	4.9					
		-1.1	6.1	26.8	19.6	4.9
July 24	3.8					
		1.6	-5.0	18.9	22.3	2.5
Aug. 2	5.4					
		0.3	-2.9	5.1	7.7	2.6
Aug. 5	5.7					
		-5.4	-1.5	1.4	-2.5	-0.4
Aug. 12	0.3					
		2.2	0.1	5.6	7.7	0.9
Aug. 20	2.5					
		4.9	6.9	70.3	68.3	9.7
Aug. 27	7.4					

phosphorus was calculated to be equivalent to about 5.52×10^5 diatom cells. According to this equivalent the recruitment of cells by growth of phytoplankton in the Inner Harbour represents the utilization of about 3.3×10^{10} micro-gram atoms of phosphate-phosphorus. This represents a concentration of about two micro-gram atoms per liter in the Inner Harbour, less than that initially available. Through advection and regeneration of organic phosphate the amount of phosphate available for photosynthesis in the Inner Harbour probably exceeds the amount indicated by the initial concentration. However, phosphate utilization by sessile plants probably reduces the amount available for use by phytoplankton.

The sequence of diatom maxima and minima in the sea during the growing season has been attributed to the grazing action of zooplankton whose maxima tend to alternate with those of the phytoplankton (Fleming, 1939). There appears to be some relation between the concentration of zooplankton and changes in phytoplankton concentration in the Inner Harbour. However, changes in the standing crop appear to be more closely related to variations in the rate of advection of cells into the Inner Harbour than to changes in the rate of removal of cells by grazing (figs. 32, 33).

Figure 34 and the vertical distribution of diatoms early in the spring bloom suggest that recruitment due to growth may exceed that resulting from advection at that time. Following this may be a period when advection contributes more cells than reproduction. In late summer reproduction appears to increase in importance as postulated previously.

The mean standing crop in the Inner Harbour was about 13.1×10^{15} cells. The mean recruitment by advection was about 2.8×10^{15} cells per day. Grazing removes about 4.5×10^{15} cells per day. Thus the mean rate of addition of cells by growth necessary to maintain the mean population was 1.7×10^{15} cells per day. According to this, advection recruits about one and a half times as many cells as cell division in the Inner Harbour. In calculating grazing rates, only bivalves, copepods, copepodids, zoea of crab, polychaete larvae and nauplii of copepods and cirripedes were considered. Such benthonic organisms as barnacles, sponges, and some polychaetes are also filter feeders and occur in the Inner Harbour. Present in the plankton samples but not counted were rotifers which were moderately abundant at times and were observed feeding on diatoms in fresh plankton samples. Probably present in the Harbour but not in the plankton samples are the larger and more active Copepoda and later larval stages of Decapoda. The pump used in plankton sampling may have failed to capture representative numbers of some of the forms counted, such as copepodids and zoea. Thus it appears that number of grazers used in the calculations were minimal. If this is the case the calculated removal of phytoplankton by grazing is too small. Since the recruitment resulting from reproduction of phytoplankton was taken to be the difference between the total crop (standing crop plus amount removed by grazing) and the recruitment by advection, the reproduction rate of phytoplankton should be higher than was calculated. The possibility of advection and regeneration of nutrients suggests that sufficient phosphate should be available for a significant increase in the calculated recruitment resulting from cell division.

Several probable sources of error exist in the calculation of the relative magnitude of the contributions of growth and advection to the total crop of phytoplankton in Inner Ladysmith Harbour.

a) It was assumed that water exchange in the Inner Bay was entirely the result of a two-layer circulation. It has been pointed out that horizontal mixing may also operate. Neglect of horizontal mixing in calculating the recruitment of phytoplankton due to water exchange will result in too high a value for the recruitment of cells from this source.

b) The renewal rate used may be in error.

c) The renewal rate was assumed constant which may not be the case.

d) The concentrations of phytoplankton and zooplankton at Station I were assumed to represent the mean for the Inner Harbour. Data from the summer of 1955 suggest that error from this source may be considerable and variable.

e) Variation in the grazing rate due to the effects of temperature changes on the activity of the grazers was neglected.

f) The fact that the numbers of grazers used in calculating grazing rates was minimal has been discussed above.

IV. CONCLUSIONS

1. The configuration of the shoreline and distribution of depth in Ladysmith Harbour have important effects on the distribution of phytoplankton. Shore configuration divides the Harbour into a shallow inner bay and a deeper outer portion. The shallow depths of the Inner Harbour limit the production of phytoplankton directly by restricting the depth of the euphotic zone. In addition no deep reservoir of nutrients is available there and competition between sessile and planktonic plants is higher in the Inner Harbour than to seaward due to the shallow depth. A second effect of the higher relative concentration of sessile plants occurs in late summer when large amounts of *Zostera* and bottom dwelling algae die and decompose, releasing nutrients which become available for use by phytoplankton. The configuration of the shoreline and distribution of depth also tend to restrict circulation and vertical mixing in the Inner Harbour with consequent effects on the distributions of salinity and temperature.

2. Freshwater discharge has no direct effect on production of phytoplankton during the growing season. However, its influence on salinity distributions in spring may result in vertical and longitudinal variations in the composition of phytoplankton in Ladysmith Harbour. Drainage is important

in helping to maintain the pressure forces resulting in the two-layer circulation.

3. Salinity gradients in Ladysmith Harbour have no direct effect on the production of phytoplankton, but are important in conjunction with temperature gradients in determining the composition of the phytoplankton. Changes in salinities appear to be associated with changes in the composition of the phytoplankton. Salinity gradients and changes in them have important effects on the phytoplankton through their influence on the distribution of density and thus circulation.

4. Temperature gradients in Ladysmith Harbour are such that their influence on metabolic rates result in a higher rate of turnover of biological products in the Inner Harbour. Growth, respiration, grazing and the rate of regeneration of nutrients should all proceed at a higher rate in the Inner Harbour than to seaward. The importance of a higher rate of nutrient regeneration from organic combination in the Inner Harbour is enhanced by the shallow depth. Temperature gradients in Ladysmith Harbour are associated with longitudinal variations in the generic composition of the phytoplankton. The effect of temperature gradients on density distributions is important in determining the circulation.

5. A large proportion of the water in Inner Ladysmith Harbour enters and leaves the inner bay each day due to tidal action. Temperature, salinity, the concentration of phytoplankton and the composition of the phytoplankton at any location in

Ladysmith Harbour tend to vary over each tidal cycle. The proportion of water in the Inner Harbour involved in tidal action and the existence of a jet stream through the Gap during periods of maximum tidal current suggest that horizontal mixing may be important in controlling the properties of the water in the Inner Harbour.

6. The mean distribution of velocity with depth over twenty-four hour periods and longitudinal gradients of salinity temperature and density indicate that a two-layer system of circulation operates in Ladysmith Harbour. Throughout most of the year outflow occurs in the upper layer and inflow in the lower layer. When dilution from seaward takes place in midsummer this circulation is reversed and inflow occurs in the upper layers.

7. The mean rate of water renewal in the Inner Harbour is about 30 percent of the mean volume per day and probably varies between 10 and 50 percent per day.

8. Water exchange in the Inner Harbour affects the distribution of phytoplankton both directly and indirectly. Through both maintaining and changing the properties of the water in the Inner Harbour water exchange exerts control on the abundance and composition of phytoplankton. In spring and early summer exchange tends to maintain the salinity by removing fresh water and entrained salt water in the upper layer and advecting more saline water inward in the lower layer. In midsummer a series of dilutions are brought about by water exchange.

Throughout the growing season (except during dilution) the circulation tends to replace warm water in the Inner Harbour with colder water, thus controlling the rise in temperature which would otherwise result from the excess of radiation during the growing season.

Thus, while the rate of water exchange in the Inner Harbour is low enough to permit the development of endemic phytoplankters, water renewal through its control of salinity and temperature is important in determining the species which may flourish. However, if the rate of additioh of new cells to the endemic circulation falls below a level determined by the circulation, the composition of phytoplankton in the Inner Harbour will depend on the forms advected inward although temperature and salinity could be such that endemic forms would develop if they could reproduce.

The normal circulation, with inflow in the lower layer, tends to maintain phytoplankton concentrations in the Inner Harbour by advecting cells and nutrients inward on a net basis. During dilution circulation tends to lower Inner Harbour plankton concentrations on a net basis.

9. Calculations indicate that during the period June 6, 1954 to August 27, 1954 the recruitment of phytoplankton to the Inner Harbour by advection was one and one half times the recruitment resulting from growth. While, for reasons mentioned previously, the estimate of recruitment by growth is thought to be low, it is certain that advection of cells contributed a large proportion of the total crop of phytoplankton

in the Inner Harbour during this period.

10. Grazing is responsible for most of the removal of phytoplankton from the Inner Harbour. However, fluctuations in the net rate of advection of cells into the Inner Harbour were closely associated with changes in the standing crop of phytoplankton.

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