

HETEROTROPHIC GLUCOSE UPTAKE AND RESPIRATION IN LAKE KINNERET

T. BERMAN, O. HADAS & U. MARCHAIM.

Israel Oceanographic & Limnological Research Ltd., Kinneret Limnological Laboratory, P.O.B. 345 Tiberias, Israel.

Received April 5, 1978

Keywords: Lake Kinneret; Glucose heterotrophy; Glucose Respiration

Abstract

The turnover times of glucose, averaged for 0-10 m in the upper waters of Lake Kinneret and measured by the addition of single or multiple concentrations of substrate, ranged from 23 to 188 hours and 1 to 87 hours respectively. Potential uptake rates (estimated as V_{max}) ranged from 0.095 to 1.94 μg glucose $\text{l}^{-1}\text{h}^{-1}$, while measured uptake rates varied from 0.09 to 1.1 μg glucose $\text{l}^{-1}\text{h}^{-1}$. Concentrations of dissolved carbohydrates and glucose averaged 0.71 mg glucose equivalents l^{-1} and 39 μg glucose l^{-1} respectively. No evident relationships between glucose cycling and any fractions of dissolved organic matter, phytoplankton biomass or primary productivity were found. Turnover times were generally most rapid immediately after the decline of the spring *Peridinium* bloom. The respiration percentage of incorporated glucose ranged from 25% to 61% with highest values during the summer months. Respiration may be influenced by the nature of the indigenous bacterial population as well as by temperature. Daily heterotrophic glucose carbon uptake was about 9% of the photosynthetic incorporation and could provide a bacterial yield of about 7×10^4 cells $\text{ml}^{-1}\text{d}^{-1}$.

Introduction

The metabolism of glucose in aquatic environments has often been studied as a general indicator of microbial heterotrophic activity (e.g. Wright & Hobbie, 1969; Allan, 1973; Overbeck, 1975; Albright, 1977). We have investigated the uptake and respiration of this compound in Lake Kinneret, a warm (13-30°C) monomictic lake in northern Israel (Serruya, 1978). A distinctive feature of this lake is the annual bloom of the dinoflagellate *Peridinium cinctum* which reaches concentrations of 124 g

freshweight m^{-2} . At other times of the year, the algal standing crop averages about 22 g freshweight m^{-2} (Berman & Pollinger, 1974). Previous reports from this laboratory have dealt with ecological aspects of the phytoplankton (Pollinger & Berman, 1977) and the zooplankton (Gophen & Landau, 1977). Bacterial nitrification and denitrification have been quantitated and some specific organisms have been studied in detail (Cavari, 1977a; 1977b). In this communication we summarize our findings on the utilization of glucose by microbial heterotrophs and on the concentrations of dissolved carbohydrates and glucose in Lake Kinneret and relate these data to the organic carbon flux in the lake.

Methods

For experiments to determine glucose turnover times, V_{max} (maximum uptake rate), and respiration by microplankton, we adapted the basic technique of Wright & Hobbie (1965) and Hobbie & Crawford (1969). Lake samples taken from near surface (1 or 3 m) at a central lake station, representative for the pelagic waters (Berman & Elias, 1972) were incubated without shaking in the dark at room temperature ($20 \pm 2^\circ\text{C}$). Appropriate additions (0.04, 0.1, 0.2, 0.4 and 0.8 μCi per 10 ml lake water of uniformly labelled ^{14}C -labelled glucose, specific activity 287 nCi mmole^{-1}) were made to sealed, sterile flasks in which were suspended small holders with glass filter (GF/C) wicks soaked in 0.5 ml Hyamine hydrochloride. Incubation was stopped by adding 6% TCA, and 0.05% HgCl in 40% formalin (Wood, 1973). We could detect no apparent losses of incorporated ^{14}C -glucose from cells treated with this fixative in contrast to reports of such

losses in samples poisoned with HCl or other strong acids (Ramsey, 1976). After shaking the flasks for 1 hour to ensure maximum absorption (> 96%) of released CO₂ by the Hyamine soaked wicks, samples were filtered through presoaked 0.45 mμ Millipore filters, which were then rinsed with about 5 ml of filtered lake water. Radioactivity on filters and wicks was counted separately by scintillation in Aquasol (New England Nuclear) fluor in order to estimate the retained and respired carbon respectively. Preliminary experiments showed that the uptake of glucose was linear for at least 3 hours (Berman & Stiller, 1977) and, therefore, we used a 1 hour incorporation period for our experiments.

To follow seasonal changes of glucose turnover in the lake, we ran two series of experiments, from September 1974 to June 1975 and subsequently from October 1976 to July 1977. In these experiments only a single concentration of ¹⁴C-glucose was added (Parsons & Strickland, 1962). Samples were taken from several depths at the central lake station, ten ml of each sample was placed in a sealed sterile flask with a Hyamine soaked wick (see above) and 0.1 μCi of uniformly labelled ¹⁴C-glucose (6 μg glucose l⁻¹) was added. The flasks were incubated and the samples treated as described previously. Incubation of the first experimental set was at room temperature but the second series was run on the research vessel at ambient air temperatures immediately after sampling.

Attempts to utilize the Hicks & Carey (1966) assay for glucose were unsuccessful, probably because of the ionic composition of the Lake Kinneret water and subsequently a new method was developed (Cavari & Phelps, 1977). Dissolved carbohydrates were determined by the phenol-sulfuric-acid method (Strickland & Parsons, 1968) on water filtered through Whatman GF/C filters.

Results

1. Glucose turnover times, uptake rates and respiration

In Table 1 we show the average turnover (or residence) times for glucose in the 0 to 10 m water layer determined for two series (October 1974 to June 1975 and October 1976 to July 1977). For both experimental sets, turnover times during the winter months were slower than in summer. In Fig. 1 we show two typical depth profiles of turnover times and respiration from February 1975 (homothermic conditions) and July 1975 (stratified conditions).

For the second experimental series, ambient glucose

concentrations were also measured (Cavari *et al.*, 1977), and we could therefore calculate the absolute rates of glucose uptake. These rates (averaged from 0 to 10 m) ranged from 0.09 to 1.1 μg glucose l⁻¹h⁻¹.

Respiration (or mineralization) in the upper water layer, expressed as the percentage of the total glucose uptake which was released as CO₂, ranged from 27% to 59%. The percentage respiration for the first series of experiments (incubation at room temperature) was somewhat lower than for the second experimental series (on deck incubation). Not unexpectedly the highest levels of respiration tended to occur during the warm summer months, this trend was most pronounced in multiple concentration addition experiments (see below and Table 2).

2. Experiments with multiple concentration additions of substrate

By varying the concentrations of added ¹⁴C-glucose, more details of the uptake characteristics of the microplankton may be obtained (Wright & Hobbie, 1965; Allen, 1969). In contrast to other reports (Vaccaro & Jannasch, 1967; Overbeck, 1975) a saturation type response was always found in Kinneret waters. Generally good fits for the Woolf modification of the Michaelis-Menton curve were observed, with correlation coefficients ranging from 0.81-0.99. Although subject to several qualifying assumptions (Wright, 1973; Williams, 1973), such experiments can provide estimates of maximal uptake rates (V_{max}), turnover times (T), and a quantity (K_t + S) which represents the sum of the substrate affinity and ambient substrate concentrations and thus gives an upper estimate for ambient concentrations (Table 2).

Turnover times calculated from these experiments showed a similar seasonal pattern to those estimated from single concentration addition experiments. In absolute terms, however, multiple concentration addition experiments gave much more rapid glucose turnover times especially in the summer months. Nevertheless, even the fastest rates that we found are still slower than those reported for other eutrophic lakes (Allen, 1973). Furthermore, these experiments indicated maximal values for ambient glucose concentrations which were considerably lower and fluctuated less than those measured in Lake Kinneret directly by the method of Cavari & Phelps (1977). In this series of experiments, which were run at room temperature, the percentage of respired substrate ranged from 25 to 61% (average 43.9 ± 12%) and was lower in winter than in summer months.

Table 1: Single substrate concentration addition experiments : Glucose Turnover Times (T), Uptake Rates and Respiration (R) with concomitant phytoplankton data*

Series 1					Series 2					
Date	T (hrs)	R (%)	Algal Biomass ($\text{g}\cdot\text{m}^{-2}$)	Primary product ($\text{mgC m}^{-2}\text{d}^{-1}$)	Date	T (hrs)	R (%)	Glucose uptake ($\mu\text{g l}^{-1}\text{h}^{-1}$)	Algal Biomass ($\text{g}\cdot\text{m}^{-2}$)	Primary product ($\text{mgC m}^{-2}\text{d}^{-1}$)
<u>9/74</u>	23	31	20.5	1861	<u>10/76</u>	81	57	1.07	18.4	1558
<u>10/74</u>	38	31	36.0	1996	<u>11/76</u>	45	37	1.10	22.2	1470
<u>11/74</u>	52	36	27.0	1056	<u>12/76</u>	89	47	0.55	8.1	936
<u>12/74</u>	102	27	16.5	979	<u>1/77</u>	188	46	0.09	9.7	1147
<u>1/75</u>	159	33	16.6	500	<u>2/77</u>	94	36	0.62	54.8	1773
<u>2/75</u>	129	29	29.3	1702	<u>3/77</u>	109	57	0.30	128.0	2038
<u>3/75</u>	123	36	41.6	2196	<u>4/77</u>	73	59	0.48	163.1	4256
<u>4/75</u>	100	41	83.4	2539	<u>5/77</u>	67	48	0.60	161.2	2306
<u>5/75</u>	79	55	104.8	3266	<u>6/77</u>	48	44	0.95	29.7	1498
					<u>7/77</u>	37	53	0.85	20.5	1354
\bar{X}	89	35	41.7	1788	\bar{X}	83	48	0.66 ⁺	59.6	1834

* Average of two monthly measurements. For glucose experiments, results are based on average of samples taken from 0,1,3,5, and 10 m. Algal biomass and productivity from Pollinger and Berman (1978).

+ The average uptake rate of glucose for the entire trophogenic layer, 0 to 20 m, was $0.61 \mu\text{g l}^{-1}\text{h}^{-1}$.

3. Concentrations of dissolved carbohydrates and glucose

In conjunction with our studies of glucose uptake, we also measured dissolved carbohydrates and glucose in Lake Kinneret. The average monthly concentrations of these compounds measured for the 0-10 m water layer at a central station in Lake Kinneret did not show any clear seasonal trends (Fig. 2). Similarly neither dissolved organic nitrogen or dissolved organic phosphorus exhibited distinct seasonal fluctuations during the period of this study (Berman, unpublished). In the case of dissolved carbohydrate there was an overall increase in concentrations in 1976 compared to 1975 which may reflect the breakdown of the larger standing crops of phytoplankton in 1976. The average concentration of dissolved carbohydrates (DOC) in the 0 to 10 m layer from January 1975 to August 1976 was 0.71 (S.D. ± 0.33) mg glucose carbon equivalents l^{-1} . At present due to technical difficulties, we have no reliable data on DOC levels in Lake Kinneret although some measurements indicate that these con-

centrations were usually between 5 to 10 mg C l^{-1} . Therefore, we estimate that between 7 to 14% total DOC was carbohydrate carbon.

Glucose concentrations, averaged from 0 to 10 m, are also shown in Fig. 2. From October 1976 to July 1977, glucose ranged from 13 to $106 \mu\text{g l}^{-1}$, with an average value of $38.9 (\pm 17.5) \mu\text{g l}^{-1}$. Thus in terms of carbon, glucose made up only about 2 to 3% of the dissolved carbohydrate pool. Similarly in ocean waters, measurements of glucose concentrations also indicate that this compound forms only a very minor portion of the ambient DOC (Parsons & Takahashi, 1973). However, in Starr Lake, Vermont, Allen (1973) found that glucose carbon constituted about 11% of the total dissolved organic carbon pool.

Several attempts were made to identify the dissolved sugars in Lake Kinneret waters. Samples were concentrated 100 to 500 fold by lyophilization, and desalted by passing through Amberlite Resin-MB3. Subsequent

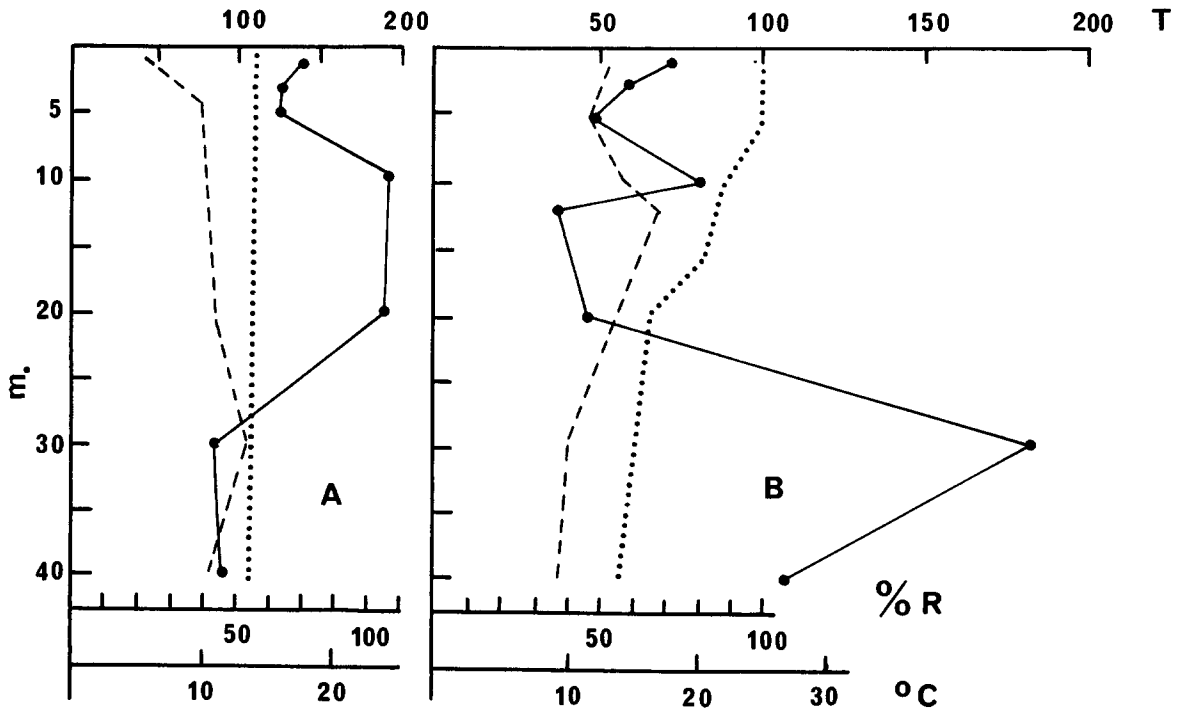


Fig. 1. Lake Kinneret: Depth profile of glucose turnover times (●-●-●-●), in hours; percentage respiration of incorporated glucose (---); and temperature (.....), C. A: 12 February 1975; B: 29 May 1975.

separation and tentative identification by paper chromatography indicated that glucose was indeed the major monosaccharide present. No other sugars, with the exception of traces of fructose, were detected using this method.

Discussion

Despite high standing crops of zooplankton (Gophen, 1972) and phytoplankton (Berman & Pollinger, 1974) and relatively warm temperatures in Lake Kinneret, the uptake rates and turnover times of glucose which have been observed are low in comparison to those reported for many temperate, eutrophic lakes (Allen, 1973; Hall, 1975; Wetzel, 1976). In contrast to other workers (Allen, 1973; Overbeck, 1975), we found no correlations between the turnover times of glucose and either standing crops of algae or primary production (Tables 1 and 2). Also, there did not appear to be any clear relationship between heterotrophic glucose uptake rates and the concentrations of any of the dissolved organic fractions which we assayed. Albright (1977) reported correlations between glucose heterotrophic potentials (V_{max})

and DOC in the waters of Georgia Straight, Vancouver, but not in the Fraser River and its estuary. Allen (1969) noted a direct relationship between the concentrations of DOC and the standing crops of phytoplankton in Lake Lotsjon. However, as Allen (1977) demonstrated, the susceptibility of various molecular weight fractions of the soluble organic pool to bacterial uptake can be very different, and thus there may not necessarily be any direct correlation between heterotrophic activity and total DOC.

The parameter V_{max} has been found to relate reasonably well with the numbers and activities of heterotrophic bacteria (Allen, 1969). Our values for V_{max} in the upper Kinneret waters (1 to 3 m) ranged from 0.095 to 1.94 $\mu\text{g glucose l}^{-1}\text{h}^{-1}$. By comparison, Overbeck (1975) reported V_{max} of 0.2 to 1.2 $\mu\text{g glucose l}^{-1}\text{h}^{-1}$ for Plussee, an eutrophic lake with temperatures ranging from about 4 to 22°C. Allen (1973) found higher values for V_{max} , up to 13.25 $\mu\text{g glucose l}^{-1}\text{h}^{-1}$, in eutrophic lakes in Vermont and Sweden during summer months, and Hall (1975) reported V_{max} ranging from 1 to 2.05 $\mu\text{g glucose l}^{-1}\text{h}^{-1}$ in nutrient supplemented limnocorrals in Lake Ontario. The relatively higher values for V_{max}

Table 2: Glucose Parameters from multiple concentration addition experiments with concomitant phytoplankton data*

Date	V_{\max} ($\mu\text{g l}^{-1}\text{h}^{-1} \times 10^{-2}$)	T (hours)	$(K_t + S_n)$ ($\mu\text{g l}^{-1}$)	R (%)	Correl. coef. (r)	Algal biomass ($\text{g}\cdot\text{m}^{-2}$)	Primary production ($\text{mgC m}^{-2}\text{d}^{-1}$)
16. 1.75	20.9	10	26	37	0.81	16.6	500
26. 2.75	12.3	66	8	45	0.99	29.3	1702
29. 4.75	27.2	45	12	61	0.93	83.4	2539
28. 5.75	167	2	4	60	0.99	104.8	3266
20. 6.75	100	1	1	58	0.97	35.7	2229
9. 7. 75	194	4	8	55	0.96	37.9	2291
21.10.75	34.0	25	9	29	0.95	26.6	1946
30.12.75	12.0	62	8	33	0.90	25.6	1194
21. 3.76	9.5	87	8	25	0.88	60.5	2076
10. 5.76	16.4	58	9	37	0.89	145.4	2124
21. 6.76	15.1	22	4	45	0.99	67.9	2497
12.7.76	37.6	27	10	42	0.97	14.5	1288
\bar{X}	53.8	34	8.9	43.9	-	56.5	1803

* All glucose data were derived from samples taken at 1 or 3 m depth. The phytoplankton measurements (Pollinger and Berman, 1978) were monthly average values.

which we found in May to July 1975 might be attributed to bacteria developing on organic material released from the decline of the *Peridinium* bloom. However no sharp rise was noted for these months in 1976, even though algal standing crops had been higher than in the preceding year. The decrease in turnover times towards the end of the *Peridinium* bloom which occurred from May 1975 and from June 1976 could also indicate an enhancement of glucose utilization due to a proliferation of heterotrophic microorganisms on dead cell material at this period.

Since carbohydrates might be expected to be readily available as heterotrophic substrates, the concentrations which we observed in the Kinneret should have provided a good source for bacterial development. As we have noted, however, glucose cycling by heterotrophs does not appear to be very rapid in this lake. This situation may be attributed to relatively low bacterial numbers or low metabolic activity, or both. Some reasons for this may be proposed. High standing crops of zooplankton, which are known to graze actively on bacteria (Gophen *et al.*, 1974),

may be responsible for maintaining a low level of bacterial populations. Cavari (1977b) has presented data showing that denitrification rates in Kinneret waters are enhanced by the addition of orthophosphate and it is therefore possible that phosphorus limitation may also be partly responsible for the observed low glucose heterotrophic activity. Furthermore, substrates other than glucose are certainly actively utilized for heterotrophic metabolism. If these compounds are in rapid flux they may not be detectable in high concentrations in the water but nevertheless they could support considerable bacterial growth. Indeed, Hoppe (1976) and Overbeck (1975) have shown that glucose may not always be a good choice as a representative substrate for measuring heterotrophic activity.

The respiration of incorporated glucose which was observed in these studies was generally higher than has been found for colder waters (Hobbie & Crawford, 1969; Hall, 1975; Overbeck, 1975) and it would be interesting to know if our respiration values are typical for warm lakes, Temperature may also have an indirect effect on respiration

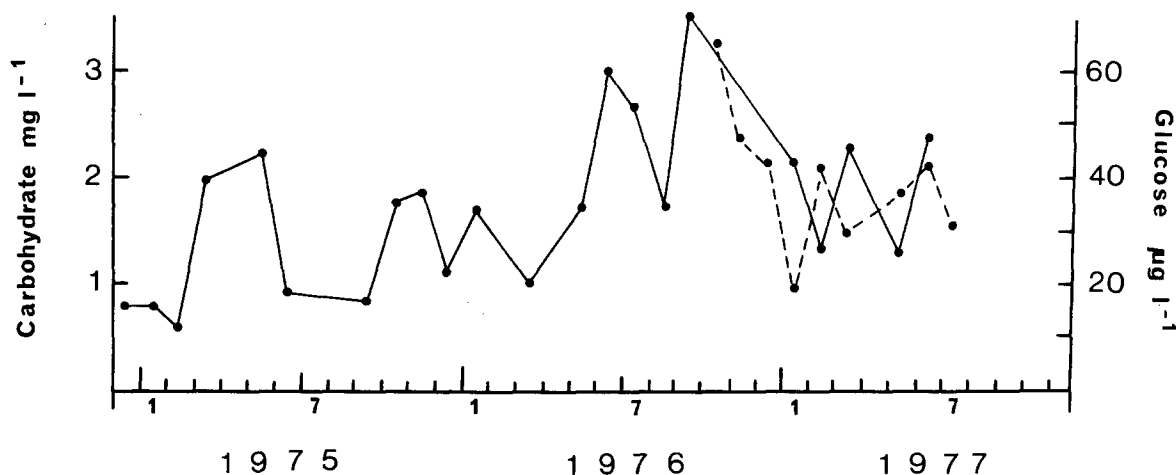


Fig. 2. Lake Kinneret: Seasonal variations in concentrations, carbohydrates (●-●-●-●), mg glucose equivalents l⁻¹ and glucose (●-●-●-●) µg l⁻¹ averaged for the water layer from 0 to 10 m.

rates. As mentioned previously, both the first series of single concentration addition experiments (from October 1974 to May 1975) and the multiple addition experiments showed increased summer respiration rates even though the sample incubations were carried out at room temperatures which did not change very greatly over the year. Thus to some extent, respiration rates may be also an intrinsic property of the microbial populations present, and these, in turn, may be somewhat determined by temperature. The second set of experiments, from October 1976 to July 1977, which were run at ambient air temperatures on board the research vessel, showed a less clear seasonal pattern and had generally higher levels of respiration.

Although both single and multiple concentration addition experiments gave similar seasonal patterns of respiration and turnover times, they showed considerable differences in absolute values for glucose turnover times. Also the glucose uptake rates measured directly in the second series of single substrate addition experiments were unexpectedly close to the maximum potential rates (V_{max}) and glucose concentrations assayed directly were usually greater than ($K_1 + S$) estimations (Table 2).

Turnover times for organic compounds obtained by single or multiple concentration additions of substrates have been recently compared by Gocke (1978). His study indicated that the former technique might lead to an overestimation of turnover times if the amount of added substrate in single addition experiments is large in relation to ambient concentrations. In our situation, both the apparent ambient glucose concentrations (see below) and

the amount of added substrate were much higher than in Gocke's study, and thus the single addition experiments probably overestimated turnover times. Also, it should be noted that our data from multiple concentration addition experiments were based on water samples from one depth only, whereas the results from single addition experiments represent averaged values from several depths from 0 to 10 m. Thus, although the two techniques which we used to study glucose uptake are complementary, in our case the data from the two methods cannot be easily compared on an absolute basis. Gocke's work suggests that the more accurate results are obtained by the more tedious method of multiple concentration additions. Cavari (unpublished) has found rapid short term fluctuations of glucose concentrations in natural water samples placed in autoclaved bottles. Samples which were assayed in the laboratory approximately one hour after being taken often had different ambient concentrations of glucose than were initially present. This phenomenon may also partly explain the lower glucose concentrations and more rapid turnover times which we found in multiple concentration addition experiments and certainly merits future investigation.

In terms of ambient concentrations, glucose carbon constituted only a small fraction (< 1%) of the total DOC in the lake water. The glucose uptake rates measured from October 1976 to July 1977 averaged 0.24 µg glucose carbon l⁻¹h⁻¹ for the trophogenic layer (0 to 20 m), that is, approximately 120 mg glucose carbon m⁻²d⁻¹. During the same period, apparent net photosynthetic carbon fixation averaged 1834 mg C m⁻²/day sunlight⁻¹. If we

assume conservative respiration losses of about 25% of the fixed carbon from algae during the night hours, the true net photosynthetic incorporation was 1375 mg C m⁻²d⁻¹. Therefore, in the trophogenic layer, daily heterotrophic glucose carbon uptake was approximately 9% of the amount of carbon fixed by primary production. Of the heterotrophic glucose fixation, if about 45% was respired, then about 66 mg C m⁻²d⁻¹ of bacterial biomass should have been synthesized in the trophogenic layer or about 3.3 mg bacterial C m⁻³d⁻¹. This amount of carbon would give an average bacterial standing crop of about 7 x 10⁴ cells ml⁻¹ growing on glucose (We have assumed a negligible role here for heterotrophic algae although Pollinger & Berman (1976) have shown that these are fairly common in Lake Kinneret).

Clearly, glucose heterotrophic uptake and respiration in the water column can only account for a small portion of the total DOC flux. Although we have no good data, it is unlikely that there has been a drastic increase in DOC over the past decade. *Peridinium* blooms, have been an annual feature of the lake for at least eighty years (Serruya, 1978). The organic carbon of the sediments is low in relation to many eutrophic lakes and shows no recent increases (Serruya *et al.*, 1974). Over the long term period then, no obvious trend to increasing levels of either particulate or dissolved organic matter is evident and respiration losses at all trophic levels must serve to maintain the balance of organic carbon. Our studies using glucose have only elucidated a part of the undoubtedly multi-substrate bacterial heterotrophic activities in Lake Kinneret. Future research, using naturally formed DOC as substrates, should give a more complete picture of the bacterial metabolism in this lake.

Summary

1. We have studied glucose uptake in Lake Kinneret by both single (Parsons & Strickland, 1962) and multiple (Wright & Hobbie, 1965) concentration addition techniques from October 1974 to July 1977.

2. Turnover times determined by single concentration additions to samples from 0 to 10 m ranged from 23 to 188 hours. For an experimental series from October 1976 to July 1977, measured glucose concentrations averaged 39 µg glucose l⁻¹ for 0 to 10 m depth. Glucose uptake rates for the same period varied from 0.09 to 1.1 µg glucose l⁻¹h⁻¹.

3. From multiple concentration addition experiments

with samples taken from 1 or 3 m depths, we obtained turnover times ranging from 1 to 87 hours, maximum uptake rates V_{max} , from 0.095 to 1.94 µg glucose l⁻¹h⁻¹ and $(K_t + S)$ from 1 to 26 µg glucose l⁻¹.

4. Despite reasonably high, ambient concentrations of carbohydrates (average 0.71 mg glucose equivalents l⁻¹), glucose turnover times and uptake rates are relatively slow in comparison to those reported for temperate, eutrophic lakes (e.g. Allen, 1973; Hall, 1975; Wetzel, 1976). This situation in Lake Kinneret may be due to limitation of the bacterial populations by intense zooplankton grazing or to low phosphorus availability.

5. Respiration, expressed as the percentage of total glucose uptake released as CO₂, ranged from 25 to 61%. Although the highest values were observed during the summer months, respiration rates appeared to be affected not only directly by temperature but also by the composition of the indigenous microbial population.

6. Heterotrophic glucose carbon uptake in the trophogenic zone was about 9% of the daily photosynthetic carbon fixation and could provide a bacterial yield of about 7 x 10⁴ cells ml⁻¹d⁻¹.

Acknowledgement

We are grateful to Mrs. U. Pollinger and Dr. S. Serruya for data on phytoplankton biomass and water temperatures respectively and to Dr. B. Z. Cavari for useful discussions. This research was supported by Grant No. 351 from the U.S.-Israel Binational Science Foundation (B.S.F.), Jerusalem, Israel.

Contribution No. 165 of Israel Oceanographic & Limnological Research Ltd.

References

- Albright, L. J. 1977. Heterotrophic bacterial dynamics in the Lower Frazer River, its estuary and Georgia Strait, N.C., Canada. *Mar. Biol.* 39: 203-211.
- Allen, H. J. 1969. Chemo-organotrophic utilization of dissolved organic compounds by planktic algae and bacteria in a pond. *Int. Rev. ges. Hydrobiol.* 54: 1-33.
- Allen, H. L. 1973. Dissolved organic carbon patterns of utilization and turnover in two small lakes. *Int. Rev. ges. Hydrobiol.* 58: 617-624.
- Allen, H. L. 1977. Dissolved organic matter in lakewater: characteristics of molecular weight size-fractions and ecological implications. *Oikos*. (in press).

- Berman, T. & Elias, Y. 1973. Lake Kinneret: Synoptic studies of chlorophyll concentrations. Proc. 4th Israel Ecol. Soc. F. 19-27.
- Berman, T. & Pollinger, U. 1974. Annual and seasonal variations of phytoplankton, chlorophyll and photosynthesis in Lake Kinneret. *Limnol. Oceanogr.* 19: 31-54.
- Berman, T. & Stiller, M. 1977. Simultaneous measurement of phosphorus and carbon uptake in Lake Kinneret by multiple isotopic labelling and differential filtration. *Microbiol. Ecol.* 3: 279-299.
- Cavari, B. Z. 1977a. Nitrification potential and factors governing the rate of nitrification in Lake Kinneret. *Oikos* 28: 285-290.
- Cavari, B. Z. 1977b. Denitrification in Lake Kinneret in the presence of oxygen. *Freshwat. Biol.* 7: 385-392.
- Cavari, B. Z. & Phelps, G. 1977. Sensitive enzymatic assay for glucose determination in natural waters. *Appl. Environ. Microbiol.* 33 (6): 1237-1243.
- Cavari, B. Z., Phelps, G. & Hadas, O. 1978. Glucose concentrations and heterotrophic activity in Lake Kinneret. *Verh. Int. Ver. Limnol.* 20: (in press).
- Gocke, K. 1978. Comparison of methods for determining the turnover time of dissolved organic compounds. *Mar. Biol.* 42 (2): 131-140.
- Gophen, M. 1972. Zooplankton distribution in Lake Kinneret (Israel), 1969-1960. *Israel J. Zool.* 21: 487-498.
- Gophen, M., Cavari, B. Z. & Berman, T. 1974. Zooplankton feeding on differentially labelled algae and bacteria. *Nature* 247 (5440): 390-394.
- Gophen, M. & Landau, R. 1977. Trophic interactions between zooplankton and sardine populations in Lake Kinneret during the period 1973-1975. *Oikos* 29: 166-174.
- Hall, K. J. 1975. Effect of nutrient enrichment on the heterotrophic uptake of organic solutes by microorganisms. *Verh. Inter. Ver. Limnol.* 19: 280-285.
- Hicks, S. E. & Carey, F. G. 1968. Glucose determination in natural waters. *Limnol. Oceanogr.* 13: 361-363.
- Hobbie, J. E. & Crawford, C. C. 1969. Respiration corrections for bacterial uptake of dissolved organic compounds in natural waters. *Limnol. Oceanogr.* 14: 528-532.
- Hoppe, H. G. 1976. Determination and properties of actively metabolising heterotrophic bacteria in the sea, investigated by means of microautoradiography. *Mar. Biol.* 36: 291-302.
- Overbeck, J. 1975. Distribution pattern of uptake kinetics responses in a stratified eutrophic lake (Plussee ecosystem study IV). *Verh. Inter. Ver. Limnol.* 19: 2600-2615.
- Parsons, T. R. & Strickland, J. D. H. 1962. On the production of particulate organic carbon by heterotrophic processes in sea water. *Deep Sea Res.* 8: 211-222.
- Parsons, T. R. & Takahashi, M. 1973. *Biological Oceanographic Processes*. Pergamon Press. Oxford. 186 p.
- Pollinger, U. & Berman, T. 1976. Autoradiographic screening for potential heterotrophs and estimation of relative phototrophic activity of natural phytoplankton populations in Lake Kinneret. *Microbiol. Ecol.* 2: 252-260.
- Pollinger, U. & Berman, T. 1977. Quantitative and qualitative changes in the phytoplankton of Lake Kinneret, Israel, 1972-1975. *Oikos* 29 (3): 418-428.
- Ramsey, A. J. 1976. The effect of acidification on measurements of microbial uptake of radioactive glucose in freshwater. *Limnol. Oceanogr.* 21: 767-940.
- Serruya, C. 1978. *Lake Kinneret: Monographiae Biologica*. Dr. W. Junk b.v. Publishers, The Hague. 480 p.
- Serruya, C., Edelstein, M., Pollinger, U. & Serruya, S. 1974. Lake Kinneret sediments nutrient composition of the pore water and mud water exchanges. *Limnol. Oceanogr.* 19 (3): 489-508.
- Serruya, C., Pollinger, U. & Gophen, M. 1975. The nitrogen and phosphorus distribution in Lake Kinneret with emphasis on dissolved nitrogen. *Oikos* 26 (2): 1-8.
- Strickland, J. P. H. & Parsons, T. R. 1968. *A practical handbook of seawater analysis* Bull. Fish. Res. Bd. Can. 167: 311 p.
- Vaccaro, R. F. & Jannasch, H. W. 1967. Variations in uptake kinetics for glucose by natural populations in seawater. *Limnol. Oceanogr.* 12: 540-542.
- Wetzel, R. C. 1975. *Limnology*. W. B. Saunders Co. Phila. 743 p.
- Williams, P. J. LeB. 1973. The validity of the application of simple kinetic analysis to heterogeneous microbial populations. *Limnol. Oceanogr.* 18: 159-165.
- Wood, L. W. 1973. Monosaccharide and disaccharide interactions on uptake and catabolism of carbohydrates by mixed microbial communities. In: *Estuarine Microbial Ecology*. Eds. L. H. Stevenson & R. R. Colwell. U.S.C. Press. Columbia S.C. 181-197.
- Wright, R. T. 1973. Some difficulties in using ¹⁴C-organic solutes to measure heterotrophic bacterial activity. In: *Estuarine microbial Ecology*. Eds. L. H. Stevenson & R. R. Colwell. U.S.C. Press. Columbia S.C. 199-217.
- Wright, R. T. & Hobbie, J. E. 1965. The uptake of organic solutes in lake water. *Limnol. Oceanogr.* 10: 22-28.