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The Coupling of Bacterial and Phytoplankton Production in Redberry Lake, Saskatchewan - an Oligotrophic, Prairie, Saline Lake with high DOC Concentration

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ABSTRACT

Bacterial and phytoplankton production were concurrently measured for 2 years in Redberry Lake, an oligotrophic, saline prairie lake, together with a range of environmental variables. Correlative relationships were used to evaluate the hypothesis that phytoplankton DOC was an important substrate for bacterioplankton. The mean DOC concentration was 35.8 mg l^{-1} while the mean concentration of total dissolved lipid was 125.9 μg l^{-1}. Chlorophyll concentrations were usually <1 μg l^{-1} but were as great as 12.7 μg l^{-1} just above the sediments at 16 m. Maximum volumetric rates of primary production (A_{max}) ranged from 3.2 to 31.6 mgC m^{-3} hr^{-1} at 2 m while areal, euphotic zone ($\overline{\times}=15.2$ m) production varied from 246 to 976 mgC m^{-2} d^{-1}. The mean number of bacteria was 7.98×10^{6} cells ml^{-1}. Published regression equations to predict bacterial numbers from mean chlorophyll concentration underestimated the mean number of bacteria in Redberry Lake. Volumetric rates of bacterial production were low at all depths, ranging from 0.01 to 0.2 mgC m^{-3} hr^{-1}, giving an average daily rate of 26.1 mgC m^{-2} d^{-1}. Gross bacterial production was calculated to be able to consume an average of 17.7%, or a maximum of 35.7%, of daily primary production. Bacterial production was correlated with primary production and water temperature at most depths while daily water column bacterial and phytoplankton production were correlated over the 2 years. Based on the data from the current study and previous studies on microbial limiting factors in this lake, we concluded that the correlations between bacterial and phytoplankton production were due to both the dependence of bacteria on phytoplankton for a supply of labile DOC and the co-limitation of both populations by inorganic nutrients (N and P).

Key words : bacterial production, primary production, saline lakes

INTRODUCTION

Although most prairie lakes are naturally eutrophic because of high nutrient loadings, high solar radiation flux, shallowness, internal nutrient

regeneration and extended freeze-up (BARICA, 1987) there are also a number of deeper, oligotrophic, saline lakes. As with other surface water bodies in this region, these oligotrophic lakes are interspersed between agricultural fields where activities, such as the use of pesticides to the operation of feedlots, may affect them. They are also important nesting and rearing habitats for waterfowl and have high recreational value.

Bacteria are generally accepted as the prime decomposers of organic carbon and regenerators of minerals in aquatic systems. Potentially they play a fundamental role mitigating the impacts of organic contaminants in prairie lakes (WAISER and ROBARTS, 1997), yet the microbial ecology of prairie lakes remains essentially unstudied. TUMBER *et al.* (1993) studied seasonal changes of bacterial cell volume in oligotrophic, saline Redberry Lake and hypertrophic, hyposaline Humboldt Lake, Saskatchewan. In Humboldt Lake cell volume was most strongly correlated with phytoplankton production. In Redberry Lake, however, it was correlated with ciliate abundance and chlorophyll concentration in the epilimnion and with ciliate abundance and primary production in the hypolimnion. In a later study of Humboldt Lake, ROBARTS *et al.* (1994) found that bacterial production was correlated with primary production and water temperature. WAISER and ROBARTS (1997) demonstrated co-limitation of Redberry Lake bacteria by not only nitrogen and phosphorus availability, but also by labile dissolved organic carbon (DOC) as well.

In view of these data, we anticipated that bacterial production in Redberry Lake would be low and that, in the absence of a major allochthonous source of labile DOC, bacterial production would be regulated by labile DOC produced by phytoplankton. We present here detailed spatial and temporal analyses of the abundance and production of bacterioplankton and phytoplankton in Redberry Lake as well as an examination of variations in bacterial production. This was done in an attempt to identify environmental factors regulating bacterial production. In addition, correlative relationships were used to evaluate the hypothesis that phytoplankton DOC is an important substrate for bacterioplankton. Magnitudes of areal bacterial and phytoplankton production were also compared. The results demonstrated that phytoplankton production was in excess of bacterioplankton requirements for organic carbon.

MATERIALS AND METHODS

Bacterial production was measured for two years in Redberry Lake (52°43′ N, 107°09′W), a saline (TDS, 20.9 g l^{-1}), oligotrophic (maximum euphotic zone Chl, 5.5 mg m^{-3}) prairie lake located in south-central Saskatchewan (ROBARTS *et al.*, 1992). The water column (maximum depth = 16 m) remains aerobic throughout the year. Sulphate is the dominant anion (93.1%) with a concentration of 130,208 μM (HAMMER, 1978). Ice formation typically occurs in early November and attains a thickness of >1 m by January while breakup usually occurs in early May. The depth to which 1%

of surface photosynthetically available radiation (PAR) penetrates (euphotic zone) averages 15.2 m during the ice-free period, frequently reaching bottom sediments (ROBARTS *et al.*, 1992). Additional details of the physical-chemical and biological characteristics of the lake can be found in ARTS *et al.* (1992), ROBARTS *et al.* (1992), TUMBER *et al.* (1993) and EVANS *et al.* (1996).

Water samples were collected from a central, deep-water station (16 m) with an opaque 8-L Niskin water sampler (internal diameter, 7 cm ; length, 71.5 cm). The sampler was held vertically and samples were collected from the surface to the bottom at 2 m intervals. Sampling in 1989 was biweekly and monthly in 1990 between May and October. Samples were also collected during ice-cover in January, February and March from surface (just beneath the ice), 8 m and 16 m. Unstable ice-conditions prevented sampling in the intervening months.

Physical and chemical parameters

Water temperature was measured at about mid-day with a Cole-Parmer 8502-20 thermistor at the depth intervals given above.

Water samples taken from 0, 10 and 16 m were analysed for particulate and dissolved nitrogen and phosphorus, dissolved (DOC) and particulate organic carbon (POC) and dissolved silica (ENVIRONMENT CANADA, 1992). Additional samples for NO_2+NO_3-N and soluble reactive phosphorus (SRP) were also collected from 4 m.

We measured total dissolved and particulate lipids as indicators of immediate and latent energy resources available to bacteria. Duplicate water samples were collected using an 8 litre Niskin sampler at 0.5 and 16 m depths (4 samples) during 1989. Water was filtered through a 150 μm Nitex mesh to remove zooplankton and then placed in 4 litre amber-coloured glass bottles in a darkened cooler partially filled with ice. On each sampling trip duplicate bottles were also filled with 'Super-Q' (Millipore) water and treated identically to lake water samples. A surrogate spike of ketone (20.0 μg hexadecanone) was added initially (on the first sampling day only) to the blanks so that extraction efficiency ($\bar{\times}=84\%$) could be estimated. Final lipid concentrations were corrected for this extraction efficiency.

Upon returning to the laboratory 1.0 litre of the 150 μm screened lake water was immediately filtered through a pre-combusted (400°C) Whatman GF/C filter (1.2 μm) into a 1 litre separatory flask. This filtered fraction was designated as the dissolved fraction. An additional 2 litres of lake water from the same source bottle was filtered through the same GF/C filter (total 3 litres filtered). The material remaining on the GF/C filter was designated as the particulate fraction. The concentration of lipids in the dissolved and particulate fractions was determined using the methods of ARTS *et al.* (1997).

Chlorophyll a (from 9 depths) was extracted in boiling (78°C) 90% ethanol and determined fluorometrically after correction for phaeopigments (NUSCH, 1980). Additional details of the field and laboratory protocols for

all of the above analyses can be found in ROBARTS *et al.* (1992).

Biological parameters

Volumetric and areal rates of phytoplankton primary production were measured using the *in situ* ^{14}C-light and dark bottle technique (ROBARTS *et al.*, 1992) concurrently with rates of bacterial production (see below).

Water samples (10 ml) were also collected from nine depths for bacterial numbers. Water was placed in sterile glass tubes and preserved with Lugol's iodine solution. Bacterial counts were done using epifluorescence microscopy and DAPI stain (TUMBER *et al.*, 1993).

Bacterial production and growth rates were calculated from the rate of [*methyl*-^{3}H] thymidine (TdR) incorporation into bacterial DNA. Water samples of 10 ml were transferred to sterile screw-top glass tubes. For each sample there were two live tubes and one control tube. Killed controls were prepared by the addition of 0.5 ml of 5M NaOH (ROBARTS and WICKS, 1989).

Working solutions of TdR (80–85 Ci nmol^{-1}, The Radiochemical Centre, Amersham, U.K.) were prepared daily with sterile distilled water. TdR was added to each tube to give a final concentration of 18 nM in order to saturate, but not inhibit, bacterial uptake (ROBARTS and ZOHARY, 1993). The tubes were attached to an incubation harness and returned to the depths from which they had originated. Incubation times were 1 hour in summer and up to 3 hr in winter. Preliminary experiments indicated that the TdR concentration used should have prevented isotope dilution (but possibly not intracellular isotope dilution) and that the rate of TdR incorporation was linear over the incubation periods (ROBARTS and ZOHARY, 1993).

Thymidine incorporation was stopped, and the samples preserved, by addition of 0.5 ml of 5M NaOH. The tubes were then stored on crushed ice until labelled DNA was extracted and purified using phenol/chloroform and ethanol, usually within 3 hr, but always within 24 hr, of NaOH addition to samples. Labelled DNA was radioassayed in a liquid scintillation counter.

Bacterial production was calculated as :

$$\text{Production (mgC m}^{-3}\text{ hr}^{-1}) = \text{TdR} \times 318 \times 1/\text{p} \times \text{C/DNA}$$

where TdR = mol thymidine incorporated into DNA

318 = average molecular weight of the four nucleotides in DNA

p = proportion of thymine in DNA (average = 0.25)

C/DNA = 6.2 for the range of bacteria found in Redberry Lake (SIMON and AZAM, 1989, Table 5 ; TUMBER *et al.*, 1993).

Bacterial growth rates (10^9 cells m^{-3} hr^{-1}) were calculated as production/mean carbon content per cell. We calculated mean carbon content per cell for bacteria from 2 m in Redberry Lake between May 1989 and March 1990 (TUMBER *et al.*, 1993) to be 16.28 ± 1.36 (S.E.) fg C cell^{-1}. The time needed for bacteria to double was calculated as cell numbers/cell production per day while specific growth rates were calculated as ln2/cell doubling time. Integrated bacterial production for the euphotic zone and water column were obtained planimetrically from production versus depth plots.

Statistical Analyses

The time-series data from each depth were not pooled but instead analysed in nine separate categories to remove the possibility of autocorrelation with depth (LEGENDRE and TROUSSELLIER, 1988). Bivariate correlations were determined using Spearman Rank analysis.

RESULTS

A pronounced thermocline developed each year so that the lake remained stratified between May and October (Fig. 1). Surface water temperatures ranged between -1.0 (January) and 21.8 °C (July). At 16 m water temperature rarely exceeded 4 °C except during fall overturn when a temperature as high as 7.6 °C was recorded in October 1990. The lake had an ice cover by November 23 (1989) and became ice-free again by May 4 (1990).

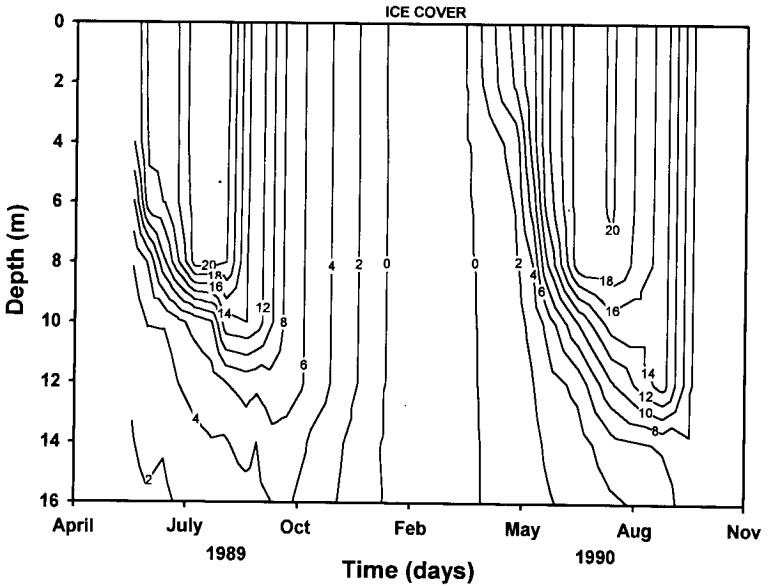

Fig. 1 Depth-time diagram of water temperature (°C) in Redberry Lake, Saskatchewan. Ice cover was Nov. 23 to May 4.

There were no distinct seasonal cycles of TDP (total dissolved phosphorus), SRP, or silica concentrations, but silica tended to be lowest in July-August each year (ROBARTS *et al.*, 1992 ; EVANS *et al.* 1996). SRP ranged between 11 and 68 $\mu g\ l^{-1}$ ($\bar{x} = 21\ \mu g\ l^{-1}$). The $NO_2 + NO_3$-N was usually $< 2\ \mu g\ l^{-1}$ but increased to 12-15 $\mu g\ l^{-1}$ beneath the ice (ROBARTS *et al.*, 1992). NH_3-N was usually $< 30\ \mu g\ l^{-1}$, but during mid-winter was almost twice this concentration. As noted by ROBARTS *et al.* 1992 and EVANS *et al.*, (1996) even though there was a marked thermocline in the lake, there was no significant gradient in nutrient concentrations with depth.

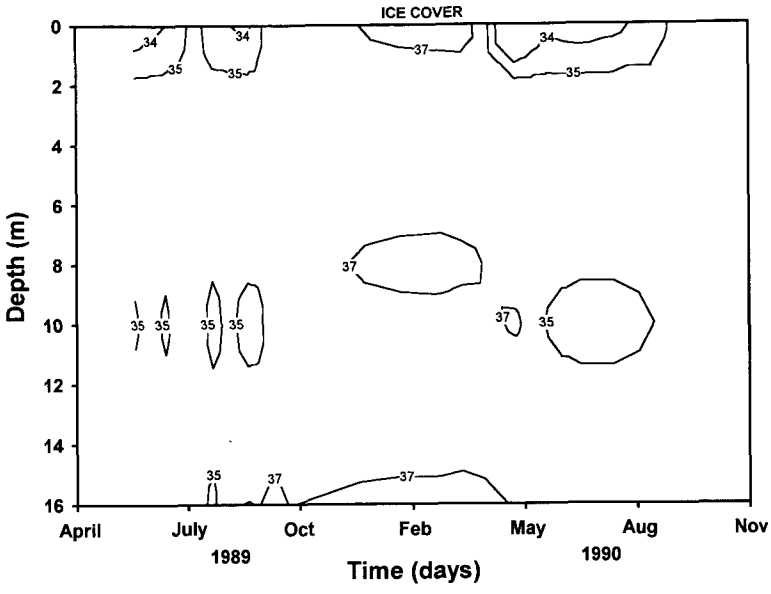

Fig. 2 Depth-time diagram of DOC (mg l^{-1}) concentration in Redberry Lake, Saskatchewan.

Redberry Lake waters are characterized by high concentrations of non-coloured DOC (Fig. 2). DOC varied between 31.6 mg l^{-1} at the surface in May to 39 mg l^{-1} at 16 m in March ($\overline{\times}=35.8$ mg $l^{-1}\pm0.2$ mg l^{-1} SE over the 2 years). The DOC concentration was significantly greater in the hypolimnion than in the epilimnion (t-test, $P<0.001$). Despite such high concentrations of DOC, the euphotic zone, as noted above, had a mean depth of >15 m due to the non-coloured nature of this material.

Total dissolved lipid concentrations ranged between 9.7 μg l^{-1} in May and 339 μg l^{-1} in October (Fig. 3). Particulate lipids basically decreased between early and late summer but started to increase again in fall. The highest concentration of 275 μg l^{-1} was measured in June and the lowest was 12.9 μg l^{-1} recorded in August. Changes in particulate lipids followed the seasonal changes of diatoms in Redberry Lake (ARTS *et al.*, 1997). Variations in dissolved lipid were weakly correlated to DOC ($r=0.44$, $P=0.05$) whereas those of particulate lipid were positively correlated with Si ($r=60$, $P=\leq0.01$) and NO_2+NO_3-N ($r=0.66$, $P\leq0.01$) and inversely with daily, areal primary production (see below ; $r=-0.67$, $P\leq0.01$).

Not unexpectedly, the concentrations of particulate nitrogen ($\overline{\times}=34$ μg l^{-1}, range 10-154 μg l^{-1}) and particulate organic carbon ($\overline{\times}=367$ μg l^{-1}, range 100-996 μg l^{-1}) were lowest during winter (ROBARTS *et al.*, 1992). Chl *a* concentration followed a similar pattern ; on several dates it was greatest at 16 m but was otherwise relatively uniformly distributed throughout the water column (Fig. 4). With the exception of SRP ($r=0.22$, $n=102$, $P<0.05$), ROBARTS *et al.* (1992) found no significant correlation between nitrogen, phosphorus or silica concentrations and chlorophyll concentration.

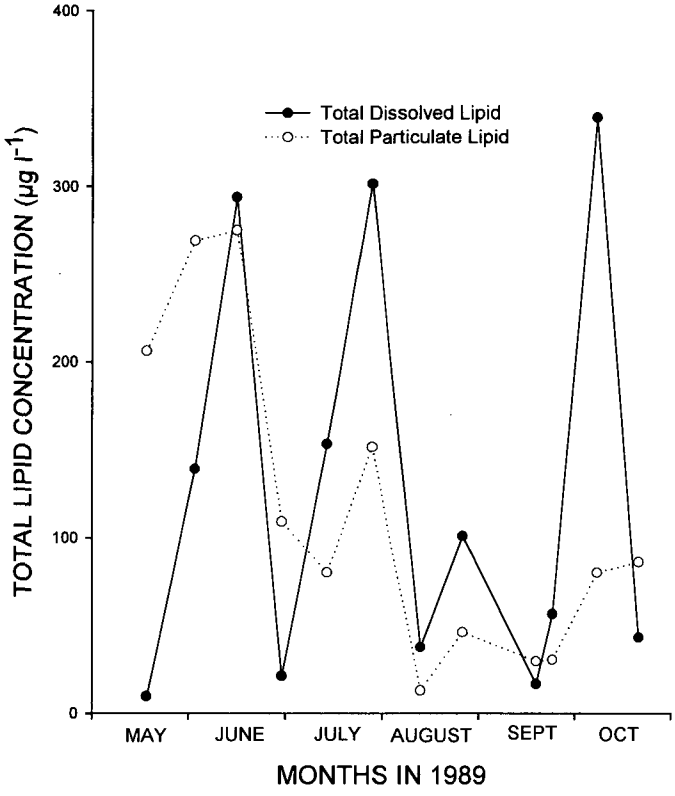

Fig. 3 Changes in total particulate and dissolved lipid concentrations in Redberry Lake.

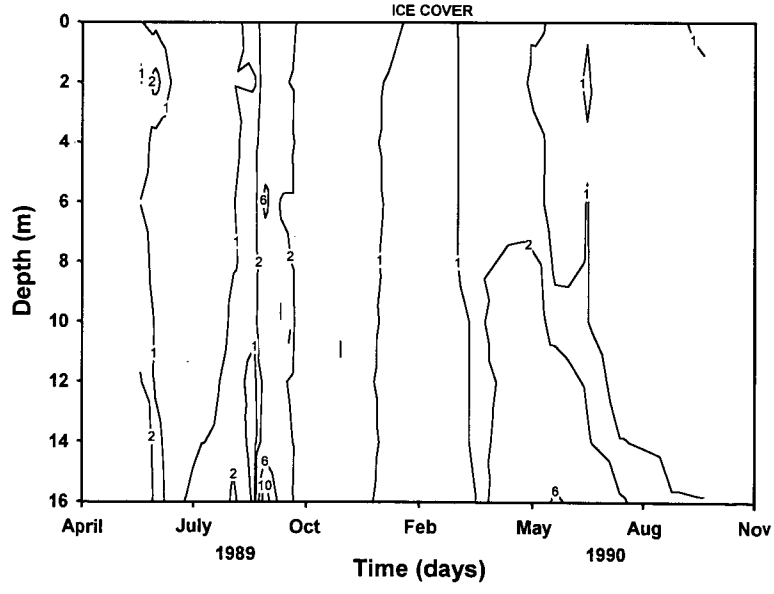

Fig. 4 Depth-time diagram of chlorophyll *a* concentration (μg l^{-1}) in Redberry Lake, Saskatchewan (Data from ROBARTS *et al.*, 1992).

Chl *a* was not correlated ($P \geq 0.5$) with either particulate or dissolved lipid concentrations.

The maximum volumetric rate of primary production varied from 3.2 mgC m^{-3} hr^{-1} in June 1990 to 31.6 mgC m^{-3} hr^{-1} in August 1989 (Fig. 5 ; ROBARTS *et al.*, 1992) and occurred above the thermocline (*cf.* Fig. 1). These rates were markedly lower in 1990 than in 1989. Water temperature was a major determinant of the chlorophyll *a*-specific primary production rate ($r=0.84$; ROBARTS *et al.*, 1992). Even though the chlorophyll peak was frequently located in the hypolimnion, this region did not support high rates of primary production due to low water temperatures and light levels (ROBARTS *et al.*, 1992). When integrated for the euphotic zone, daily phytoplankton production was between 246 and 976 mgC m^{-2} d^{-1} (see Fig. 8).

Bacterial numbers varied from 1.80 to 18.28×10^6 cells ml^{-1} ($\overline{X} = 7.98 \pm 0.20 \times 10^6$ ml^{-1} SE) (Fig. 6). There was no clear depth-distribution pattern but cell numbers tended to be greatest after ice-out (notably in 1990) and lowest under ice-cover. The strongest correlation between bacterial numbers and other environmental variables was with surface primary production ($r = 0.61$, $P = 0.01$). A similar correlation occurred at 8 m but otherwise bacterial numbers and primary production were not significantly correlated. Bacterial numbers were also inversely correlated with the DOC concentration at the surface ($r = -0.51$, $P = 0.02$) ; similar correlations were not found at greater depths.

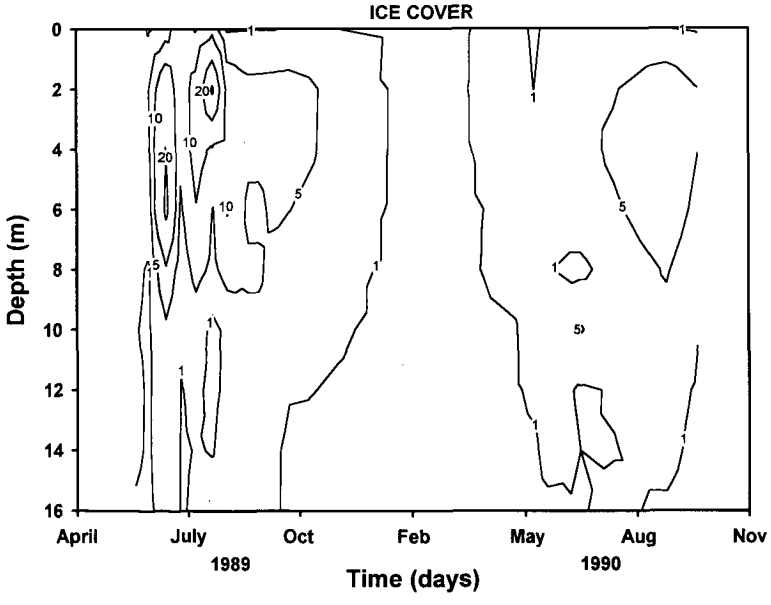

Fig. 5 Depth-time diagram of the volumetric rate of phytoplanktonic primary production (mgC m^{-3} hr^{-1}) in Redberry Lake, Saskatchewan (Data from ROBARTS *et al.*, 1992).

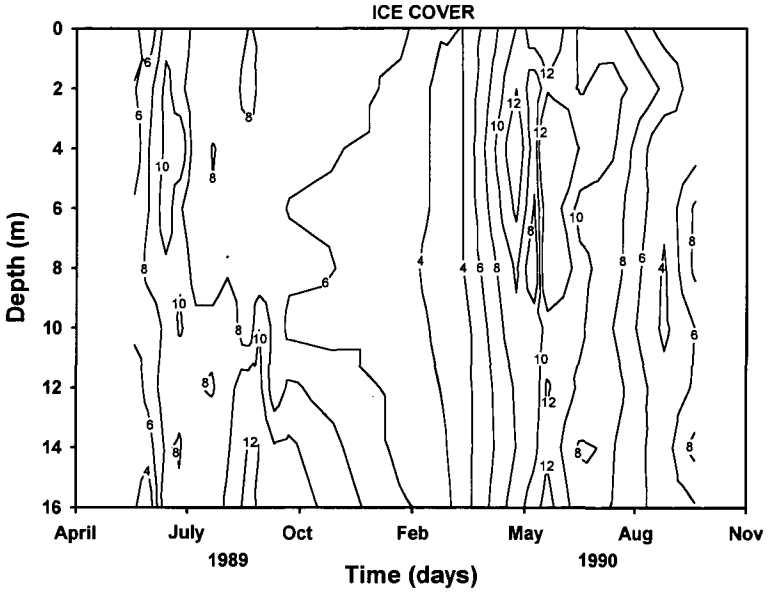

Fig. 6 Depth-time diagram of bacterial numbers (10^6 cells ml^{-1}) in Redberry Lake, Saskatchewan.

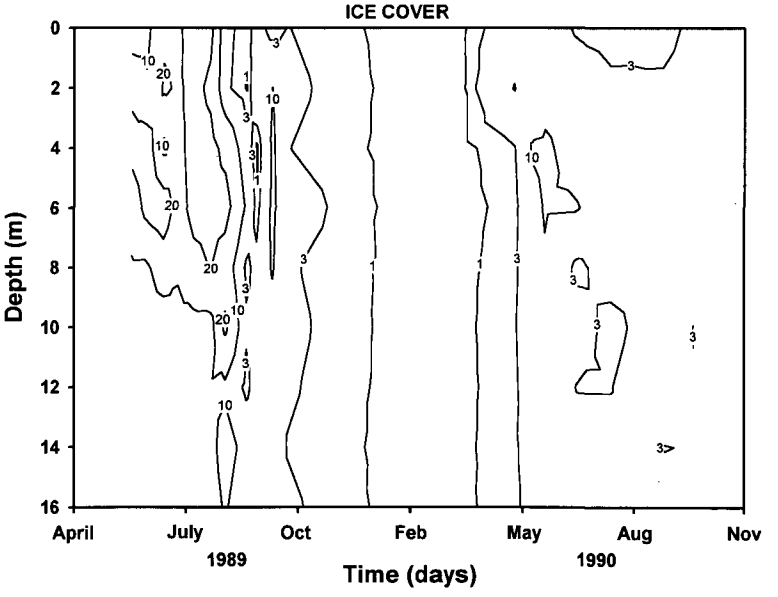

Fig. 7 Depth-time diagram of heterotrophic bacterial production (pmol TdR l^{-1} hr^{-1}) in Redberry Lake, Saskatchewan.

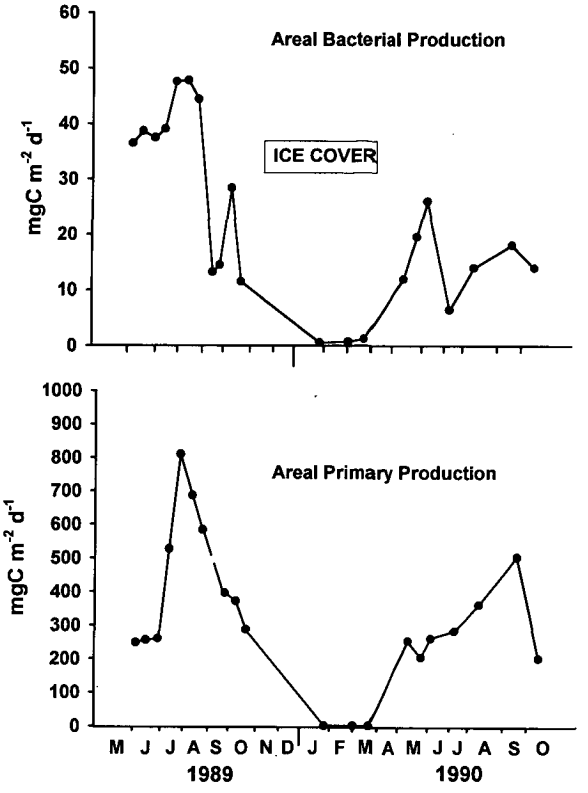

Fig. 8 Seasonal changes in heterotrophic bacterial production (mgC m^{-2} d^{-1}) and phytoplankton primary production (mgC m^{-2} d^{-1}) (ROBARTS *et al.*, 1992) in Redberry Lake, Saskatchewan.

Bacterial production varied from 0.07 to 25.9 pmol TdR l^{-1} hr^{-1} ($\bar{X}$ = 7.7 pmol TdR l^{-1} hr^{-1}) with lowest rates recorded during under ice conditions in winter (Fig. 7). Production was generally greatest above the thermocline during the ice-free period and was higher in 1989 than in 1990, similar to the trend in primary production (Fig. 5). Bacterial production was significantly correlated with water temperature and volumetric rates of primary production (Table 1).

Volumetric rates of bacterial production as carbon during the ice-free season were very low at all depths, ranging from 0.01 to 0.2 mgC m^{-3} hr^{-1} (Table 2). Under ice rates were about one order of magnitude lower or 0.001 to 0.004 mgC m^{-3} hr^{-1}. Extrapolated to daily values for the water column, rates averaged 26.1 mgC m^{-2} d^{-1} during the ice-free period and only 0.9 mgC m^{-2} d^{-1} from January to March (Fig. 8). The mean ratio of daily bacterial production to daily phytoplankton production was 6.2 (range = 1.9 − 12.5), excluding under-ice data. Bacterial production was corrected for respiration using a growth yield of 0.35 (ROBARTS *et al.*, 1994). The results indicated that on average the heterotrophic bacterial population could consume 17.7%, or a maximum of 35.7%, of daily primary production.

Table 1. Summary of Spearman rank correlation coefficients (r) between volumetric bacterial production (pmol TdR l^{-1} hr^{-1}), water temperature and volumetric primary production in Redberry Lake, 1989-1990. Only coefficients with $p \leq 0.05$ are given ; NS = $p > 0.05$, * = $p \leq 0.05$, ** = $p \leq 0.001$, n = 23-26.

Depth	Water Temperature (°C)	Primary Production (mgC m^{-3} hr^{-1})
Surface	0.70**	0.70**
2 m	0.37^{NS}	0.51*
4 m	0.48*	0.10^{NS}
6 m	0.61*	0.55*
8 m	0.66**	0.53*
10 m	0.10^{NS}	0.20^{NS}
12 m	0.29^{NS}	0.59*
14 m	0.32^{NS}	0.57*
16 m	0.76**	0.62*

Seasonal changes in the daily rate of bacterial production were correlated with water temperature ($r = 0.63$, $P = 0.012$) and daily primary production ($r = 0.58$, $P = 0.01$). An increased predictive capability was not achieved by using stepwise multiple regression analysis using these, or the other concurrently measured variables.

Bacterial cell production varied from 0.01 to 12.56×10^9 cells m^{-3} hr^{-1}, giving population doubling times of 18 to 1,323 days during the ice-free season (Table 2). Not unexpectedly, population doubling times were significantly longer under the ice, ranging from 544 to 7,999 days. These doubling times are generally longer than those measured in hypertrophic Humboldt Lake (range 4.7 to 275 days during the ice-free season) by ROBARTS *et al.* (1994).

DISCUSSION

Relatively few analyses of bacterial dynamics have been made in oligotrophic freshwater systems over annual periods (COVENEY and WETZEL, 1995). Most studies for oligotrophic waters are of marine systems. Redberry Lake is an inland saline lake whose chemistry is dominated by magnesium and sulphate ions. Although unlike marine systems, it is typical of the prairie and Great Plains regions of North America. These prairie systems also tend to have high concentrations of non-coloured dissolved organic carbon (>10 mg l^{-1}) (CURTIS and ADAMS, 1995) and high SRP concentrations. Little of the phosphorus or DOC is biologically available (WAISER and ROBARTS, 1995 ; 1997).

Bacterial production in Redberry Lake during the ice-free period averaged about 8 $nmol^{-1}$ TdR m^{-3} hr^{-1} (Table 2) placing it at the lower end of values measured in other marine and freshwater systems. This level is similar to

Table 2. Bacterial production and growth rate in Redberry Lake during the ice-free periods of 1989-1990, calculated from the rate of thymidine incorporation into DNA. Data given are the mean and the range.

Depth	Bacterial production (nmol TdR m^{-3} hr^{-1})	Cell production (10^{12} m^{-3} hr^{-1})	Specific growth rate (hr^{-1})	Doubling time (hr)	Carbon production (mgC m^{-3} hr^{-1})
0 m	7.8	3.65	0.008	225	0.06
	1.1-25.8	0.01-12.50	0.001-0.030	23-711	0.01-0.20
2 m	9.5	4.58	0.010	158	0.07
	0.8-22.4	0.39-10.85	0.001-0.027	26-969	0.01-0.18
4 m	11.5	5.57	0.014	175	0.09
	0.5-25.9	0.24-12.55	0.001-0.040	18-1323	0.01-0.20
6 m	12.4	6.00	0.013	117	0.10
	1.3-25.9	0.63-12.56	0.001-0.031	22-633	0.01-0.20
8 m	8.4	1.13	0.009	142	0.07
	1.7-20.3	0.16-3.00	0.001-0.024	29-537	0.01-0.16
10 m	6.5	0.86	0.007	150	0.05
	1.1-21.9	0.13-2.30	0.001-0.019	37-646	0.01-0.17
12 m	5.6	2.69	0.006	172	0.04
	1.8-9.4	0.87-4.55	0.001-0.014	49-544	0.01-0.07
14 m	5.7	2.76	0.005	151	0.04
	2.6-13.8	1.26-6.69	0.002-0.012	60-309	0.02-0.11
16 m	5.9	2.85	0.007	155	0.05
	2.2-10.9	1.07-5.28	0.002-0.026	27-352	0.02-0.09

that found in oligotrophic Lawrence Lake, Michigan (COVENEY and WETZEL, 1995) but lower than that reported for oligotrophic Mirror Lake, New Hampshire (OCHS *et al.*, 1995). This probably occurred because of higher chlorophyll concentrations in Mirror Lake (~3 to 35 μg l^{-1} from April to November), concentrations that were significantly higher than in either Redberry (Fig. 4) or Lawrence lakes. Although the average bacterial production rate for Humboldt Lake, a nearby hypertrophic and hyposaline lake, was 100 $nmol^{-1}$ TdR m^{-3} hr^{-1} (ROBARTS *et al.*, 1994), the much lower rates in Redberry Lake probably reflect lower nutrient levels, algal standing crops and phytoplankton production compared to Humboldt Lake (ROBARTS et al., 1992). In Lawrence Lake water temperature was significantly correlated with bacterial numbers and production but these were not significantly correlated with either chlorophyll concentration or primary production (COVENEY and WETZEL, 1995). OCHS *et al.* (1995) found that water temperature explained >50% of the variance in bacterial production in Mirror Lake. Similarly, in Redberry Lake water temperature seemed to be an important factor associated with changes in bacterial production (Table 1) which was also the case in Humboldt Lake (ROBARTS *et al.*, 1994). Moreover, bacterial production was also significantly correlated with volumetric and areal primary production in both lakes (Table 1, Figs. 6 & 7 ; ROBARTS *et al.*, 1994).

As recently noted by RIVKIN and ANDERSON (1997) a positive correlation between bacterial and phytoplankton production does not unequivocally prove a causal relationship of organic carbon limitation of bacterial production. If both bacteria and phytoplankton are constrained by the availability of the same resource, then their production would covary and be correlated. As noted above, both bacteria and phytoplankton have been shown to be co-limited by nitrogen and phosphorus in Redberry Lake (WAISER and ROBARTS, 1995) while in addition, bacteria can also be limited by labile DOC (WAISER and ROBARTS, 1997). As well, areal primary production has been shown to be correlated with phosphorus in Redberry Lake (ROBARTS *et al.*, 1992). We can conclude that the correlations between bacterial and primary production in the present study were due to both the dependence of bacteria on phytoplankton for a supply of labile DOC and the co-limitation of both populations by inorganic nutrients. This occurred in spite of the large DOC pool in this lake (Fig. 2) which was essentially ($<1\%$ of the DOC) unavailable to bacteria (WAISER and ROBARTS, unpubl. data). Therefore, the apparent coupling between bacterial and phytoplankton production in Lawrence and Redberry lakes resulted from different mechanisms. In Lawrence Lake this coupling stemmed mainly from similar responses of both components to common regulating factors and not from direct metabolic links (COVENEY and WETZEL, 1995).

Several regression equations have been developed for predicting bacterial numbers and production from chlorophyll concentrations and primary production rates (BIRD and KALFF, 1984 ; COLE *et al.*, 1988). BIRD and KALFF's and COLE *et al.*'s regression equations use mean chlorophyll concentration, but both underestimated bacterial numbers in Redberry Lake (Table 3). Conversely, although the equations to predict bacterial production from primary production have wide confidence limits, the mean predicted values for bacterial production were higher than measured rates. A similar situation was found for hypertrophic Humboldt Lake (ROBARTS *et al.*, 1994) located in the same prairie region as Redberry Lake. The reasons for the discrepancies between measured and predicted values are not obvious. In Redberry Lake bacteria are co-limited by phosphorus, nitrogen and labile DOC (WAISER and ROBARTS, 1995, 1997). This and the general lack of correlation between bacterial numbers and environmental parameters we measured, indicate that the majority of the bacterial population may be in a non-active state. This would also account for the very long population doubling times calculated for Redberry Lake (Table 2) since the calculation assumes that all bacterial cells are active and growing.

On the basis of low measured rates of bacterial production compared to the predicted rates, both on a volumetric and areal basis (Table 3), it would appear that bacterial production in Redberry Lake was generally low compared to other systems. COLE *et al.*'s (1988) models, however, were constructed with few data from lakes with chlorophyll as low as those in Redberry Lake or Lawrence Lake. Furthermore, when making such comparisons it is essential to remember the various factors used to convert rates of

Table 3. Measured and predicted numbers of bacteria and bacterial production in Redberry Lake during the ice-free season. Data are bacterial numbers ($\times 10^6$ cells ml^{-1}), mean euphotic zone chlorophyll *a* concentration ($\mu g\ l^{-1}$), mean volumetric bacterial and primary production ($mgC\ m^{-3}\ d^{-1}$) and mean areal bacterial and primary production ($mgC\ m^{-2}\ d^{-1}$).

Parameter	Measured Value	Predicted Value	Model
Bacterial numbers from chlorophyll	8.16±0.40 (95% CL)	1.25±0.43–2.94 (95% CL)	BIRD and KALFF (1984)
	8.16±0.33 (90% CL)	1.39±0.49–3.00 (90%)	COLE *et al.* (1988)
Volumetric bacterial production from volumetric primary production	1.5±0.16 (90% CL)	7.9±1.0–26.5 (90% CL)	COLE *et al.* (1988)
		10.0±1.1–35.9 (90% CL)*	COLE *et al.* (1988)
Areal bacterial production from areal primary production	26.1±5.3 (90% CL)	138.6±47.7–305 (90% CL)	COLE *et al.* (1988)

* Bacterial production obtained with TdR method only.

TdR incorporation into carbon units. We used a theoretical factor (0.5×10^9 cells $nmol^{-1}$ TdR incorporated) but an empirical conversion factor of 1.94×10^9 cells produced per nmol of TdR incorporated has been determined for Redberry Lake (R.A. SNYDER, U.S. EPA, Gulf Breeze, Florida, unpubl. data). It has been argued (ROBARTS and ZOHARY, 1993; ROBARTS *et al.*, 1994) that such empirical factors, derived from growing bacteria in flasks for 24 hr, may be biased. However, if we had used this factor our bacterial production rates would have been much closer to predicted mean values (Table 3). Since a wide range of conversion factors were used by authors in the studies that were incorporated into the regression equations, we can conclude that bacterial production in Redberry Lake relative to the standing crop of phytoplankton was not significantly lower than that found in other lakes of similar trophic status and phytoplankton primary production. COVENEY and WETZEL's (1995) data for Lawrence Lake supports this conclusion.

LE *et al.* (1994) predicted that systems with coupled (correlated) algal and bacterial production are characterized by molar inorganic N : P ratios > 40. In Redberry Lake the mean N : P ratio was 4.6. Variations in bacterial production were correlated to phytoplankton production in Redberry Lake (Table 1, Fig. 8) but based on LE *et al.*'s model they should not have been. In Lawrence Lake the N : P ratio was >330, leading COVENEY and WETZEL (1995) to conclude that the relationships between algal and bacterial production in this lake, where the direct release of DOC from phytoplankton was not the dominant substrate source for bacteria, were consistent with LE *et al.*'s (1994) model. Therefore, is the model of LE *et al.* (1994) not applicable to prairie saline lakes or is there some aspect of the chemistry of these waters that invalidates the model ?

Redberry Lake water is characterized by relatively high concentrations of

inorganic phosphorus. Using ^{32}P-kinetics, WAISER and ROBARTS (1995) calculated that the upper bound for biologically available phosphorus in Redberry Lake was only 0.05 μg l^{-1} when the chemically measured concentration was 16 μg l^{-1}. If this difference is characteristic of the relationship between chemically measured and biologically available phosphorus in Redberry Lake for significant periods of the year, then the N : P ratio would exceed 40. On this assumption then, our conclusion that bacterioplankton depend upon phytoplankton for labile DOC was consistent with LE *et al.*'s (1994) model.

For Lawrence Lake COVENEY and WETZEL (1995) calculated that low and high estimates of bacterial production over 2 years exceeded phytoplankton production by factors of 1.33 and 3.35. They concluded that net metabolism in the pelagic zone was heterotrophic, a state which was probably supported by littoral macrophytic and periphytic production, and that water temperature played a primary role in regulating seasonal bacterial production rates. There are no extensive beds of macrophytes in Redberry Lake. However, because of the high transparency of the water, it is possible that benthic algal production could be significant, although this has not been investigated. The demonstrated limitation of bacterial production by labile DOC in this lake (WAISER and ROBARTS, 1997) indicated that there were no other significant autochthonous or allochthonous labile DOC sources for bacterioplankton. In Redberry Lake, bacterial production consumed a maximum of 35.7% of phytoplankton production suggesting that primary production could fulfill the organic carbon requirements of the bacterial populations. Assuming that the factors used to calculate gross daily bacterial production were not significantly in error, then the lack of consumption of a larger proportion of primary production may have been due to inorganic nutrient limitation (N or P). If this were the case, then the pool of labile DOC in Redberry Lake should be fairly large, but it was not. Since our measured rates of bacterial production were in approximately the right proportion relative to primary production as in other aquatic systems, what is the fate of the autochthonously produced dissolved and particulate organic carbon ? Much of it may accumulate in the sediments which have an organic carbon content of about 13% (range 8.5-18.5% ; VAN STEMPVOORT *et al.,* 1993), which is high for lakes. Clearly there is a need for a study to examine the means by which this could occur and to determine whether this is a plausible explanation for the discrepancy between the seemingly large excess of phytoplankton organic carbon and the very small pool of labile DOC in the water column.

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