Factors related to heterotrophic bacterial and flagellate abundance in temperate rivers

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ABSTRACT: Thirty-one rivers of varying trophic status located in Ontario and Quebec, Canada, were sampled in order to determine the factors related to heterotrophic bacterial and flagellate abundance. Bacterial abundance ranged from 1.80×10^6 to 9.92×10^6 cells ml^{-1} and flagellate abundance ranged from 1.18×10^3 to 17.4×10^3 cells ml^{-1} . There was a highly significant, positive relationship between bacterial abundance and both total phosphorus ($R^2 = 0.55$) and chlorophyll *a* ($R^2 = 0.55$). Bacterial abundance was not related to dissolved organic carbon concentration which ranged from 4.6 to 13.0 mg l^{-1} . A significant positive relationship was observed between heterotrophic flagellate abundance and both heterotrophic bacterial abundance ($R^2 = 0.46$) and total phosphorus ($R^2 = 0.52$). Neither bacterial nor flagellate abundance was significantly related to water residence time. No relationship between zooplankton biomass and bacterial or flagellate abundance was observed, possibly because of the low biomass of zooplankton in the rivers (mean = 11.3 $\mu\text{g l}^{-1}$ dry mass). Results suggest that in rivers there is little transfer of energy from the microbial food web to the planktonic food web due to the scarcity of metazoan zooplankton.

KEY WORDS: Bacteria · Flagellates · Rivers · Nutrients · Zooplankton

INTRODUCTION

The importance of microbial food webs in marine and lentic freshwaters has been recognized for the past decade (Azam et al. 1983, Cole et al. 1988). These webs can be visualized as 'microbial loops', in which heterotrophic bacteria convert dissolved organic matter of autochthonous or allochthonous origin into particulate organic carbon (Azam et al. 1983, Berninger et al. 1991, Findlay et al. 1991). The heterotrophic bacteria are then grazed by heterotrophic flagellates and small ciliates (Porter et al. 1985, Berninger et al. 1991) which, in turn, may be consumed by larger ciliates, microzooplankton and cladocerans (Gasol & Vaqué 1993).

In temperate lakes heterotrophic bacterial abundance has been related to measures of lake productivity such as chlorophyll *a*, total phosphorus or dissolved organic carbon concentrations (Bird & Kalff 1984, Tranvik 1989, Currie 1990, Tzaras & Pick 1994), sug-

gesting that predatory control of bacteria may be of minor importance (Gasol & Vaqué 1993). Heterotrophic flagellate abundance has been positively correlated with heterotrophic bacterial abundance (Berninger et al. 1991) and a negative relationship between flagellates and zooplankton has been suggested (Dolan & Gallegos 1991, Pace & Funke 1991).

The overwhelming majority of studies concerning freshwater microbial food webs have been conducted in lentic environments with comparatively little research focused on heterotrophic bacteria and protozoa in temperate rivers (Edwards & Meyer 1986, Carlough & Meyer 1990, Dolan & Gallegos 1991, Findlay et al. 1991). The microbial food web could be particularly important to carbon and nutrient dynamics in rivers due to the often high loadings of allochthonous organic matter (Edwards & Meyer 1986, Findlay et al. 1991, Sabater et al. 1993), and low zooplankton abundances (Pace et al. 1992, Basu & Pick 1996). Under such conditions, significant carbon flow to benthic invertebrates and nutrient regeneration may occur via the microbial food web.

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The abundance of heterotrophic bacteria in rivers can be high. Edwards (1987) observed an average abundance of 1.5×10^{10} cells l^{-1} in the Ogeechee River (USA). As in lakes, the primary consumers of heterotrophic bacteria in rivers appear to be heterotrophic flagellates (Carlough & Meyer 1990), though benthic filter-feeding invertebrates can also be significant consumers of planktonic bacterial biomass (Meyer 1990). Yet, the chemical and biotic factors influencing the abundance of heterotrophic bacteria and flagellates in rivers, and the effect of hydrological factors such as discharge or water residence time, have not been examined.

The objective of the present study was to determine the factors most strongly related to (and hence potentially regulating) heterotrophic bacterial and flagellate abundance in 31 north-temperate rivers. We tested the following hypotheses: (1) that bacterial abundance is positively related to measures of productivity (nutrients, chl *a*, dissolved organic carbon), (2) that flagellate abundance is positively related to bacterial abundance, (3) that flagellate abundance is negatively re-

lated to zooplankton biomass, and (4) that both bacterial and flagellate abundances are positively related to water residence time.

METHODS

Thirty-one rivers of varying trophic status located in eastern Canada were sampled in July 1994 (Table 1). The rivers drain areas located on either the Canadian Shield (granitic bedrock) or the Great Lakes, St. Lawrence Lowlands (sedimentary bedrock). The watersheds of the rivers range from completely forested to agricultural. All the rivers are fifth order or larger and have mean annual discharges greater than $8.0 \text{ m}^3 \text{ s}^{-1}$ (Water Survey of Canada 1990). The sampling sites on the rivers were located close to Water Survey of Canada gauging stations and not near any inflowing tributaries or within 10 km of headwater lakes.

Heterotrophic bacteria and flagellate samples were collected mid-channel at each river site using a 4 m vertically integrated tube. Usually the entire water col-

Table 1. River locations with dissolved organic carbon (DOC), heterotrophic bacteria, and heterotrophic flagellate concentrations for July 1994 sampling. S: rivers located on the Canadian Shield; L: rivers located in the Great Lakes/St. Lawrence Lowlands

River	Latitude (N)	Longitude (W)	DOC (mg l^{-1})	Bacteria ($\times 10^6$ cells ml^{-1})	Flagellates ($\times 10^3$ cells ml^{-1})
Madawaska (S)	45° 30'	77° 10'	6.0	3.05	3.10
Bonnechere (S)	45° 30'	76° 50'	6.5	3.80	3.95
Mississippi (S/L)	45° 20'	76° 15'	7.0	3.43	4.95
Rouge (S)	45° 50'	74° 40'	5.8	3.56	1.26
du Lievre (S)	45° 40'	75° 35'	5.7	1.80	1.55
South Nation (L)	45° 20'	75° 5'	12.6	3.95	8.94
Gatineau (S)	45° 40'	75° 55'	6.5	2.12	2.01
Picanoc (S)	45° 43'	75° 55'	5.3	3.24	1.58
Magnetewan (S)	45° 46'	80° 35'	5.1	2.95	2.05
French (S)	46° 2'	80° 43'	4.8	3.18	2.33
Mattawa (S)	46° 20'	78° 45'	5.5	3.01	3.04
Temagami (S)	46° 38'	80° 8'	5.8	2.25	1.55
Sturgeon (S)	46° 26'	79° 58'	5.3	2.86	2.40
Amable (S)	46° 20'	77° 15'	5.5	3.42	2.01
Veuve (S)	46° 26'	80° 10'	13.0	5.14	2.51
Trent (L)	44° 20'	77° 55'	6.7	7.69	2.77
Napanee (L)	44° 20'	76° 50'	9.9	4.33	1.18
Salmon (L)	44° 15'	77° 5'	8.4	3.66	1.21
Moir (L)	44° 20'	77° 20'	8.2	3.21	3.03
Burnt (S/L)	44° 30'	78° 42'	5.5	3.57	4.10
Otonabee (S/L)	44° 25'	78° 15'	6.1	5.88	3.88
Skootamata (S/L)	44° 30'	77° 15'	8.6	3.16	1.60
Saugeen (L)	44° 12'	81° 11'	6.0	4.67	3.33
Ausable (L)	43° 3'	81° 38'	4.6	7.93	17.40
North Thames (L)	43° 14'	81° 12'	5.4	9.92	11.50
Nith (L)	43° 25'	80° 43'	5.8	9.10	13.90
Thames (L)	42° 51'	81° 25'	5.8	7.47	7.70
Conestogo (L)	43° 36'	80° 40'	5.9	5.17	1.47
Maitland (L)	43° 51'	81° 15'	6.1	2.66	1.42
Grand (L)	43° 6'	80° 11'	5.5	7.58	4.66
Rideau (L)	45° 27'	75° 42'	6.7	4.44	3.80

umn was sampled, as river depths rarely exceeded 4 m. Subsamples (100 ml) of whole river water were preserved immediately with 10% glutaraldehyde buffered with 0.1 M sodium cacodylate and stored at 4°C in the dark until enumeration within 3 mo. Bacterial and flagellate samples were stained with 4',6-diamidino-2-phenylindole (DAPI) added at a 3:1 sample-to-DAPI ratio. Enumeration was performed using epifluorescence microscopy at 1500× magnification (Porter & Feig 1980). Bacteria were filtered onto 0.2 µm and flagellates onto 1.0 µm Irgalen black stained Nucleopore filters. At least 500 cells from approximately 10 randomly selected fields were enumerated for bacterial abundance. For heterotrophic flagellates, between 70 and 120 cells were counted from random transects (Tzaras & Pick 1994). Samples containing large amounts of inorganic particulate material were diluted in 10 ml of filtered (0.2 µm) distilled water and subsampled prior to enumeration.

For chl *a*, vertically integrated water samples were filtered through Whatman GF/F filters, chl *a* was extracted using DMSO and acetone (Burnison 1980) and concentrations were calculated using the equations of Jeffrey & Humphrey (1975). Chemical analyses for total phosphorus (TP) and total nitrogen (TN) were performed at the Regional Municipality of Ottawa-Carleton, Surface Water Quality Laboratories by standard methods (Basu & Pick 1995). TP was determined by acid digestion to orthophosphorus followed by reaction with ammonium molybdate and ascorbic acid. Nitrate + nitrite was determined by reducing nitrate to nitrite, diazotizing with sulfanilamide, and coupling with ethylenediamine dihydrochloride. Total Kjeldahl nitrogen was determined by converting organically bound nitrogen to ammonium sulfate via acid digestion, then analyzing for ammonia. TN was the sum of nitrate + nitrite and Kjeldahl nitrogen concentrations. Dissolved organic carbon (DOC) concentration was determined using the UV oxidation method as outlined in the Analytical Methods Manual of Environment Canada (1979).

Triplicate vertically integrated crustacean zooplankton samples were collected mid-channel by pumping 30 l of water through a 64 µm Nitex mesh plankton net. Rotifer samples were collected by filtering 4 l of water through a 35 µm Nitex mesh screen. Samples were preserved with 4% chilled formalin sucrose (Haney & Hall 1975). Crustaceans were enumerated under a dissecting microscope, rotifers under an inverted microscope. Biomass estimates for crustaceans were determined using length-dry mass relationships (Dumont et al. 1975, Bottrell et al. 1976) and biomass estimates for rotifers were determined using biovolume-dry mass relationships (Dumont et al. 1975, Ruttner-Kolisko 1977). Further details are described in Basu & Pick (1996).

Discharge values for the rivers were obtained from Water Survey of Canada gauging sites. Discharge was calculated as the mean of the daily discharges for the period 7 d prior to and including the sampling date (Pace et al. 1992). Watershed area for each river was obtained from the Water Survey of Canada which calculates upstream watershed area at each gauging site (Water Survey of Canada 1990). Water residence time (an estimate of the time the water has been in the river system or, in other words, its 'age' at the sampling site) was calculated using the formula:

$$R = 0.08 A_d^{0.6} / Q^{0.1} \quad (1)$$

where *R* represents water residence time at the sampling site (days), *A_d* represents watershed area upstream of the sampling site (km²) and *Q* represents river discharge (m³ s⁻¹) (Soballe & Kimmel 1987).

Statistical analysis was performed using Systat 5.03 (Systat Inc. USA). Model I linear regression analysis was used to identify predictive relationships between variables, however, because both independent and dependent variables had measurement error, Model II regression (geometric mean) was used to derive functional relationships between variables (Sokal & Rohlf 1981). Regressions plotted in the figures are Model I, but both Model I and Model II equations are included in the figure captions. All parametric tests satisfied the assumptions of normality (Wilkes-Shapiro test) and homoscedasticity (Levene's test) following logarithmic transformation of the data and all log transformed equations were corrected for bias (Sprugel 1983).

RESULTS

Means and ranges of the measured variables are given in Tables 1 & 2. Further physical, chemical and biotic variables can be found in Table 1 of Basu & Pick (1996).

There was a significant positive relationship between bacterial abundance and both TP and chl *a* (Fig. 1). Bacterial abundance was also positively related to TN, however, the coefficient of determination (*R*²) for this relationship was lower than those for the TP-bacteria or chl *a*-bacteria relationships (for TN: *p* < 0.001, *R*² = 0.47). There was no significant relationship between bacterial abundance and DOC (*p* = 0.89).

Bacterial abundance was not significantly related to rotifer biomass (*p* = 0.47), crustacean zooplankton biomass (*p* = 0.69) or total zooplankton biomass (rotifer + crustacean biomass) (*p* = 0.89). Bacterial abundance was also not significantly related to water residence time (*p* = 0.22).

There was a significant positive relationship between heterotrophic flagellate abundance and both

Table 2. Means ($\pm$ SE) and ranges of measured variables for rivers sampled in Ontario and Quebec during July 1994. n = 31 sampled rivers

Variable	Mean ($\pm$ SE)	Range
Bacterial abundance ($\times 10^6$ cells ml^{-1})	4.46 (± 0.38)	1.80–9.92
Flagellate abundance ($\times 10^3$ cells ml^{-1})	4.07 (± 0.70)	1.18–17.40
Chl <i>a</i> ($\mu\text{g l}^{-1}$)	6.62 (± 1.17)	1.77–27.62
Rotifer biomass ($\mu\text{g l}^{-1}$ dry mass)	2.27 (± 0.85)	0.016–22.6
Crustacean biomass ($\mu\text{g l}^{-1}$ dry mass)	8.99 (± 6.38)	<0.1–196.0
TP ($\mu\text{g l}^{-1}$)	32.0 (± 7.60)	7.3–212.3
TN ($\mu\text{g l}^{-1}$)	1117.6 (± 219.5)	272.0–5318.0
DOC (mg l^{-1})	6.6 (± 0.4)	4.6–13.0
Water residence time (d)	7.32 (± 0.70)	3.28–19.38

bacterial abundance and TP (Fig. 2). Flagellate abundance was also significantly related to chl *a* ($p < 0.001$, $R^2 = 0.50$) and TN ($p < 0.001$, $R^2 = 0.44$). There was no significant relationship between flagellate abundance and DOC ($p = 0.52$) or water residence time ($p = 0.98$).

There were no significant relationships between flagellate abundance and rotifer biomass ($p = 0.25$), crustacean biomass ($p = 0.97$), or total zooplankton biomass (rotifer + crustacean biomass) ($p = 0.26$). Furthermore, there were no significant relationships between the residuals of the flagellate-bacteria or flagellate-TP regressions and any zooplankton variables ($p > 0.05$ for rotifer, crustacean, and total zooplankton biomass).

DISCUSSION

In temperate lakes, heterotrophic bacterial abundance has been positively correlated with chl *a* and TP (Bird & Kalff 1984, Currie 1990, Tzaras & Pick 1994). A link between planktonic bacteria and algae was postulated by Bird & Kalff (1984). Bacterial growth was believed to be carbon limited and algae were hypothesized to be the main suppliers of DOC used by bacteria. However, Currie (1990) and Tzaras & Pick (1994) observed that the relationship between bacterial abundance and TP was often stronger than that between bacterial abundance and chl *a*. Bacteria can compete effectively with algae for the uptake of phosphorus (Lean & White 1983, Currie & Kalff 1984) and Currie (1990) argued that phosphorus directly influences both algal and bacterial abundance. The positive relationships we observed between bacterial abundance and both chl *a* and TP indicate that similar processes may occur in temperate rivers, with bacteria responding

Fig. 1. Significant relationships between (A) total phosphorus (TP) concentration and heterotrophic bacterial abundance [Model I (shown); log bacterial abundance = $6.46 + 0.38 \log \text{TP}$, Model II; log bacterial abundance = $6.30 + 0.50 \log \text{TP}$] and (B) chl *a* concentration and heterotrophic bacterial abundance [Model I (shown); log bacterial abundance = $6.62 + 0.45 \log \text{chl } a$, Model II; log bacterial abundance = $6.52 + 0.61 \log \text{chl } a$] for rivers sampled during July 1994. Dashed lines represent 95% confidence intervals

directly to TP, as well as to organic carbon produced by phytoplankton. Alternatively, both phytoplankton and bacteria may respond independently to TP.

We did not observe a significant relationship between bacterial abundance and DOC. This contrasts with many lake studies in which a positive DOC-bacteria relationship has been observed (Tranvik 1989, Berninger et al. 1991, Tzaras & Pick 1994). A relation-

Fig. 2. Significant relationships between (A) heterotrophic bacterial abundance and heterotrophic flagellate abundance [Model I (shown); $\log \text{flagellate abundance} = -4.62 + 1.31 \log \text{bacterial abundance}$, Model II; $\log \text{flagellate abundance} = -8.98 + 1.98 \log \text{bacterial abundance}$] and (B) total phosphorus (TP) concentration and heterotrophic flagellate abundance [Model I (shown); $\log \text{flagellate abundance} = 3.11 + 0.66 \log \text{TP}$, Model II; $\log \text{flagellate abundance} = 2.85 + 0.97 \log \text{TP}$] for rivers sampled during July 1994. Dashed lines represent 95% confidence intervals

ship between bacterial abundance and DOC may only be evident when a high fraction of total DOC is labile and available for bacterial consumption. In rivers, a large proportion of total DOC may be refractory and unavailable for bacterial use. Most of this non-labile DOC could be of allochthonous, terrestrial origin (e.g. vascular plant detritus) (Findlay et al. 1991). Up to 70%

of total DOC inputs to streams is refractory to bacterial degradation (Wetzel & Manny 1977). Sabater et al. (1993) concluded that there was a good correspondence between low molecular weight (MW) DOC and bacterial abundance. They suggested that low MW fractions of DOC are more readily utilized by bacteria and that uptake of medium and high MW DOC fractions is slower and possibly inhibitory. In our study rivers, a large proportion of total DOC may have been of a high MW, refractory nature, unavailable for bacterial use.

A positive relationship was observed between heterotrophic flagellate and bacterial abundance. Berninger et al. (1991) observed similar results across a range of freshwater environments. The positive correlation between flagellates and bacteria may be indicative of a predator-prey relationship as heterotrophic flagellates are the primary consumers of bacteria in freshwaters (Porter et al. 1985). However, other studies have concluded that in lakes the relationship between flagellates and bacteria is often weak or eliminated due to metazoan grazing on the flagellates (Gasol & Vaqué 1993, Tzaras & Pick 1994). Because zooplankton biomass was often very low in the rivers, there may have been little grazing of flagellates by metazoans. Instead, resource control of flagellates by bacteria may have dominated.

We also observed a positive relationship between flagellates and TP. Bacterial turnover can be very rapid and standing stock of bacteria may be a poor indicator of actual supply rates of bacteria to flagellates (Tzaras & Pick 1994). Since P may partially regulate bacterial growth, TP may represent a less variable measure of bacterial supply rates to heterotrophic flagellates. Alternatively, the positive relationship between flagellates and TP may result from protozoans directly responding to nutrients, though this possibility remains little explored (Pace & Funke 1991).

We observed no effect of water residence time on heterotrophic bacterial or flagellate abundances though water residence time significantly influenced zooplankton biomass (Basu & Pick 1996). As water residence time increased both rotifer and crustacean zooplankton biomass increased. The relatively long generation time of zooplankton (days to weeks) makes them more susceptible to advective loss in short residence systems (Pace et al. 1992, Basu & Pick 1996). In comparison, the generation times of bacteria and protists are much shorter (hours to days). The average water residence time at the river sites was 7.3 d and the minimum was 3.3 d. This appeared to be sufficient time for bacteria and protozoans to develop in the rivers as no relationship with residence time was observed.

The limitation of zooplankton development due to short water residence times meant that zooplankton

biomass in the rivers was low (mean = $11.3 \mu\text{g l}^{-1}$ dry mass of total zooplankton). In addition, the dominant zooplankton in the rivers were rotifers and small crustaceans (e.g. *Bosmina* sp.). Large cladocerans such as *Daphnia* sp. (which can exert significant grazing pressure on flagellates; Pace & Funke 1991) were much less abundant. The lack of any relationship between zooplankton biomass and either flagellate or bacterial abundance may be due to these low levels of biomass and the dominance of small taxa.

As mentioned, this contrasts with studies conducted on lakes and estuaries in which zooplankton grazing was observed to have significant effects on flagellate and bacterial abundances (Dolan & Gallegos 1991, Pace & Funke 1991, Gasol & Vaqué 1993). In lakes the microbial loop may be coupled to the classical food web, with metazoan grazing of flagellates and bacteria serving as the link. In rivers, however, with low zooplankton abundance, there may be little transfer of energy from the planktonic microbial food web to planktonic metazoans. Instead, the major importance of the microbial loop in temperate rivers may be the remineralization of organic matter into small nutrient molecules (CO_2 , PO_4^{3-} , NH_4^+) (Goldman & Caron 1985).

At present, the study of river food webs lags a decade behind that of lake food webs. Our conclusions with respect to the importance of the microbial loop to higher trophic levels and nutrient remineralization remain speculative and we did not account for possible temporal variation in microbial abundances and processes. Furthermore, our results may only be applicable to north temperate rivers of moderate size, not to larger rivers or rivers in tropical or arctic climates.

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