Phytoplankton and zooplankton development in a lowland, temperate river

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Abstract. The longitudinal and seasonal patterns of plankton development were examined over 2 years in a lowland, temperate river: the Rideau River (Ontario, Canada). Following an initial decrease in phytoplankton and zooplankton biomass as water flowed from the headwaters into the Rideau River proper, there was an increase in chlorophyll *a* (chl *a*) and zooplankton biomass with downstream travel. At approximately river km 60, both phytoplankton and zooplankton reached their maximum biomass of 27 µg l^{-1} (chl *a*) and 470 µg l^{-1} (dry mass), respectively. Downstream of river km 60, the biomass of both planktonic communities declined significantly despite increasing nutrient concentrations and favorable light conditions. These downstream declines may be due to the feeding activity of the exotic zebra mussel (*Dreissena polymorpha*) which was at high density in downstream reaches (>1000 individuals m^{-2}). There was no evidence for longitudinal phasing of phytoplankton and zooplankton, as increases and decreases in chl *a* and zooplankton biomass appeared to coincide. Overall, chl *a* was best predicted by total phosphorus ($R^2 = 0.43$), whereas zooplankton biomass was best predicted by chl *a* ($R^2 = 0.20$). There was no evidence for significant grazing effects of zooplankton on phytoplankton biomass.

Introduction

Planktonic organisms can attain significant densities in large lowland rivers where residence times and low flow rates allow sufficient time for growth and reproduction (Margalef, 1960; de Ruyter van Steveninck *et al.*, 1990a). However, little research has focused on the regulation of phytoplankton and zooplankton development and the interactions between these two communities in rivers (Reynolds, 1988; Köhler, 1993; Thorp *et al.*, 1994).

The factors regulating river plankton abundance may be hydrological (discharge, water residence time), chemical (nutrient concentrations), physical (light conditions) and biotic (grazing, competition) (Reynolds, 1988; Moss *et al.*, 1989). An inverse correlation between phytoplankton biomass and river discharge has been demonstrated (Jones, 1984; Jones and Barrington, 1985; Reynolds, 1988). Other researchers have concluded that river phytoplankton is more strongly regulated by nutrient concentrations. A significant positive relationship between river phytoplankton abundance and total phosphorus concentration has been observed (Soballe and Kimmel, 1987; Moss *et al.*, 1989; Basu and Pick, 1996; Van Nieuwenhuyse and Jones, 1996).

Owing to the turbulent and often turbid conditions found in many rivers, light conditions may regulate river phytoplankton development (Krogstad and Lovstad, 1989; Cole *et al.*, 1992). In deep sections of rivers, when the depth of mixing is greater than the depth of the photic zone, it is possible that algal cells are exposed to light levels below the threshold for net growth (Lewis, 1988; Cole *et al.*, 1992).

In comparison to phytoplankton, there has been less attention devoted to the zooplankton of rivers. Pace *et al.* (1992) and Thorpe *et al.* (1994) observed zooplankton abundance to be negatively correlated with river discharge in the

Hudson and Ohio rivers (USA), respectively. Similarly, Basu and Pick (1996) observed that across a range of 31 rivers in Ontario, Canada, zooplankton biomass was positively related to water residence time. In addition, to what extent zooplankton impact algal communities in rivers remains little explored.

The present study examines the development of phytoplankton and zooplankton longitudinally and seasonally within a temperate, lowland river (Rideau River, Ontario, Canada). Our previous work on the Rideau (Basu and Pick, 1995) indicated extensive longitudinal changes in phytoplankton biomass. The objectives of this study were: (i) to describe the longitudinal and seasonal pattern of both phytoplankton and zooplankton development; (ii) to determine the factors most strongly related to phytoplankton biomass; (iii) to determine the factors most strongly related to zooplankton biomass. Variables measured included chlorophyll *a* (chl *a*), crustacean zooplankton biomass, rotifer biomass, nutrient concentrations, river discharge, light attenuation, depth and temperature. Invasion of the Rideau River by the exotic zebra mussel (*Dreissena polymorpha*) occurred in 1990 and densities have increased since (1990–1995) (Martel, 1995). Therefore, we also evaluated the potential effect that this benthic suspension feeder could have on plankton biomass.

Method

Study area

The Rideau River is located in southeastern Ontario and flows northeast for 110 km from its headwaters in Lower Rideau Lake before discharging into the Ottawa River at Ottawa (45°27′N, 75°42′W) (Figure 1). The average annual discharge of the Rideau is 38.9 m^3 s^{-1} and the watershed area at Ottawa is 3830 km^2 (Water Survey of Canada, 1990). Being lake fed, discharge does not change appreciably along the Rideau's length and there are only a few small tributaries. In summer, when river discharge is ~10 m^3 s^{-1}, it takes 15 days for water to travel from Lower Rideau Lake to the mouth of the Rideau (B.K.Basu, unpublished data). Approximately 70% of the watershed area is agricultural land, the remainder is either forested or urban (Davidson, 1990). The primary uses of the river are for recreation and water supply, and there are no major industries located along the Rideau's course.

Once month, from May to October 1994 and May to September 1995, the Rideau was sampled at 15 sites. Site 1 was located in the headwaters, while sites 2–15 were located within the river proper, upstream from the city of Ottawa. The sites were evenly spaced ~7 km apart (Figure 1).

Field sampling

Water samples were taken mid-channel using a 4 m vertically integrated tube and it was assumed that the water column was vertically homogeneous (Basu and Pick, 1995). Five 2 l samples were taken for algal chl *a* and three 300 ml samples were taken for measurement of total phosphorus (TP), soluble reactive phosphorus (SRP) and total nitrogen (TN) concentrations. For chl *a*, water samples were
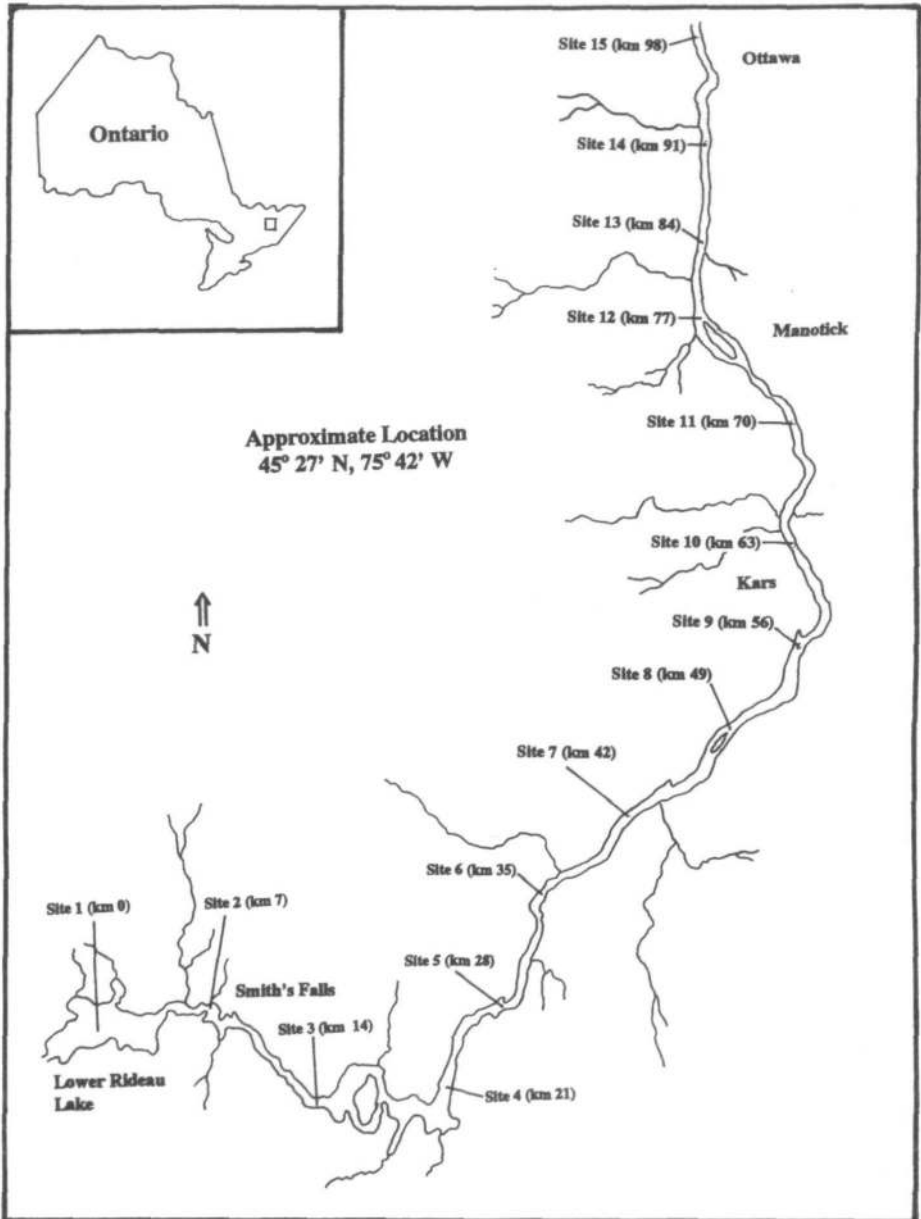
238

Fig. 1. Location of sampling sites (numbered 1–15) in the Rideau River, Ontario. Distances in parentheses refer to the number of kilometers downstream from site 1 in Lower Rideau Lake (km 0).

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 and Humphrey (1975). Chemical analysis to determine TP, SRP and TN

concentrations was performed at the Regional Municipality of Ottawa-Carleton, Water Quality Laboratories by standard methods (Basu and Pick, 1995).

Zooplankton were sampled mid-channel at sites 1, 3, 5, 7, 9, 12 and 14 following methods described in Basu and Pick (1996). Triplicate macrozooplankton (clado-cerans and copepods) samples were collected by pumping 30 l of water through a 64 μm Nitex mesh plankton net. Triplicate microzooplankton (rotifers) samples were collected by filtering 4 l through a 35 μm Nitex mesh screen. Samples were preserved with 4% formalin–sucrose (Haney and Hall, 1975).

Zooplankton abundance was determined by enumerating either whole samples or counting at least 120 individuals in subsamples of each replicate. Cladocerans and copepods were counted under a dissecting microscope (50×), and rotifers under an inverted microscope (80×). Crustaceans and rotifers were identified to genus level following Thorp and Covich (1991) and Stemberger (1979). Biomass estimates for crustaceans and rotifers were determined using methods described in Basu and Pick (1996). Total zooplankton biomass (dry mass) was the sum of crustacean and rotifer biomass.

Depth was measured with an LCR 400ID depth sounder (Marine Information, USA) and temperature was measured with a mercury thermometer. Light attenuation coefficients were calculated using irradiance measurements obtained with a Li-Cor 185B 4π underwater photometer (Li-Cor, USA). Euphotic depth (1% light level) to mixing depth ratios were calculated using attenuation coefficients and assuming that mixing depth was equivalent to the total depth. The shallow depth of the Rideau (usually 3–5 m) justified this assumption.

Discharge values were obtained from the Water Survey of Canada, which maintains a continuous gauging site at Ottawa. Discharge was calculated as the average of the daily discharges for the period 7 days prior to and including the sampling date (Pace *et al.*, 1992; Basu and Pick, 1995).

Statistical analysis

Statistical analysis was performed using Systat 5.03 (Systat Inc., USA, 1993) software. Polynomial regression was used to quantify longitudinal patterns of variables. The inclusion of site 1 (Lower Rideau Lake, km 0) during polynomial regression analysis created significance at third- and fourth-order levels. Therefore, because site 1 was not located in the Rideau River proper and the most parsimonious regression models were desired, we did not include site 1 during the derivation of equations. Linear regression and correlation were used to identify relationships between variables. All parametric tests performed satisfied the assumptions of normality and homoscedasticity following any required logarithmic transformation of the data.

Results

Longitudinal and seasonal development of chlorophyll a

The longitudinal patterns in chl *a* for the sampling months of 1994 and 1995 are shown in Figure 2. In all months for both 1994 and 1995, there was a decrease in

chl *a* as the water flowed from site 1 (Lower Rideau Lake, km 0) into the Rideau River proper at site 2 (km 7). With the exception of May 1994, October 1994 and July 1995, the subsequent development of chl *a* along the river proper could be described using a second-order polynomial including km and km^2 terms as significant independent variables. Chl *a* increased with downstream travel, peaked, and then decreased (Figure 2). The longitudinal kilometer at which the peak in chl *a* occurred ranged from km 54 to km 76 and was most often located near km 60 (Figure 2). To obtain the most general second-order polynomial describing the longitudinal development of chl *a* in the Rideau, the data from all the months (of second order) were combined and an overall second-order equation derived (chl $a = -1.29 + 0.47$ km $- 0.004$ km^2, $P = 0.001$, $R^2 = 0.35$). Using this equation, we estimated that peak chl *a* occurred at km 59.3.

The longitudinal pattern of chl *a* in May 1994 and October 1994 was best described using a first-order (simple linear) regression. In these months, chl *a* continued to increase with downstream travel (Figure 2). The longitudinal pattern of chl *a* for July 1995 was not predictable even upon trial of a tenth-order polynomial (Figure 2).

Longitudinal and seasonal development of zooplankton biomass

The longitudinal development of zooplankton biomass in the Rideau River could not be described using polynomial regressions ($P > 0.05$ for all months up to fifth order). However, several patterns were repeated from month to month and across years (Figure 3). For all months of both 1994 and 1995, there was a decrease in total zooplankton biomass from site 1 (Lower Rideau Lake, km 0) to the first riverine zooplankton sampling site (site 3, km 14). This decrease in zooplankton biomass was often very large (e.g. August 1994, June 1995) (Figure 3).

Following this initial decrease, zooplankton biomass tended to increase downstream (Figure 3). After peaking at site 9 (km 56) or site 12 (km 77), zooplankton biomass usually fell, often with very low levels recorded at site 14 (km 91).

Longitudinal and seasonal trends in nutrient concentrations

The longitudinal pattern in TP for the sampling months of 1994 and 1995 is shown in Figure 4. In contrast to the second-order pattern exhibited by chl *a*, the longitudinal trend in TP for most months was a simple linear increase in TP with downstream travel (Figure 4). Seasonally, TP tended to be higher in the summer months (June, July and August) (Figure 4).

In comparison to TP, longitudinal and seasonal patterns in SRP were less evident. SRP was low (<10 μg l^{-1}) along most of the Rideau, but increased at sites 13 (km 84), 14 (km 91) and 15 (km 98). At these downstream sites, SRP was often >20 μg l^{-1}. As with SRP, identifiable longitudinal or seasonal patterns in TN were difficult to establish. Gradual increases in TN were sometimes observed, as were high concentrations at sites 13 (km 84), 14 (km 91) and 15 (km 98) for several months (>1000 μg l^{-1}).
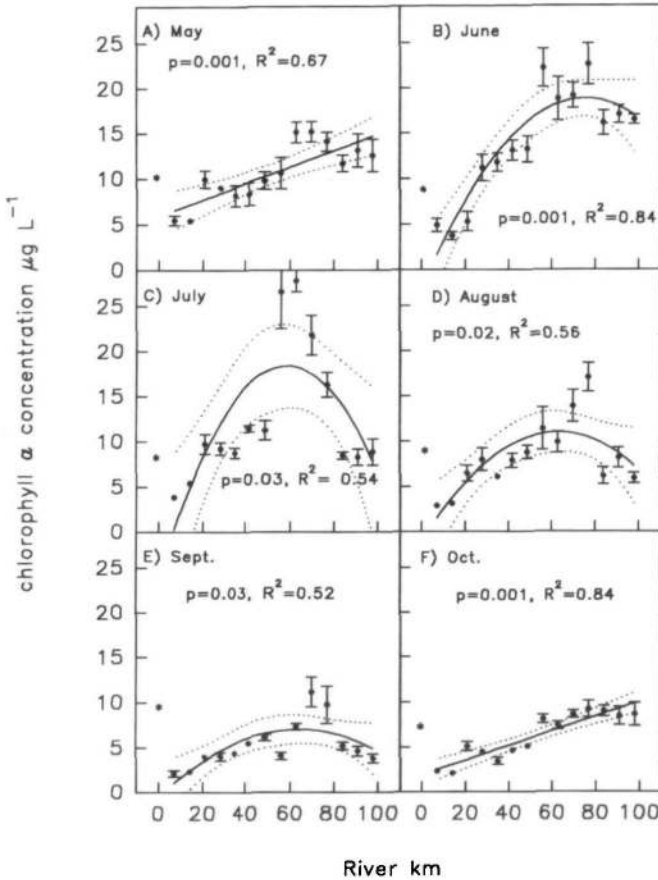
Fig. 2. Longitudinal pattern of chl *a* concentration in the Rideau River for the sampling months of 1994 (**A–F**) and 1995 (**G–K**). Plotted are means for each site ± 1 SD. Significant first- or second-order regressions between chl *a* and river km are indicated by solid lines with 95% confidence intervals (dotted lines). Site 1 (Lower Rideau Lake, km 0) was not included in the regression analysis (see the text) and is represented by an asterisk (*).

Hydrological and physical variables

In the Rideau River, high discharges (>150 m^3 s^{-1}) associated with spring snow melt were followed by lower and more stable discharges (10–20 m^3 s^{-1}) throughout the summer and fall (Basu and Pick, 1995). Water temperatures for both 1994 and 1995 also showed the expected seasonal trend with the maximum temperature recorded in July of both years (~25°C). Only in May and October of 1994 were water temperatures below 10°C. Longitudinal differences in temperature were <2°C.

The euphotic depth to mixing depth ratio for all sites and all dates in the Rideau was usually >0.6 ($Z_{eu}:Z_m$ > 0.6 for 153 out of 165 observations) and, due to the shallow depths, often the entire water column was euphotic ($Z_{eu}:Z_m \geq 1.0$). $Z_{eu}:Z_m$ was never below 0.4.
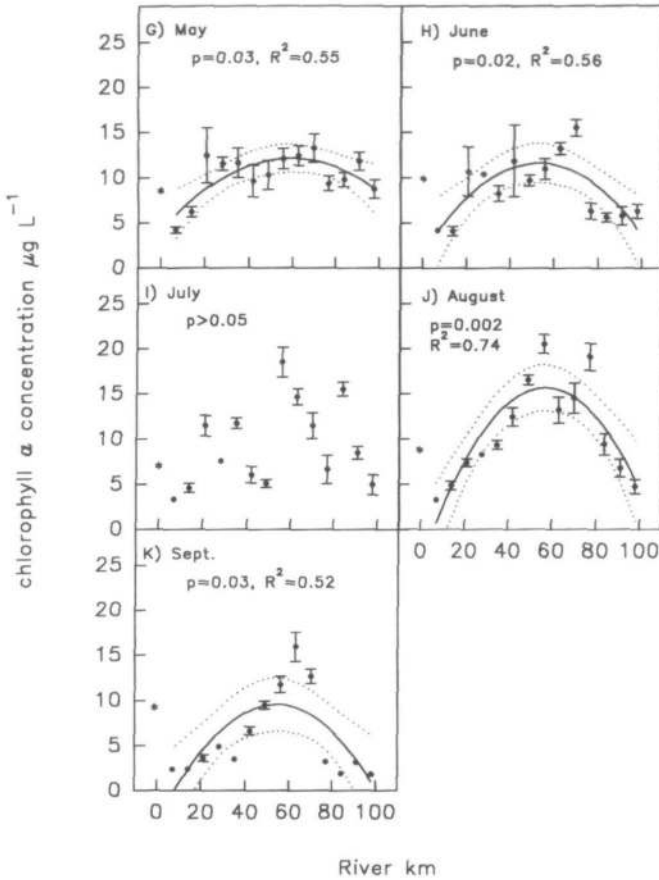
Fig. 2. Continued.

Determinants of algal and zooplankton biomass

Chl *a* concentration in the Rideau River for 1994 and 1995 was best predicted using a simple linear regression including TP concentration as the only independent variable (Figure 5). Log chl *a* was also significantly related to log TN in 1994 ($P = 0.001$, $R^2 = 0.13$), but not in 1995 ($P = 0.32$). In neither year was log chl *a* significantly related to log SRP concentration (for 1994, $P = 0.12$; for 1995, $P = 0.06$). We did not derive a multiple regression equation predicting chl *a* from all the nutrient variables due to high multicollinearity between TP and TN ($P = 0.001$, $R = 0.72$), TP and SRP ($P = 0.001$, $R = 0.54$), and SRP and TN ($P = 0.001$, $R = 0.56$).

Chl *a* was not significantly related to temperature (for 1994, $P = 0.57$; for 1995, $P = 0.25$) and mean chl *a* for each month was not related to discharge for each month (for 1994, $P = 0.10$; for 1995, $P = 0.89$).

In both 1994 and 1995, zooplankton biomass in the Rideau was best predicted using a simple linear regression including chl *a* as the independent variable (Figure 6). Zooplankton biomass was not significantly related to TP in either year
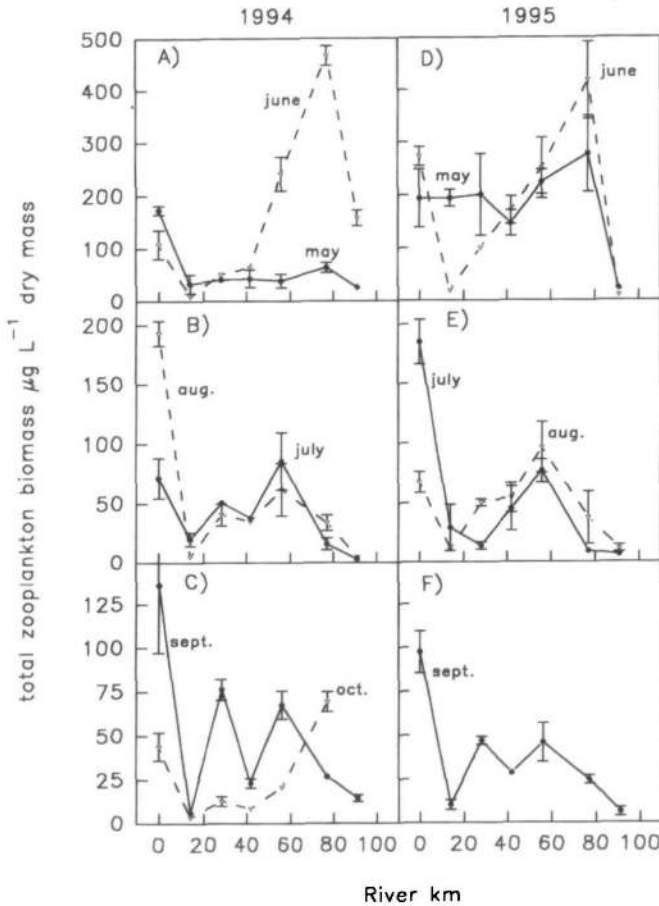
243

Fig. 3. Longitudinal pattern of zooplankton biomass in the Rideau River for the sampling months of 1994 (**A–C**) and 1995 (**D–F**). Plotted are means ± 1 SD. Note the change in scale between panels (y-axis). (Data for site 14, October 1994, were not available.)

(for 1994, $P = 0.37$; for 1995, $P = 0.58$). Zooplankton biomass was also not significantly related to temperature (for 1994, $P = 0.95$; for 1995, $P = 0.52$) and mean monthly zooplankton biomass was not significantly related to discharge (for 1994, $P = 0.15$; for 1995, $P = 0.67$).

Discussion

There was a distinct longitudinal pattern in chl a within the Rideau River. The initial decrease in chl a as water flowed from Lower Rideau Lake into the river proper has been previously observed (Basu and Pick, 1995). Other researchers have observed similar decreases in algal biomass during such lentic to lotic transitions. Köhler (1993) suggests that algae that develop in lentic waters are ill-suited to lotic conditions and Uehlinger (1993) observed that phytoplankton

244

flowing out of a lake incurred physiological damage upon entering a river. Dense growths of macrophytes at the outflow of Lower Rideau Lake may also contribute to losses of phytoplankton by intercepting and enhancing sedimentation of algae (Talling and Rzoska, 1967) and providing a favorable habitat for herbivores.

Following the initial decrease in algal biomass, chl a increased with downstream travel until concentrations peaked at km 60 (site 10). Downstream increases in algal biomass have been observed in many other rivers (Greenberg, 1964; Capblancq and Descamps, 1978; Jones, 1984; Descy et $al.$, 1987; de Ruyter van Steveninck et $al.$, 1990a,b) and generally these increases have been associated with an increased time available for plankton to develop. However, nutrient concentrations in rivers also increase downstream (Jones, 1984; Moss et $al.$, 1984; Jones and Barrington, 1985; Garnier et $al.$, 1995). Total phosphorus in the Rideau continued to increase along its course, while maximum SRP and TN values were recorded at the most downstream sites. Downstream increases in nutrients may be attributed to continuous loading from agricultural and municipal sources, as well as a high degree of association between the river and its watershed. Therefore, increasing algal biomass in the Rideau with downstream travel is not surprising, given that increasing time for development coincides with increasing nutrient concentrations. However, from km 60 to km 98, chl a decreased in most months. This decrease occurred despite a lengthening residence time and still increasing nutrient concentrations. What factors may have contributed to the decrease in algal biomass downstream of km 60?

Cole et $al.$ (1992) concluded that in deep sections of the turbid Hudson River (USA), the depth of mixing was greater than the depth of the euphotic zone (Z_{eu}:Z_m ~0.2). This resulted in phytoplankton cells remaining below the 1% light level long enough to make net algal growth impossible. Alpine and Cloern (1988) suggested that light limitation should be considered when Z_{eu}:Z_m is <0.2. In the Rideau, Z_{eu}:Z_m was usually >0.6 and, due to shallow depths (3–5 m), often the entire water column was euphotic. Light limitation of phytoplankton growth in the Rideau was unlikely.

It has been observed that grazing by zooplankton may contribute to decreases in phytoplankton biomass in the downstream reaches of large rivers (Descy et $al.$, 1987; de Ruyter van Steveninck et $al.$, 1990a,b; Gosselain et $al.$, 1994). De Ruyter van Steveninck et $al.$ (1990a) suggested that plankton communities in rivers are 'spatially phased'. River phytoplankton with a higher intrinsic rate of growth will develop further upstream, while zooplankton will lag behind phytoplankton and develop further downstream. Significant grazing may then occur once a high biomass of zooplankton has developed.

In the Rideau, however, there was no evidence for phasing of the plankton communities. The pattern of zooplankton development resembled the pattern of chl a with no lags observed. Zooplankton biomass decreased as water flowed from Lower Rideau Lake to km 14 (site 3) within the river proper. This decrease may be associated with the lentic to lotic transition, as discussed with respect to phytoplankton. A true river zooplankton community then developed in the Rideau, as there was an increase in zooplankton biomass as water flowed downstream. This increase in zooplankton was followed by large downstream decreases in biomass.
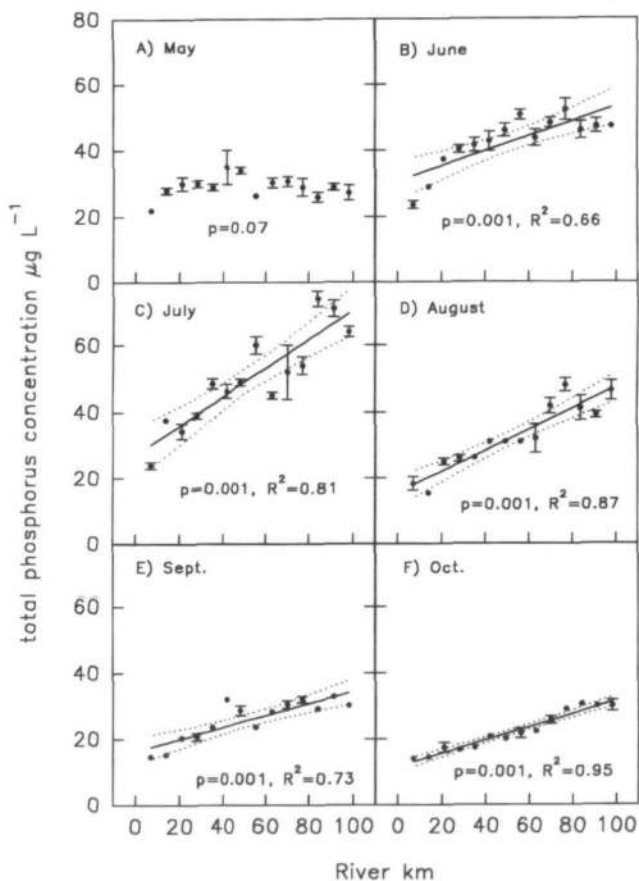
Fig. 4. Longitudinal pattern of TP concentration in the Rideau River for the sampling months of 1994 (**A–F**) and 1995 (**G–K**). Plotted are means for each site ± 1 SD. Significant first- or second-order regressions between TP and river km are indicated by solid lines with 95% confidence intervals (dotted lines). Note the change in scale between panels (*y*-axis).

In order for zooplankton grazing to contribute significantly to the decrease in chl *a* a high biomass of zooplankton at the downstream sites would be required (de Ruyter van Steveninck *et al.*, 1990a,b). Instead, we observed decreases in zooplankton biomass downstram of km 60 and the zooplankton community was dominated by rotifers and small crustaceans (e.g. *Bosmina* sp.). Large zooplankton with high filtration capacities (e.g. *Daphnia* sp.) were much less abundant (mean *Daphnia* sp. biomass at river sites 12 and 14 was 17.2 μg l^{-1} dry mass).

To determine the potential impact of zooplankton grazing in the downstream reaches of the Rideau, theoretical filtration rates were multiplied by zooplankton densities. The densities of crustaceans and rotifers were calculated as the mean densities from site 12 and site 14 for both 1994 and 1995. For a mean density of 65 individuals l^{-1} and a mean filtration rate of 1 ml individual^{-1} day^{-1} (Knoechel and Holtby, 1986; Mazumder *et al.*, 1992), crustacean zooplankton could filter 6.5% of
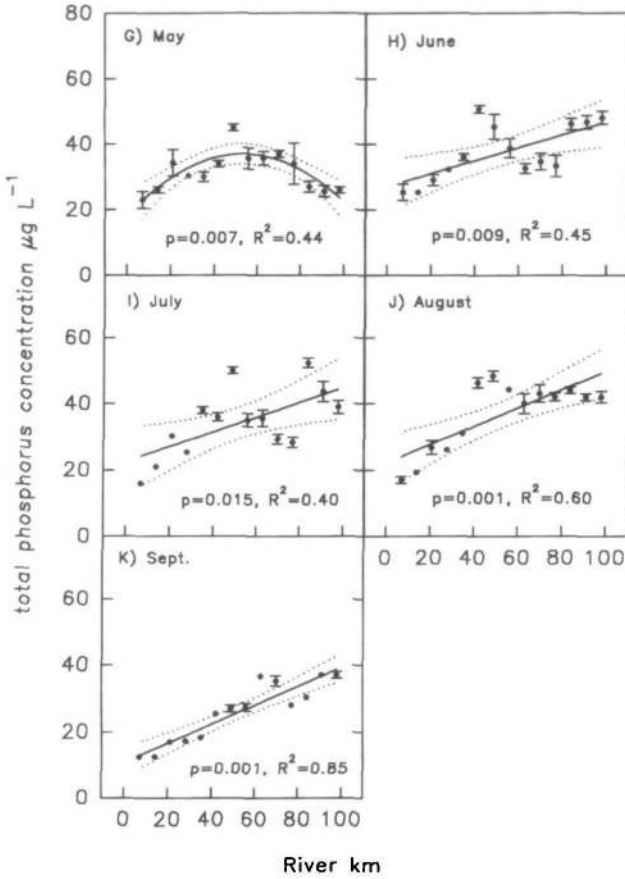
246

Fig. 4. Continued.

the water column per day. Rotifers, with a mean density of 500 individuals l⁻¹ and a mean filtration rate of 60 μl individual⁻¹ day⁻¹ (Mazumder *et al.*, 1992), could filter 3% of the water column per day. This level of filtration was unlikely to have caused the substantial decrease in phytoplankton biomass. What factors may have contributed to the decreases in both algal biomass and zooplankton biomass downstream of km 60?

There is a distinct longitudinal pattern in the distribution of *D.polymorpha* within the Rideau (Martel, 1995). In both 1994 and 1995, low densities were recorded upstream, whereas densities downstream (km 60–98) were several orders of magnitude higher (Figure 7) (Martel, 1995; A.Martel, unpublished data). This pattern may be attributed to an increased availability of rocky substrates in the downstream reaches of the Rideau (Martel, 1995).

To address the possibility that the downstream colonization of the Rideau by zebra mussels was the major factor which contributed to the decrease in chl *a* and zooplankton biomass, we assumed that: (i) the average density of zebra mussels
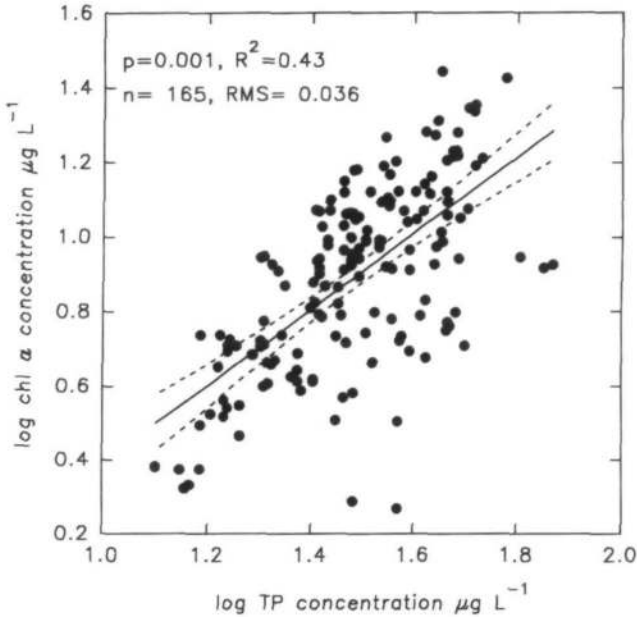
247

Fig. 5. Relationship between chl *a* concentration and TP concentration for the Rideau River (combined 1994 and 1995 data) (log chl *a* = –0.62 + 1.02 log TP). The dashed line indicates the 95% confidence interval.
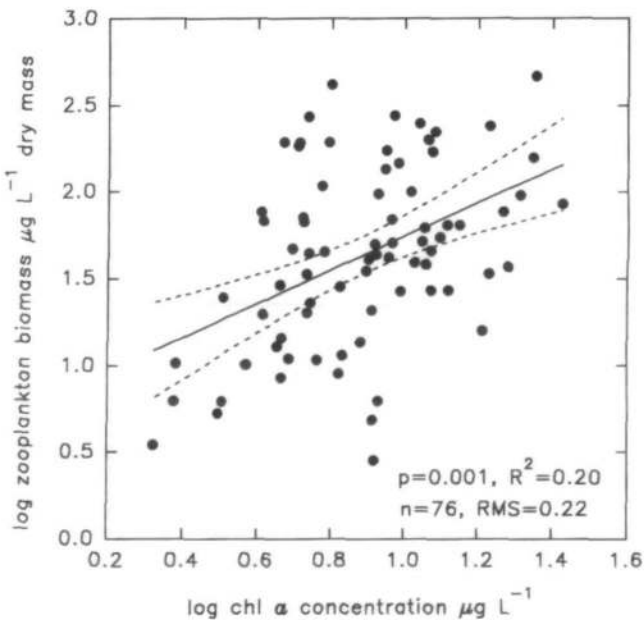
Fig. 6. Relationship between zooplankton biomass and chl *a* concentration for the Rideau River (combined 1994 and 1995 data) (log zooplankton biomass = 0.76 + 0.97 log chl *a*). The dashed line indicates the 95% confidence interval.
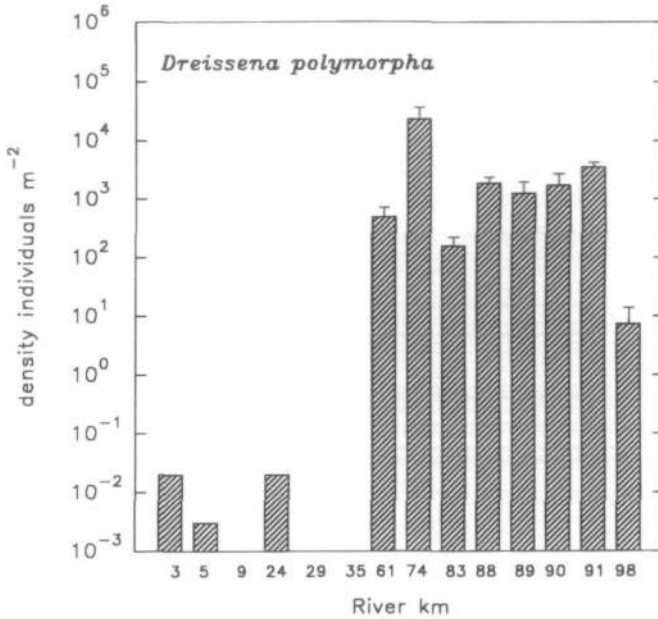
Fig. 7. Longitudinal pattern of the density of *D.polymorpha* in the Rideau River in 1994 (mean ± 1 SD). Data from Martel (1995) replotted. Note that the *x*-axis is not to scale.

from km 60 to km 98 was 1200 individuals m^{-2} (Martel, 1995); (ii) the average filtration rate was 1 l individual^{-1} day^{-1} (Kryger and Riisgard, 1988; MacIsaac *et al.*, 1992; Leach, 1993); and (iii) the coverage of total benthic area was 25%. Based on these assumptions, the zebra mussel community could theoretically filter 14.5 m^3 s^{-1}. Therefore, a substantial percentage of total river discharge could be filtered from km 60 to km 98 (Table I). On an aereal basis, zebra mussels could filter 1.2 m^3 m^{-2} day^{-1}, which assuming a 3 m water column, is ~40% day^{-1}. Such high filtration capacities have often been reported for *D.polymorpha* populations. MacIsaac *et*

Table I. Proportion of Rideau River discharge filtered from km 60 to km 98 given a zebra mussel community filtration capacity of 14.5 m^3 s^{-1} (see the assumptions in the text). Discharges are means for the period 7 days prior to and including the sampling date (see Method)

Month	River discharge (m^3 s^{-1})	Proportion filtered (%)
May 1994	47.0	30
June 1994	46.3	31
July 1994	21.3	68
August 1994	17.0	85
September 1994	9.4	100+
October 1994	19.2	76
May 1995	16.1	90
June 1995	30.6	47
July 1995	4.0	100+
August 1995	30.4	48
September 1995	2.6	100+

249

al. (1992) calculated that a 7 m water column in Lake Erie could be filtered between 3.5 and 18.8 times per day, and Reeders *et al.* (1989) reported that the entire contents of two Dutch lakes could be filtered in ~15 days. Our results indicate that downstream in the Rideau, zebra mussels have a filtration impact four times greater than that of the zooplankton community (40% day^{-1} versus 10% day^{-1}).

As has been reported many times, chl *a* can be severely depleted in the presence of *D.polymorpha* beds (Reeders and Bij de Vaate, 1990; MacIsaac *et al.*, 1992; Leach, 1993). *Dreissena polymorpha* can decrease zooplankton biomass through competition with zooplankton for suspended algal food resources, and results from Ten Winkel and Davids (1983), Sprung and Rose (1988), MacIsaac *et al.* (1991) and Bunt *et al.* (1993) suggest that zebra mussels can also be direct predators on rotifers and small crustaceans.

The filtering impacts of zebra mussels should be greatest in shallow, well-mixed water columns due to increased contact between the benthic filter feeders and suspended food particles (Bunt *et al.*, 1993). In the downstream sections of the Rideau, warm, shallow, well-mixed waters with rocky substrates appear to be a favorable habitat for zebra mussels. Given that densities of *D.polymorpha* increased substantially in 1995 (often over 50 000 individuals m^{-2}) (A.Martel, unpublished data), it seems likely that zebra mussel filtration contributed to the decrease in phytoplankton and zooplankton biomass downstream of km 60.

In May and October 1994, a decrease in chl *a* downstream of km 60 was not observed (Figure 2). In these months, water temperatures were <10°C. A positive linear relationship between bivalve filtration and temperature has been demonstrated (Jorgenson, 1990; Fisher *et al.*, 1993). It is possible that in May and October 1994 filtration rates of the resident *D.polymorpha* community were not high enough to cause a decrease in biomass and chl *a* continued to increase downstream.

Previous work on the Rideau and other rivers has demonstrated that algal biomass can be predicted from TP (Soballe and Kimmel, 1987; Moss *et al.*, 1989; Basu and Pick, 1995; Van Nieuwenhuyse and Jones, 1996). Although benthic grazing may have created conditions of low chl *a* despite high TP in the downstream reaches of the Rideau, overall, chl *a* was still best predicted by TP in 1994 and 1995 [as in 1993 (Basu and Pick, 1995)]. The low coefficient of determination for the TP-chl *a* relationship ($R^2 = 0.43$), however, indicates that additional factors, such as benthic filtration, may also regulate algal biomass in the Rideau River.

We did not observe a negative relationship between chl *a* and river discharge as has been reported in other studies (summarized by Reynolds, 1988). This may be due to a limited range of discharges over which sampling occurred. We sampled when the Rideau was open for navigation during the relatively low discharge period from May until October. These conditions always appear favorable for plankton development (Basu and Pick, 1995).

Despite the possible influence of zebra mussel filtration on zooplankton in the Rideau, zooplankton biomass was best predicted by chl *a*. No significant relationship between zooplankton biomass and discharge was observed. The positive relationship between chl *a* and zooplankton biomass is indicative of a resource

effect of phytoplankton on zooplankton. The low coefficient of determination for the chl *a*-zooplankton relationship, however, indicates that additional factors (e.g. benthic filtration) may regulate zooplankton biomass.

There was no evidence for significant grazing of phytoplankton biomass by zooplankton in the Rideau. In general, the biomass of zooplankton in rivers tends to be lower than in lakes (Basu and Pick, 1996). Furthermore, river communities tend to be dominated by smaller taxa (e.g. rotifers, nauplii and bosminids), with larger taxa (e.g. daphnids, calanoid copepods) much less abundant (Shiel *et al.*, 1982; Ferrari *et al.*, 1989; Pace *et al.*, 1992; Thorp *et al.*, 1994). As a result, significant grazing effects of zooplankton on phytoplankton may not occur with regularity in rivers.

Acknowledgements

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