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Use of size spectra and empirical models to evaluate trophic relationships in streams

Abstract—We measured the biomass size distributions of algae, protozoa, and invertebrates in several streams of Eastern Ontario and Western Québec and related assemblage biomass to nutrient (nitrogen and phosphorus) concentrations in the water. Size spectra and measurement of periphytic chlorophyll were then combined with existing empirical models to estimate primary production, invertebrate production, and grazer removal, to examine herbivory in these natural assemblages. In general, biomass of organisms increased with nutrients but the response of invertebrates was stronger than that of algae and protozoans. Secondary production (range 1.7%–4.2%) and algal removal by grazers (range 62%–175%) were high relative to primary production. This suggests that grazers exert top-down control on algae in these streams and that increases in nutrient inputs to oligo- and mesotrophic streams may benefit consumers more than primary producers.

Production and consumption rates are notoriously difficult to quantify for natural stream communities because of their taxonomic richness and complexity. Consequently, our knowledge of trophic interactions, such as herbivory in natural communities, derives mostly from short-term controlled experiments, in the laboratory or in the field, where grazers or periphyton are manipulated (Rosemond et al. 1993; Feminella and Hawkins 1995). Because controlled experiments are subject to artifacts and tend to be performed at small spatial and temporal scales, extrapolation of experimental results to real systems remains tentative. Only measurements on natural systems can confirm predictions derived from experiments.

The recent publication of empirical models predicting primary production from periphytic chlorophyll and temperature, and of allometric models of secondary production and algal removal rate by benthic invertebrates, has prompted us to integrate these models with size-based description of stream communities to obtain estimates of production and grazing pressure in unmanipulated stream communities. Such estimates for naturally occurring communities could be used to test hypotheses concerning herbivory (Oksanen et al. 1981; Cyr and Pace 1993) that, in streams, have usually been addressed in experimental settings.

We measured the size spectra of algae, protozoans, and invertebrates in nine streams of Eastern Ontario and Western Québec, covering the trophy gradient typical of the region. In this study, we quantify how biomass of these three groups vary with nutrients. We then combine measurements of periphyton chlorophyll and invertebrate size spectra with empirical equations predicting primary production (Morin et al. 1999), secondary production (Morin and Dumont 1994), and algal removal rate (Cattaneo and Mousseau 1995) by these

communities to describe how herbivore pressure varies along a trophic gradient.

The study was performed in nine sites on eight streams in Eastern Ontario and Western Québec (45°N, 75°W), spanning the regional range of trophic conditions (Table 1). Sampling took place over a 3-d period in June 1992 ~5 weeks after high spring discharge. Total phosphorus (TP) concentration in the water was estimated after potassium persulfate digestion under pressure (Menzel and Corwin 1965), and total nitrogen (TN) concentration was determined by the method of Raimbault and Slawik (1991). At each site, we sampled each of the four or five substrate categories present (sand, 0.25–2 mm particle diameter; fine gravel, 2–8 mm; gravel, 8–32 mm; cobble, 32–128 mm; and boulder, >128 mm).

Six replicate samples were collected on each sampled substrate in each station, to describe invertebrate abundance and size distribution. Sand and gravel substrates were sampled with a modified Hess sampler (Mackie and Bailey 1981), 10 cm in diameter, with a net mesh of 63 μm . The first 5 cm of substrate was collected. Cobbles were simply lifted and placed in bags. Larger boulders were placed in a tray, measured and brushed clean, and the material collected was then sieved (63 μm). Invertebrates were sorted under a dissecting microscope at 25 \times . When samples contained >200 individuals, they were separated into two fractions (>1 mm and 63 μm –1 mm) by use of sieves. The animals in the >1mm fraction were all sorted, whereas the ones in the 63 μm –1 mm fraction were subsampled with a Folsom plankton splitter until 50–200 individuals remained. The invertebrates were then measured to the nearest 0.01 mm by use of an image analysis system by summing the length of several line segments (created manually) along the central axis of the body. The coefficient of variation of repeated measures made in this manner on the same individual was between 1% and 2%. The individual dry mass (DM, in μg) was estimated by the equation $DM = L^3$, where L is body length (mm).

Three replicate samples for analysis of algae and protozoans were collected for each substratum type, as close as possible to the invertebrate samples. Sand and fine gravel were sampled with a small core (2.4 cm diam) to the depth of 1–2 cm. Gravel and cobbles were simply lifted and placed in a bowl. For boulders, small fragments were detached with hammer and chisel. Algae and protozoans were separated from sand and fine gravel by agitation and decanting. Brushing with a stiff nylon brush was used for separation from the remaining substrata. The samples were fixed with Lugols for microscopical analysis. Algae were counted in random fields of a Palmer nannoplankton chamber at 600 \times and

Table 1. Location and average conditions at each sampling site in June 1992.

| Sampling site | Coordinates | [TP] ($\mu\text{g L}^{-1}$) | [TN] ($\mu\text{g L}^{-1}$) | [Seston] (mg DM L ⁻¹) | Periphyton biomass (mg Chl <i>a</i> m ⁻²) |
|------------------|------------------|----------------------------------|----------------------------------|--------------------------------------|---|
| Corriveau | 45°41'N, 75°44'W | 2.4 | 314 | 1.3 | 11.1 |
| Rainville | 45°35'N, 75°39'W | 8.3 | 242 | 1.0 | 11.2 |
| La Pêche | 45°39'N, 76°01'W | 16.1 | 346 | 2.6 | 7.4 |
| Blackburn | 45°39'N, 75°49'W | 16.4 | 340 | 1.4 | 4.3 |
| Chelsea | 45°30'N, 75°48'W | 19.1 | 503 | 6.0 | 8.2 |
| Leamy upstream | 45°29'N, 75°48'W | 21.9 | 287 | 5.0 | 21.1 |
| Leamy downstream | 45°27'N, 75°45'W | 45.9 | 322 | 18.4 | 57.2 |
| Des Féés | 45°25'N, 75°45'W | 49.9 | 535 | 17.4 | 57.4 |
| Des Trembles | 45°26'N, 75°46'W | 54.4 | 755 | 16.7 | 52.4 |

125 \times magnification. Macroalgae and protozoa were counted in a Sedwick-Rafter chamber (125 \times magnification). Cell volumes of algae and protozoa were calculated by approximation to solids of known volume. When colonies or filaments were present, the whole volume was taken as algal size rather than the volume of the single cell. Besides microscopical analysis, periphyton biomass was estimated from the amount of chlorophyll *a* extracted by the ethanol used to preserve the substrate and benthos samples (*see* Bourassa and Morin 1995 for more details).

To have an integrated description of stream biomass at each site, we averaged mean values observed for the different substrata. Effect of substratum size on these communities is described in Cattaneo et al. (1997) for algae and in Bourassa and Morin (1995) for invertebrates. To build the biomass spectrum, we grouped individuals into logarithmic size classes corresponding to a doubling of equivalent spherical diameter (a 8 \times increase in DM between the limits of adjacent size classes).

Primary production was estimated from Chl *a* standing stock and water temperature by use of the empirical model of Morin et al. (1999) and under the assumption that carbon accounts for 50% of the ash-free dry mass of algae (Reynolds 1984). Invertebrate production was estimated from the biomass spectrum, body mass, and water temperature by use of the empirical model of Morin and Dumont (1994). Grazer removal was estimated from density and body mass of grazer taxa (Baetidae, Heptageniidae, Glossosomatidae, Helicopsychidae, Hydroptilidae, Leptoceridae, Psephenidae, Orthocladinae, and *Physo*), by use of the empirical model of Cattaneo and Mousseau (1995).

The size spectra we obtained in our streams spanned over a 10¹⁰ range of body mass. We present in Fig. 1 two examples of these size spectra from the two extreme sites along the trophic gradient. The smallest size classes were codominated by cyanobacteria (mostly Crocococcales) and small diatoms (e.g., *Achnanthes*). Larger diatoms were the dominant in the two following size classes. In the richer site (Fig. 1b), the algal distribution was bimodal, with filamentous green algae (mostly *Cladophora*) abundant in the 0.25–16 $\mu\text{g DM}$ range. Chironomids dominated the classes between 16 and 128 $\mu\text{g DM}$ at both sites. The largest size class was dominated by filter-feeder trichopterans (Hydropsychidae) in the oligotrophic Ruisseau Corriveau and by deposit-feeder oligochaetes in the rich Ruisseau des Trembles. Protozoa were

found in the trough between algae and invertebrates (Fig. 1a,b).

Biomass of algae, protozoans, and invertebrates responded differently to increases in nutrients (Fig. 2). Although algae and invertebrate biomass tended to increase with increasing TP and TN, only invertebrate biomass increased significantly with increasing TP. Protozoan biomass did not vary significantly with increases in nutrients, although their decline with increasing TP approached statistical significance ($P = 0.06$). These results suggest that, along a trophic gradient, there is also a faster increase of invertebrate biomass (the largest-sized group), compared with algae and protozoa (Fig. 2). A size increase with increasing TP within a group of organisms (e.g., algae and invertebrates) has been reported elsewhere (Cattaneo 1987; Bourassa and Morin 1995; Cattaneo et al. 1997).

The hypothesis of exploitation ecosystems (Oksanen et al. 1981) predicts that, in systems of intermediate productivity, grazing will keep vegetation depleted. As a result, an increase of trophic would translate to an increase of the ratio of secondary to primary production. The combination of empirical models with the size spectra allowed comparison of the response to nutrients by algae and invertebrates, not only in terms of biomass but also in terms of production. Our estimates indicated that the ratio of secondary production (SP) to primary production (PP) increased along the trophic gradient and therefore that invertebrate production increased faster than algal production (Fig. 3). Our results support the hypothesis of exploitation ecosystems in a natural system without the inevitable artifacts of manipulation.

Feminella and Hawkins (1995), from a meta-analysis of experimental studies in streams, determined that herbivores significantly reduce periphyton biomass in most situations (70% of the experiments). The idea of a top-down control of algae in our streams is supported by the high grazer removal relative to PP (62%–175%, Fig. 3). Our estimates of algae removal rates provide support to the view that periphytic algae can be controlled by invertebrates as well, in natural unmanipulated streams. These results, together with those of Brönmark and Weisner (1996) in natural ponds, suggest that top-down control is widespread in benthic communities.

The increase of the ratio of grazer removal to PP with increasing TP and TN (Fig. 3) implies that invertebrate impact on algae is relatively higher in eutrophic sites than in

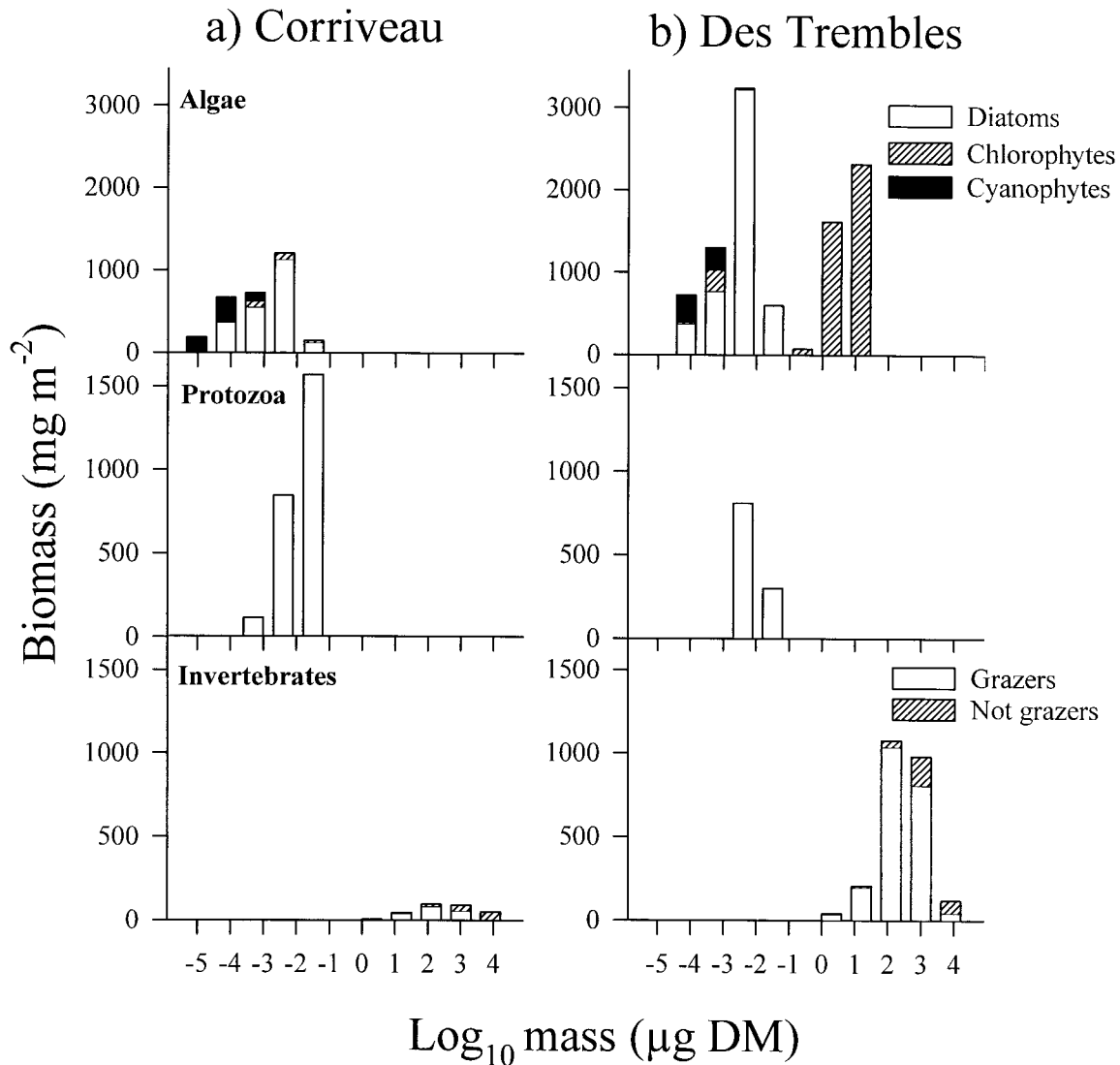


Fig. 1. Algae, protozoa, and invertebrate biomass spectra in (a) the most oligotrophic (Corriveau) and (b) most eutrophic (Des Trembles) sites. Baetidae, Heptageniidae, Glossosomatidae, Helicopsychidae, Hydroptilidae, Leptoceridae, Psephenidae, Orthocladiinae, and *Physa* were considered grazers in these streams.

oligotrophic ones. This is contrary to the pattern of proportional increase of herbivory, with PP observed in a general survey of herbivory measurements in aquatic and terrestrial ecosystems (Cyr and Pace 1993).

The estimates of production obtained by combining field measurements of chlorophyll or size spectra with empirical models are coarse, but this imprecision is unlikely to affect the major patterns described here. The PP estimates derived from periphyton chlorophyll were found by Morin et al. (1999) to be unbiased but much less precise than direct measurements. Morin and Dumont (1995) used Monte Carlo simulations to assess the magnitude of error potentially introduced by the use of empirical models to estimate SP of invertebrates. Their simulations showed that this additional source of error was significant for individual species but that estimates of production by assemblages of several species were unbiased and that their precision approached that of direct measurements. Spatial variability of abundance of

benthic algae (Morin and Cattaneo 1992) and invertebrates (Morin 1997) is generally quite large and, for both measurements and estimates of production derived from empirical models, is often the dominant factor affecting precision. However, the major trends observed here, that grazer removal is of the same order of magnitude as PP and that the ratios of SP:PP and grazer removal:PP increase with trophy, are unlikely to be artifacts. Imprecision of the models would tend to create noise and obscure trends rather than generate statistically significant patterns.

Estimates of grazer removal exceeded PP in several eutrophic sites and therefore appear to be unsustainable from periphytic algae alone in these sites. Either our estimates are biased or grazers used another source of energy. We estimated PP and grazer removal from simple means in each habitat rather than on habitat-weighted stream means, which can differ greatly. However, contrarily to other streams, biomass and size structure differed little among habitats (*see*

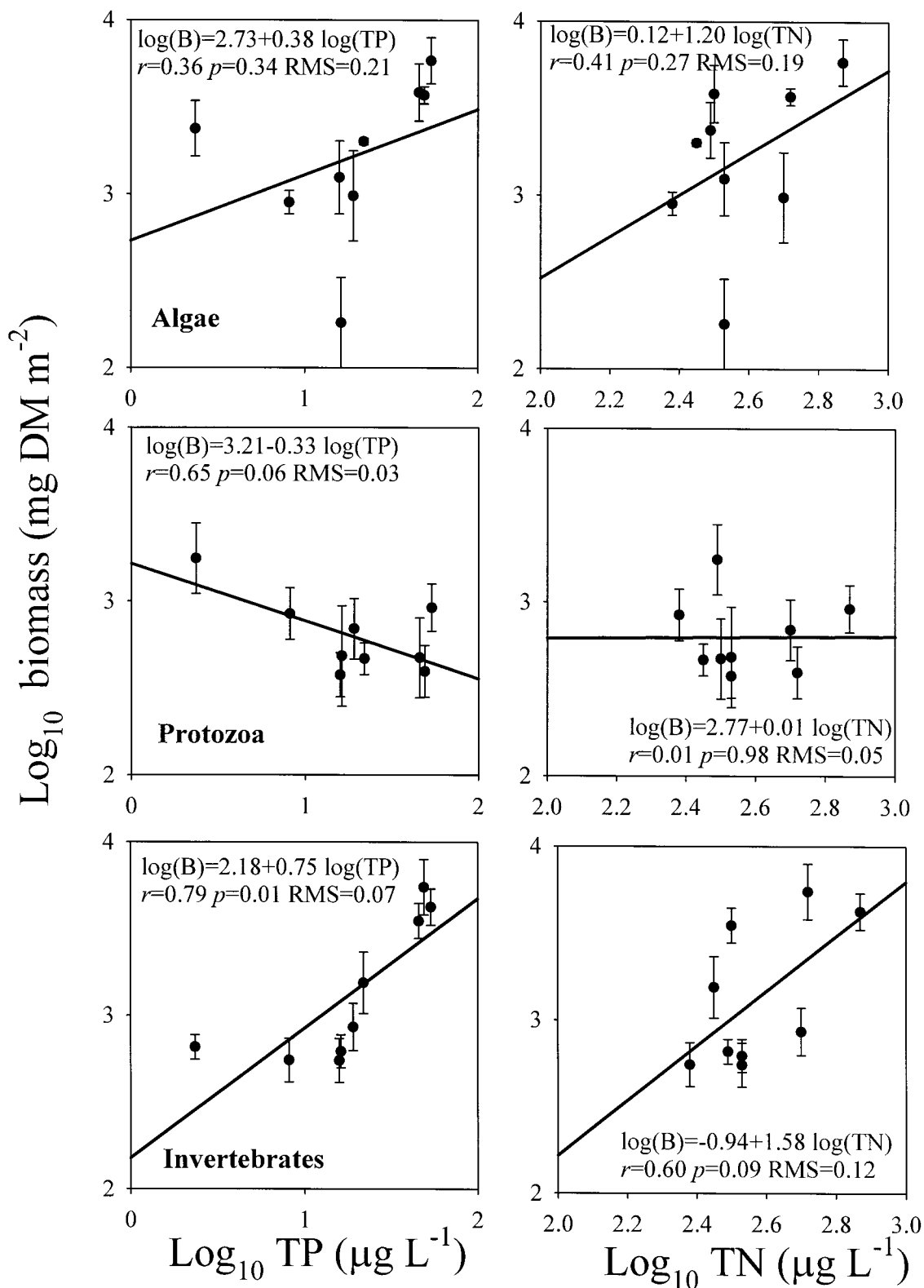


Fig. 2. Relationships between total biomass of algae, protozoa, and invertebrates and water TP and TN concentration. Data points are means and SEs, and lines are the linear regressions fitted to the data (RMS is the residual mean square of the regression).

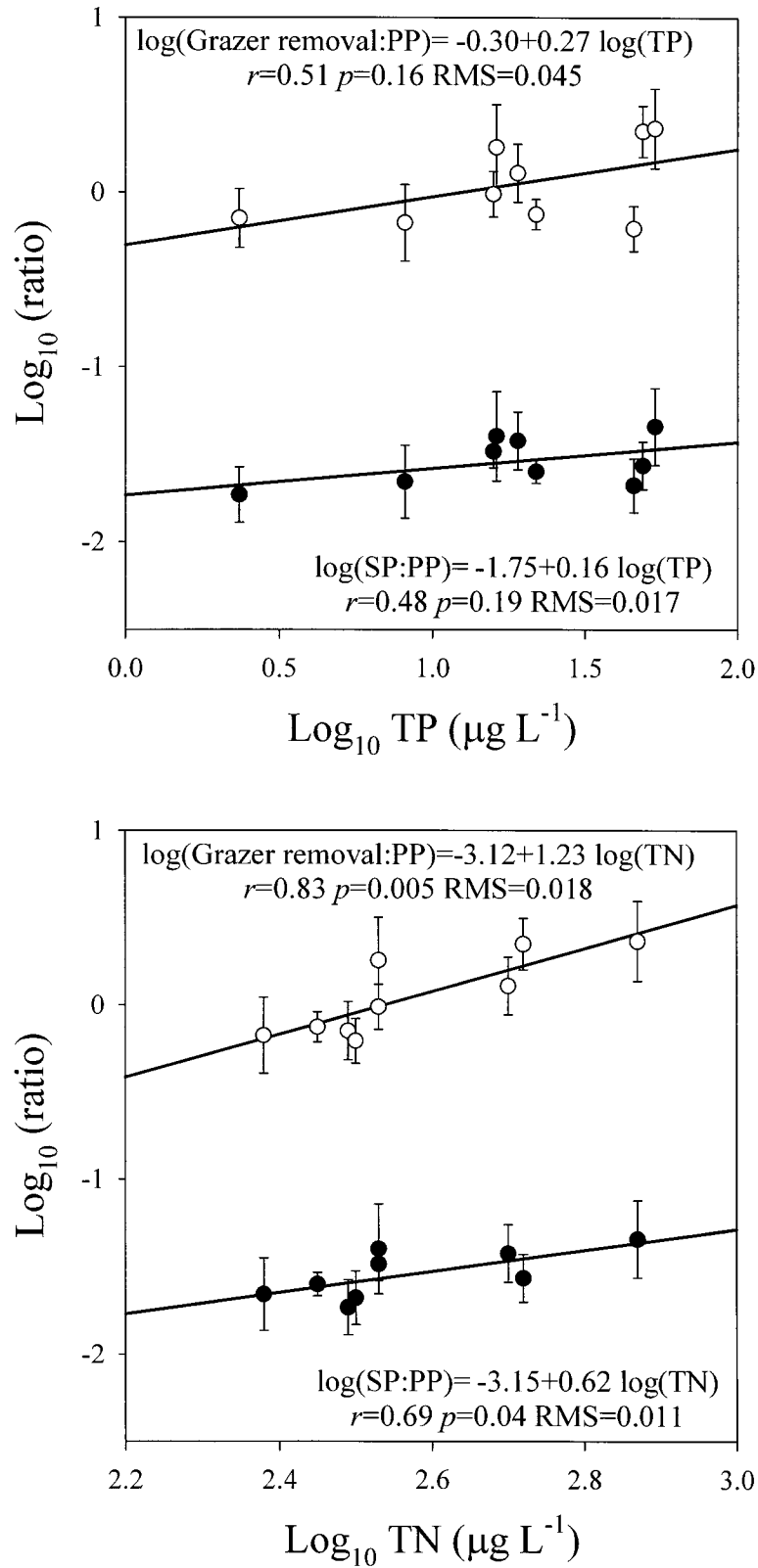


Fig. 3. Ratios (and SE) of SP:PP and of grazer removal of algae to PP as a function of TP and TN concentration in the water. Lines are the linear regressions fitted to the data.

Bourassa and Morin 1995; Cattaneo et al. 1997) at our sampling sites, and habitat-weighted means would be similar. We suspect that the heterotrophic component of the biofilm subsidizes grazing at times and are currently conducting research on this.

In the range of trophy observed in this region, our observations strongly indicate a control of periphyton biomass by herbivory. Because of our small sampling units, we could not estimate large invertebrates (i.e., crayfish) or vertebrate predators; therefore, we were unable to test eventual control of herbivores by higher trophic levels. Algal control by grazers was also suggested by a study of algal and invertebrate biomass over a trophic gradient in several Québec streams (Bourassa and Cattaneo 1998). A further increase in eutrophication could push the streams outside the range of "intermediate trophy," in which herbivory effect is stronger (Oksanen et al. 1981; Elser and Goldman 1991), and result in algal accumulation. Because our sampling was in summer in a period of stable flow, we cannot exclude the effect of abiotic control that may prevail in other seasons. We conclude, however, that, at least during the summer, moderate eutrophication of these streams results in higher invertebrate biomass rather than in unsightly accumulation of algae.

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