

Spatial patterns in fish biomass and relative trophic level abundance in a wastewater enriched river

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Abstract – It is generally accepted that nutrient enrichment of aquatic systems will lead to increased production at the top trophic level (fish). We found that in the wastewater enriched Bow River, Alberta rainbow trout (*Oncorhynchus mykiss*) biomass increased over 25-fold, and brown trout (*Salmo trutta*) biomass increased 5-fold, however total sportfish biomass did not increase below the nutrient input point source. This was due to a dramatic downstream decrease in mountain whitefish (*Prosopium williamsoni*) biomass to 2% of the average biomass upstream of the municipal effluent source. The spatial pattern over a 177-km river section encompassing the city of Calgary, showed that the increase in trout abundance approximately tracked the expected nutrient concentrations in the river, but with a downstream lag of 20–30 km. Mountain whitefish biomass over the 177 km was inversely related to the dominant trout species, rainbow trout. Invertebrate abundance, macrophyte biomass and phytoplankton biomass all increased below the wastewater treatment plant outfalls. However, periphyton data were highly variable and showed no response. We propose several hypotheses as regards the factors that may have led to the decrease in mountain whitefish, based on the data from all trophic levels and the spatial pattern for fish biomass. Proposed factors influencing the mountain whitefish decline were; altered competitive ability because of macrophyte abundance, ammonia toxicity and barriers to movement (weirs).

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Introduction

The effects of nutrient enrichment on aquatic systems have received much attention in the literature over the last several decades. Many studies focus on the anthropogenic eutrophication of lakes and rivers, and the associated negative effects, such as nuisance macrophytes, algae and the associated potential for hypoxia (Chambers et al. 1997; Sosiak 2002; Chambers et al. 2006). Other studies use experimental

fertilization (Peterson et al. 1993; Koning et al. 1998; Johnston et al. 1999) or correlations across lakes (McQueen et al. 1986; Persson et al. 1992; Mazumder 1994; Brett & Goldman 1997) to examine food web properties and fish production response to enrichment. Of these, few studies examine food webs and fish production responses to enrichment by municipal wastewater (de Bruyn et al. 2003).

The majority of data and empirical tests that involve food web response to enrichment come from lakes.

Analyses are often correlations that compare many lakes that differ in productivity. In general, these studies find patterns similar to classic theoretical predictions (Oksanen et al. 1981) where standing stock biomass of the top trophic level and alternating levels below increase because of enrichment (McQueen et al. 1986; Persson et al. 1992; Mazumder 1994; Brett & Goldman 1997; Ginzburg & Akcakaya 1992). In contrast to correlation analysis across systems, experimental fertilisation of aquatic systems has generally led to increases in adjacent trophic levels. This is expected, as the time scale at which many experiments are performed is often not sufficient to allow populations and communities to equilibrate. In the short time frame over which most manipulations are performed, standing stock increases in the lowest trophic level(s) and individual growth responses in the top trophic level(s) are expected and observed (Peterson et al. 1993; Harvey et al. 1998; Koning et al. 1998; Johnston et al. 1999). It is not possible to conclude from such studies whether top-down effects will occur in the longer term, after fish have numerically equilibrated. However, two studies of systems with long-term nutrient alteration have also resulted in increases for all trophic levels (Ginzburg & Akcakaya 1992; de Bruyn et al. 2003).

The unidirectional flow of rivers allows for the spatial partitioning of potential productivity within a single system. The response of nutrient perturbations may be displaced downstream because of nutrient spiralling and downstream flow of plant and invertebrate organisms (Newbold et al. 1981; Anderson et al. 2005). Furthermore, unlike closed systems, mobile organisms such as fish can move across productivity gradients. This changes the mechanism of biomass accumulation at the top trophic level from local reproduction to movement plus reproduction. However, if fish compete exploitatively following an ideal free distribution, then fish density should be correlated with resource production as in closed systems (Power 1984; Wootton & Power 1993; Oksanen et al. 1995). Experimental tests of trophic level interactions have been extended to rivers; however, many of these studies used enclosures that eliminate fish movement (Rosemond et al. 1993; Deegan et al. 1997; Golden & Deegan 1998; Forrester et al. 1999).

In this paper we examine the spatial patterns of three species of sport-fish in a river that receives substantial municipal nutrient inputs. The Bow River originates in the Rocky Mountains of Alberta and flows east to the city of Calgary as a low productivity river. While flowing through Calgary the river is transformed by a large point source influx of nutrients because of municipal wastewater that has been relatively constant since the late 1980s (Sosiak 2002). Further, we have incorporated available data

for nutrients, primary producers and macroinvertebrates to infer potential food web processes that lead to the spatial biomass pattern observed for the top trophic level, fish.

Study system

The Bow River has a 25,430 km² watershed and flows 619 km from its headwaters in the Rocky Mountains to its confluence with the Oldman River on the southern Alberta prairies. It flows through the city of Calgary, which has two wastewater treatment plants (WTPs) that discharge their effluent directly into the Bow River; Bonnybrook (380 million l·day⁻¹) and Fish Creek (FC) (70 million l·day⁻¹) (City of Calgary 2002). Effluent from these two WTPs comprises 97% of the municipal effluent entering the Bow River. Wastewater effluent input is typically 2–5% of river discharge. Effluent total phosphorus (TP) concentrations (0.8 mg·l⁻¹) are 30–40 times larger than background phosphorus concentrations (City of Calgary 2002). Total daily phosphorus loading is 360 kg, which is mainly from Bonnybrook WTP, 304 kg TP per day (FC contributes 56 kg). Our analysis uses available TP data as an indicator of nutrient enrichment. As phosphorus and nitrogen are associated with the same primary point source, our analysis using phosphorus should be very similar to results based on nitrogen limitation. As the Bow River flows through Calgary, it is a typical mid-order river that is relatively wide (30–60 m) and shallow (1–3 m maximum depth), and is therefore typically considered to be nutrient, not light, limited.

There are two weirs and associated water diversions within the section of river sampled for fish abundance. The purpose of the weirs is for diversion of water to irrigation canals used for agricultural and rural water supply. A telemetry study (Rhodes 2005) showed that mature rainbow trout are able to bypass both of the weirs. However, the ability of other species and smaller rainbow trout to move past these weirs remain unknown.

Methods

Fish

Sport fish abundance [rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*) and mountain whitefish (*Prosopium williamsoni*)] was estimated over a 177-km section of river, encompassing locations 'a' to 'b' (Fig. 1). The river was divided into 1-km subsections for which a total of 170 river sections were boat electrofished. The entire length of the lower Bow River study area was sampled at least once, with the exception of a 5 km reach on the

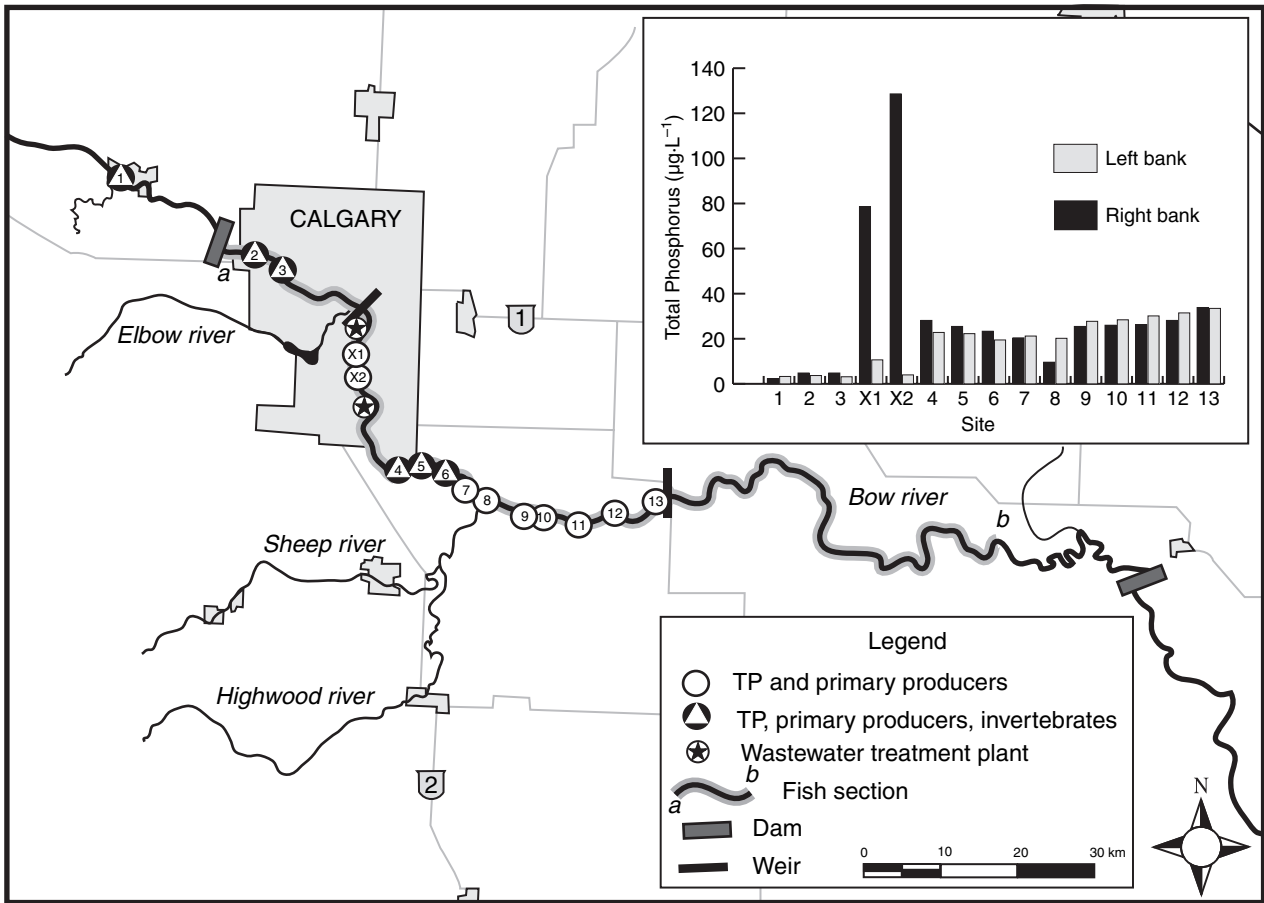


Fig. 1. Map of Bow River near Calgary, Alberta and study sites. Nutrients and primary producers were sampled at sites labelled 1–13. Macroinvertebrates were sampled at sites 1–6. Fish were sampled in 1 km sections starting at Bears paw dam and continuing for 170 km. Inlayed graph shows total phosphorus concentrations at each of the study sites.

Siksika Reserve that was inaccessible by boat, and areas immediately adjacent to weirs (for safety reasons). Fish were captured by electrofishing between 13th August and 25th September of 2001 from two boats running sections of the river simultaneously. The boats used were a Smith-Root SR18 and a Roughneck Tunnelhull. Each boat was equipped with a GPP 5.0 electrofisher unit and two fixed boom anode arrays. The electrofisher units were set to a frequency of 30 Hz and a pulse width of 3.5 ms, yielding a total power output ranging from 3.5 to 4.2 A. Effort was recorded as the number of seconds electrofished per 1 km of river. Random subsamples of fish were measured and weighed, and a further subsample was aged from each species. The central portion of the study area (45–93 km) was sampled four times to mark and recapture fish to estimate catchability. The proportion of marked individuals recovered per unit effort of electrofishing provided an estimate of the efficiency of the boat electrofishers (q) using maximum likelihood. The actual abundance (N , fish·km⁻¹)

and biomass of fish (kg·km⁻¹) could then be calculated for each 1 km section from raw catch (C) as:

$$N = C \frac{1}{qE}$$

where E is the effort in seconds per km. Fish <150 mm were much less catchable, and were eliminated from the analysis as there were no data available to assess the probability of capture for fish of this size.

Invertebrates

Macroinvertebrate abundance was estimated at three sites above, and three sites below the WTPs, corresponding to sites 1–6 of the nutrient and primary producer dataset (Fig. 1). Sampling occurred over a 2-day period in July, 2002 and 2003. At each site, three invertebrate samples were collected using a surber sampler with 500 µm mesh size. The surber sampler restricted the potential sample locations to the edges of the river where depth did not exceed 30 cm. Each

sample was preserved in 70% ethanol, and individuals were enumerated and classified to family. Families were assigned to herbivorous or carnivorous feeding groups according to Merritt & Cummins (1996) with regard to genera found in Alberta (Clifford 1991).

Phosphorus and primary producers

Samples for phosphorus concentration, phytoplankton chlorophyll *a* concentration, periphyton biomass and macrophyte biomass were collected over a 3-day period in July 2003. Thirteen locations, with sites on each bank of the river, were chosen to sample water above and below the WTPs (Fig. 1). Two extra locations were sampled immediately downstream of the WTPs where effluent had not fully mixed across the river. Water samples were collected in acid-washed polyethylene bottles, stored on ice in coolers in the field, and refrigerated until analysis. Samples were processed within 24 h for TP, following digestion with potassium persulphate, by spectrophotometry using the molybdate-blue technique (Menzel & Corwin 1965 as modified by Prepas & Rigler 1982). Chlorophyll *a* concentration was measured after filtering a known volume of water through a glass GF/C fibre filter. The chlorophyll on the filter was extracted into 90% acetone and measured fluorometrically (Turner Designs Model 10, Sunnyvale, CA, USA) with correction for phaeopigments (detection limit $0.05 \mu\text{g}\cdot\text{l}^{-1}$) (Arar & Collins 1997).

Periphyton biomass was estimated by assessing chlorophyll *a* concentration. Periphyton was collected from natural rock substrata at each sampling location at a depth of 30 cm. Five individual stones from each side of the river were randomly chosen at each location. A 1-cm^2 area of periphyton was brushed loose with a toothbrush and collected in a sample container with as little distilled water as possible. These samples were stored on ice in a closed cooler in the field until they could be frozen. In the lab, periphyton samples were filtered through a GF/C filter. When necessary samples were diluted with distilled water and subsampled. Chlorophyll *a* concentration was determined as for phytoplankton.

Macrophyte biomass was estimated by removing all above substrate macrophyte tissue within five 1-m^2 quadrats, which were randomly located in the river on the left and right banks of each sampling location. Samples were stored on ice in the field and frozen until analysis. Samples were washed with water to remove any attached sediments, epiphytes or invertebrates, then weighed and identified to species.

Analysis

We examined the relationships between phosphorus and primary (periphyton, macrophytes and

phytoplankton), secondary (herbivorous and carnivorous invertebrates) and tertiary (mountain whitefish, rainbow and brown trout) producers using regression analysis. Although all variables were continuous, the abrupt change in phosphorus concentration below the WTPs, caused some of the trophic components to cluster into high and low ranges of the log phosphorus concentration. Despite this clustering we chose a regression approach, as we were inferring continuous processes and some plots did contain intermediate points. However, a similar result would be obtained if we used the ANOVA analogue and an *F*-statistic to test the hypothesis that the cluster means increased with a categorical assessment of low and high phosphorus.

The phosphorus and primary producer data were collected from the same 13 sites (on both banks, $N = 26$). Data at the two sites between the WTPs (sites X1 and X2, Fig. 1) where the effluent had not mixed completely were not included in the regression analysis. The invertebrate samples were taken from a single bank at the first six (most upstream) primary producer sites for 2 years ($N = 12$), and can be directly cross-referenced with TP at those sites. The fish data were collected in 1-km sections along the river beginning below the first study site for the lower trophic levels. Thus, the fish data were contrasted with the TP of the last 12 study sites by using the fish abundance data for the corresponding kilometre location of the study site ($N = 12$). All data were log transformed to eliminate heteroscedasticity. The macrophytes, phytoplankton and trout datasets contained zero values and were therefore transformed as $\log(x + 1)$.

Our data were collected over a spatial gradient, and represent a temporal 'snapshot'. Therefore, our data required the assumption that the system approximates equilibrium conditions to combine data across years for the different trophic levels. We believe the assumption to be plausible, because little change has occurred in phosphorus loading to the river since 1983 and nitrogen loading since 1988 (Sosiak 2002). Sosiak (2002) also showed a consistent pattern in increased macrophyte abundance below WTPs from 1981 to 1996. The patterns in relative fish abundance above and below the WTPs seen in this paper have long been recognised by anglers as guided trips primarily occur below the WTPs. Trout abundance surveys in the early 1980s show the abundance of trout to be 3–4 times higher at a single site below the WTPs compared with a single site above the WTPs (Fernet et al. 1988).

Results

Spatial variation in fish species composition and biomass

There was a clear spatial pattern in trout biomass over the 177-km sampled section of the Bow River.

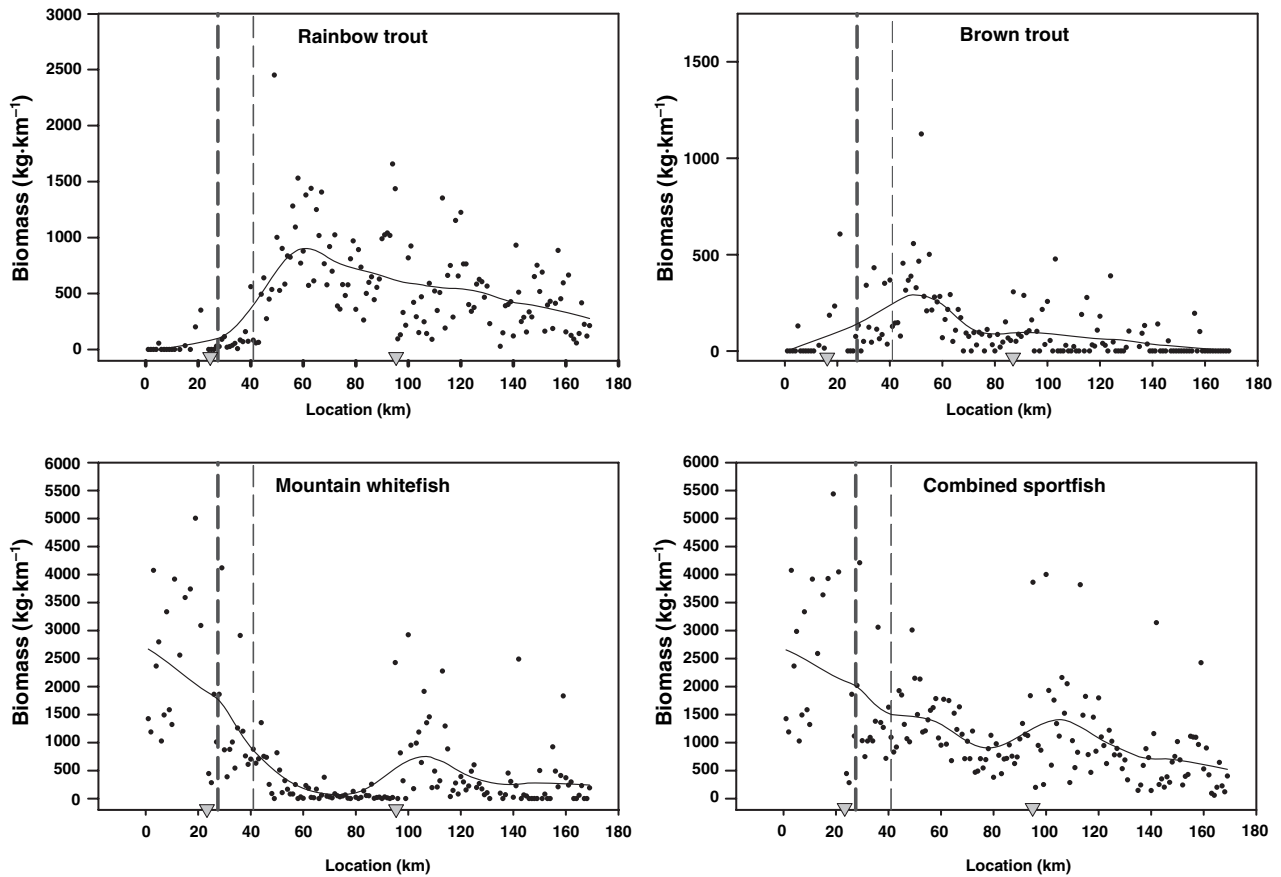


Fig. 2. Biomass ($\text{kg}\cdot\text{km}^{-1}$) of sportfish in the Bow River over 177 km section of the river (see Fig. 1). Vertical dashed lines represent the location of Bonnybrook (thick line) and Fish Creek (thin line) wastewater treatment plants. Inverted triangles indicate the position of weirs. The trend lines in the data are Loess tricube weight functions (polynomial degree = 1, sampling proportion = 0.3 and Sigmaplot 2001). Note the differences in scale on the y-axis.

Rainbow and brown trout density was low above the WTPs, but there was a large initial increase downstream of the WTPs followed by a gradual decrease with distance from the city (Fig. 2). Biomass increased over 25-fold and over 5-fold at peak locations below the WTPs for rainbow trout and brown trout, respectively. The spatial trends (Loess tricube weight function) indicate that rainbow trout biomass reached a peak at 60 km, whereas brown trout biomass was at a maximum at 48 km (Fig. 2). We calculated the spatial lag for which the nutrient perturbation manifests in trout abundance as the distance between the peak nutrient concentration and the peak in fish biomass. Bonnybrook WTP is the primary source of phosphorus loading, and was used as the nutrient input location (27 km), and distance from FC WTP (41 km) is reported in parentheses. We estimated that there is a 21 km (7 km to FC) lag in brown trout response and a 33 km (19 km to FC) lag for rainbow trout. The shorter response distance by brown trout is followed by a quicker decline in biomass downstream than for rainbow trout (Fig. 2).

The spatial pattern in whitefish biomass was the inverse of the pattern for the two trout species. A cross-correlation analysis (Systat statistical package, version 8, San Jose, CA, USA) revealed that mountain whitefish were inversely related to rainbow trout ($r = -0.266$, $N = 170$ and $P < 0.001$), but not brown trout ($r = 0.022$, $N = 170$ and $P = 0.781$). The two trout species were positively correlated ($r = 0.336$, $N = 170$ and $P < 0.001$). Whitefish abundance declined rapidly below Bonnybrook WTP and reached a minimum at 75 km (Loess tricube weight function, Fig. 2). There is a small increase in the whitefish at 95 km, which corresponds to the Carseland weir. No such trend was noted at the weir located at 23 km, suggesting that this weir did not impede movement. The whitefish biomass was very high upstream of the WTP and declined rapidly below the WTP where rainbow trout abundance was increasing rapidly.

The opposing spatial patterns of trout and whitefish led to abrupt changes in relative species abundance. At 1–20 km whitefish made up 98% of total sportfish biomass, however, by 71–90 km the two trout species

made up 97% of sportfish biomass. The increase in trout biomass was primarily because of rainbow trout, as this species constituted the majority of sportfish biomass below the point source influx of nutrients. However, after the Carseland weir at 95 km, the relative abundance of mountain whitefish increased to comprise about half of the sportfish biomass for the remaining 74 km of the study section.

Trophic structure response to enrichment

Despite a fourfold difference in TP concentration, there was no response of periphyton biomass to enrichment when comparing the sites above the WTPs with sites in well mixed water below the WTPs (Table 1, Fig. 3). However, data were also obtained at two locations where the water had not mixed completely and phosphorus concentrations were much higher on the right bank than on the left (Fig. 1). At these sites there was a more than 28-fold increase in TP from upstream values, and periphyton biomass increased over fourfold from upstream estimates. Thus periphyton was significantly correlated to TP concentration when the unmixed locations were included ($r^2 = 0.578$, $N = 30$ and $P < 0.05$). Unlike periphyton, phytoplankton significantly increased with TP concentration (Table 1, Fig. 3). Macrophytes were only present at sites below the WTPs and therefore macrophyte biomass was significantly correlated to phosphorus concentrations (Table 1).

Macroinvertebrates were classified into herbivores and carnivores; however, herbivores comprised 98.6% of the biomass. Herbivorous macroinvertebrate abundance increased below the WTPs (Table 1, Fig. 3). Carnivores did not show a significant response to phosphorus concentration. In general, macroinvertebrates responded positively to enrichment, with almost all orders increasing in abundance below the WTPs for 2002 and 2003. The only exception, Plecoptera, was a small percentage of the invertebrate community and

was not encountered below the WTPs in 2002 (Table 2). The relative increase in abundance was not constant across orders and the relative species composition changed above and below the WTPs (Table 2).

Mountain whitefish, rainbow trout and brown trout were the dominant species in the catch over the entire 177-km sample section (total catch 6653 fish). Their combined biomass did not increase in response to enrichment as predicted by food web theory, in fact, total biomass showed a slight, but nonsignificant negative response (Fig. 3, Table 1). However, significant relationships did occur when total fish biomass was divided into trout and whitefish. Combined trout biomass increased significantly (Table 1, Fig. 3) and whitefish decreased significantly (Table 1, Fig. 3) in response to enrichment.

Discussion

The advective nature of rivers leads to a net dispersal of nutrients, primary producers and invertebrates that is unidirectional. Thus there is an expected spatial lag in the response of river food webs to perturbations (Anderson et al. 2005, 2006). The most extensive data available for our study were for the sportfish abundance, which allowed for spatial visualisation over a 177-km river section. Unlike lower trophic levels, fish are able to move freely over large distances and track available resources. It is known that over 80% of mature rainbow trout migrate into the Highwood River, a tributary of the Bow River, to spawn (Rhodes 2005). Therefore, the spatial pattern in our fish data must be reset annually and maintained through movement. We expect that the trout biomass pattern tracks invertebrate production, and that the downstream spatial lag in response to nutrient inputs represents the net impact of advection, nutrient spiralling and energy flow through the food

Table 1. Results of linear regressions on log transformed data of trophic levels and their components against July total phosphorus concentration. Log transforms were generally of the form $\text{Log}(Y) = \text{Log}(X) \cdot A + B$ except for macrophytes, phytoplankton and trout where the transformation was $\text{Log}(Y + 1)$ to incorporate zero values.

Dependent variable	Intercept	Slope	<i>N</i>	r^2	<i>P</i>
Primary producers					
Phytoplanktonic chlorophyll <i>a</i> ($\mu\text{g}\cdot\text{l}^{-1}$)	-0.0362	0.256	26	0.39	<0.01
Periphytic chlorophyll <i>a</i> ($\text{g}\cdot\text{m}^{-2}$)	2.664	-0.181	26	0.014	0.56
Macrophytes ($\text{g}\cdot\text{m}^{-2}$)	-0.529	0.982	26	0.25	<0.01
Consumers					
All macroinvertebrates ($\text{number}\cdot\text{m}^{-2}$)	2.854	0.670	12	0.43	<0.05
Herbivore-detritivores ($\text{number}\cdot\text{m}^{-2}$)	2.841	0.674	12	0.44	<0.05
Carnivores ($\text{number}\cdot\text{m}^{-2}$)	1.283	0.183	12	0.015	0.71
Predators					
Combined fish ($\text{kg}\cdot\text{km}^{-1}$)	3.460	-0.339	12	0.25	0.10
Mountain whitefish ($\text{kg}\cdot\text{km}^{-1}$)	4.574	-2.080	12	0.56	<0.01
Combined trout ($\text{kg}\cdot\text{km}^{-1}$)	-1.912	3.450	12	0.89	<0.01

Trophic level abundance in an enriched river

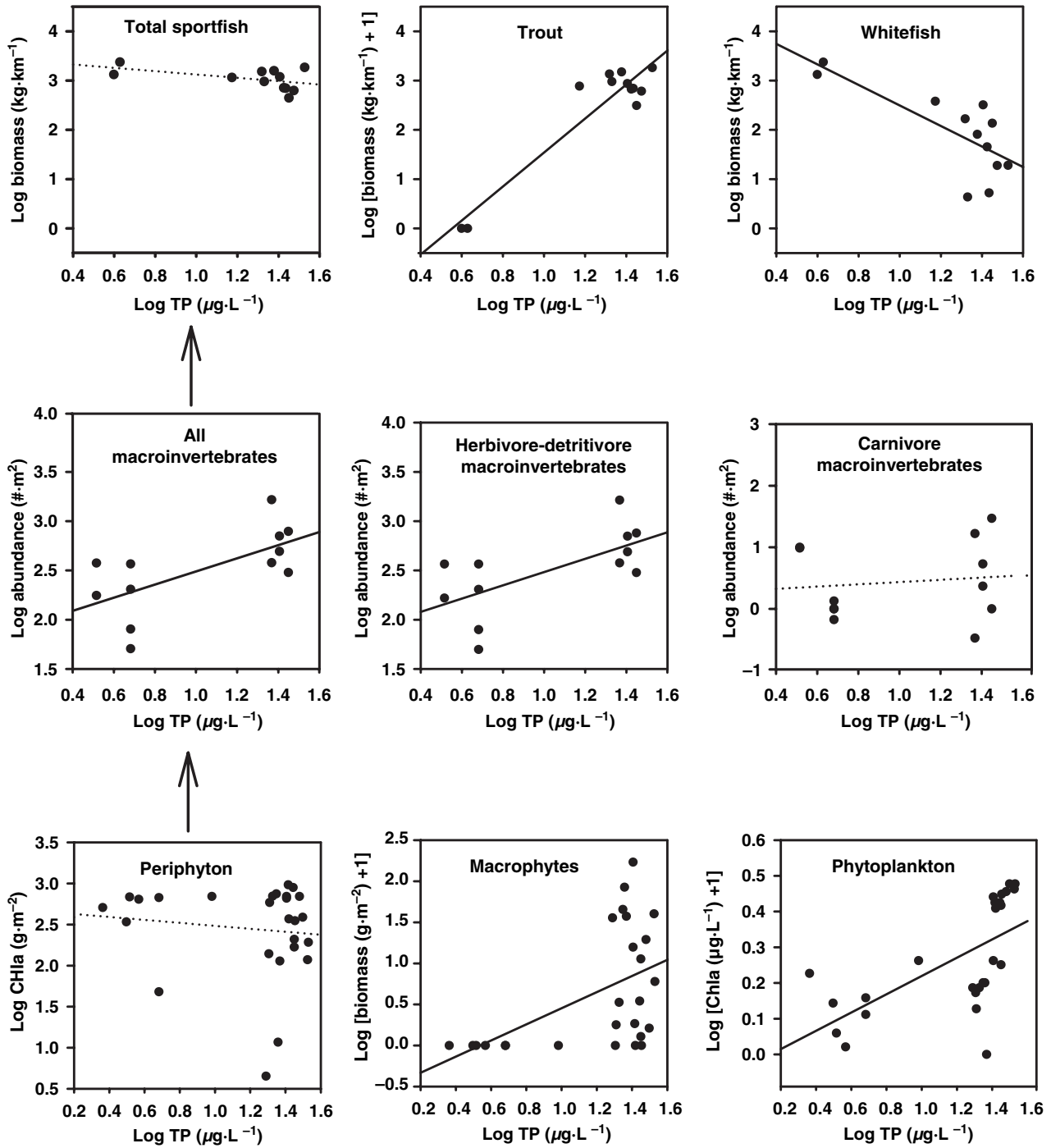


Fig. 3. The response of trophic groups to total phosphorus (TP) enrichment in the Bow River. Solid lines show significant trends, whereas, dotted lines are not significant. Arrows indicate feeding relations between the trophic groups. All data has been \log_{10} transformed [datasets with zero values were transformed as $\log(\text{data} + 1)$].

web. These processes of advection and food web dynamics are poorly understood (Anderson et al. 2006), and this study is a rare representation of the spatial scale over which these processes interact in lotic systems. Unfortunately, our invertebrate data do not have sufficient spatial distance or detail to assess rigorously the underlying mechanisms. The phospho-

rus data do not extend to the spatial scale of the fish data, and do not noticeably decline downstream within the sampling area. However, the broader spatial scale for which Sosiak (2002) measured total dissolved phosphorus indicated that phosphorus does decline downstream within the spatial range of our fish data.

Table 2. The changes in numerical density (number·m⁻²) and proportional composition for macroinvertebrates above and below the wastewater treatment plants (WTPs) in the Bow River.

Year	Numerical densities			Composition	
	Above WTPs, mean (SE)	Below WTPs, mean (SE)	+/-	Above mean	Below mean
2002					
Diptera	1822.7 (694.7)	6788.4 (846.5)	+	0.55	0.46
Ephemeroptera	1001.0 (68.4)	6314.8 (750.5)	+	0.30	0.43
Tricoptera	21.5 (6.2)	660.2 (206.9)	+	0.01	0.04
Oligochaeta	261.9 (19.0)	326.5 (79.2)	+	0.08	0.02
Amphipoda	0.0 (0.0)	437.7 (309.6)	+	0.00	0.03
Coleoptera	7.2 (3.6)	129.2 (55.2)	+	0.00	0.01
Plecoptera	129.2 (76.4)	0.0 (0.0)	-	0.04	0.00
Hemiptera	0.0 (0.0)	10.8 (10.8)	+	0.00	<0.01
Other	43.1 (6.2)	64.6 (27.1)	+	0.01	<0.01
Total	3286.6 (646.7)	14732.2 (1242.0)	+	1.00	1.00
2003					
Diptera	7172.4 (1390.8)	11632.2 (888.3)	+	0.71	0.37
Ephemeroptera	1284.5 (342.8)	13246.8 (1647.5)	+	0.13	0.42
Tricoptera	383.9 (109.5)	1837.0 (375.1)	+	0.04	0.06
Oligochaeta	965.2 (74.1)	3753.0 (1434.9)	+	0.10	0.12
Amphipoda	0.0 (0.0)	57.4 (9.5)	+	0.00	<0.01
Coleoptera	71.8 (31.3)	183.0 (28.5)	+	0.01	0.01
Plecoptera	150.7 (53.1)	186.6 (17.9)	+	0.01	0.01
Hemiptera	0.0 (0.0)	276.3 (50.6)	+	0.00	0.01
Other	50.2 (9.5)	179.4 (37.5)	+	<0.01	0.01
Total	10078.6 (3175.7)	31351.7 (1845.1)	+	1.00	1.00

Values are expressed as means of three sites with associated standard error (SE). The change in abundance below the nutrient input is summarised as an increase (+) or decrease (-). Relative composition is the proportion of numerical density represented by a given order.

The most unexpected result of this study was that the aggregated top trophic level did not increase with enrichment. This result contradicts theory based on trophic levels as ecological units and has rarely been documented (Persson et al. 1991; Hulot et al. 2000). Although the three fish species are not exact ecological equivalents, all rely on the invertebrate trophic level as a primary food source (Scott & Crossman 1973; Nelson & Paetz 1992). The overall negative trend in fish biomass was driven by mountain whitefish, which rapidly declined below the city of Calgary and overwhelmed the increase in the two trout species. The spatial cross-correlation analysis showed that rainbow trout and whitefish are inversely related. Thus the large decline in whitefish abundance could be due to a change in the relative competitive abilities of the two species associated with the wastewater effluent. Although we do not have the data necessary to investigate explicitly the competitive interaction between trout and whitefish, our data for the lower trophic levels allow us to infer processes that may affect this competitive interaction.

A change in competitive advantage could occur because of changes in species composition at the trophic level below fish. For example, invertebrate composition could change to favour species that are less vulnerable to whitefish than trout. Peterson et al. (1993) reported a decrease in the second most

abundant macroinvertebrate species, blackflies (*Prosimulium martini*), in the experimentally enriched section of an arctic river. Change in community composition within the macroinvertebrate trophic level appears to be a consistent pattern among enriched lotic systems (Peterson et al. 1993; Harvey et al. 1998; de Bruyn et al. 2003). In our study there was a switch in the dominant species from Diptera above the WTPs to Ephemeroptera below the WTPs (in 2003 only). However, although the relative abundances of invertebrate orders did change, the numerical abundance of all invertebrate orders increased. Therefore, all invertebrates preferentially consumed by mountain whitefish were more abundant below the WTPs. Thus, the spatial pattern of whitefish is not simply driven by prey limitation.

The presence of macrophytes below the WTPs may be an important factor which alters the instream habitat, and thereby influences predator-prey interactions (Diehl 1993). Mountain whitefish morphology allows them to forage effectively for invertebrates amongst the rocky substrate of rivers (Scott & Crossman 1973). The presence of macrophytes may inhibit this foraging behaviour and would thus decrease the competitive ability of mountain whitefish. Periphyton is usually the focus of stream food web studies, as it is the main food source for macroinvertebrates (Angradi 1994; France 1995). However,

macrophytes are an important part of the primary producer data because of their role in habitat structure. The hypothesis that macrophytes are altering the interaction between trout and whitefish is supported by the lag in trout and whitefish response below the WTPs. Macrophyte abundance is lagged because of the distance needed for nutrients to spiral and be incorporated into sediments where macrophytes derive their nutrients (Jackson et al. 1991).

Predation could also be a factor in the negative spatial correlation between rainbow trout and mountain whitefish. Although brown trout tend to be more piscivorous than rainbow trout (Nelson & Paetz 1992), predation by adult trout on young whitefish may depress whitefish abundance in the enriched reaches of the river. Unfortunately, we do not have the empirical data necessary to assess this hypothesis more fully.

We feel it is unlikely that the spatial pattern in fish abundance can be explained by changes in habitat quality. We do not have data on any abiotic habitat variables; however, no abrupt changes in habitat were apparent during fish sampling. Furthermore, a trout habitat suitability index for the Bow River from 0 to 70 km presented in Anderson et al. (2006) does not correlate with the fish biomass patterns in our study.

There are two potential abiotic factors that may have influenced the apparent negative effect of nutrient enrichment on whitefish. First, the Carseland fish weir at 95 km appears to inhibit mountain whitefish movement, as abundance below the weir is substantially higher than directly above it. However, the low abundance above the weir extends for a large distance of approximately 40 km, thus it does not appear that the weir is the primary factor influencing abundance. Furthermore, although our macrophyte data do not extend below the Carseland weir, Sosiak's (2002) basin wide survey found a few submerged macrophytes further downstream. Therefore, higher whitefish abundance below the weir could be due to the absence of macrophytes. A second abiotic factor that may explain the low mountain whitefish abundance downstream of the WTP is ammonia loading from the municipal effluent. The concentration of ammonia producing 50% mortality (LC_{50}) for mountain whitefish ($0.289 \text{ mg}\cdot\text{l}^{-1}$, range: $0.143\text{--}0.473$) is approximately half of the LC_{50} s reported for rainbow and brown trout (Environment Canada 2001). Sosiak (2002) reported the highest ammonia concentrations at his first sampling site below the WTPs, corresponding to approximately 60 km of our study. At that site, median ammonia concentrations between 1989 and 1996 were in the range: $0.11\text{--}0.28 \text{ mg}\cdot\text{l}^{-1}$, however, this concentration dropped to only $0.01\text{--}0.06 \text{ mg}\cdot\text{l}^{-1}$ at the Carseland weir (96 km). Therefore, it is possible that ammonia concentrations in the section of river near and above the 60 km sampling site were

sufficient to affect mountain whitefish negatively. However, the lowest abundance of whitefish is well below 60 km where the ammonia concentrations have decreased. Given the available data, we cannot conclude to what extent abiotic factors and/or the proposed competition–predation processes can explain the spatial pattern of whitefish abundance.

In the Bow River, we did not observe a positive enrichment response at the top trophic level and alternating responses at lower trophic levels, as would be predicted by classic theory (Oksanen et al. 1981). However, it is now recognised that predicting food web response to enrichment is more complicated and requires data on relative biomasses and interaction strengths of trophic groups (Abrams 1993; Biggs et al. 2000). From a management standpoint it may be more realistic to try to predict at what stage specific detrimental changes, such as, nuisance periphyton and macrophytes occur (Sosiak 2002). Our data indicate that macrophytes may be an important factor that led to the switch in dominant fish species. If nutrient inputs to the Bow River continue to increase, then macrophyte biomass could potentially reach a level where large-scale fish mortality occurs because of hypoxia. This would lead to a new community state dominated by fish species with greater tolerance for low oxygen levels below the WTPs.

This documentation of effects of enrichment of the Bow River system by municipal wastewater is an example of a common situation. Many major cities are located near water bodies, and a greater understanding of the effects of enrichment because of land use practices on aquatic systems is needed. Furthermore, fertilization projects have been implemented in some aquatic systems with the objective of increasing fish production. The rainbow and brown trout fishery in the Bow River has apparently benefited from the increase in abundance because of enrichment from sewage effluent. However, the drastic change in dominant fish species above and below the WTPs is troublesome. If anglers preferred whitefish over trout, then the enrichment of the Bow River would be viewed much more negatively. Our study is one example by which enrichment may increase or decrease abundance of species at the top trophic level.

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