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The influence of fluctuating ramping rates on the diets of small-bodied fish species of boreal rivers

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Abstract The response of aquatic organisms to flow regulation at hydro facilities has become a key issue for the development of sustainable management practices intending to reduce the impact in regulated rivers. In previous studies, unrestricted ramping rates have been found to have a negative effect on invertebrate communities and shortened the length of the food web. The decrease in the length of the food web was inferred from a significant decrease in the difference between macroinvertebrates and fish δ^{13}N signatures, equivalent to the loss of the one trophic level. A before-after-control-impact (BACI) design was applied to determine the possible effects of ramping rate restrictions on the diet of small-bodied fishes in a boreal river in northern Ontario. Stomach contents were identified to the taxonomic level of order. Using these data, abundance, diversity and taxa composition were calculated to yield an understanding of the alterations that occurred in the food web, and how fish species diets may have changed to compensate for the shift in the invertebrate trophic level. It was found that unrestricted ramping rates were associated with an increase in invertebrate abundance within the stomach contents. There was no effect from the change to unlimited ramping for both stomach content EPT abundance and species diversity, as both rivers followed a similar trend over time. After unrestricted ramping rates, a greater frequency of baseline taxa and a lower frequency of predatory macroinvertebrates were found within the altered river stomach contents compared to what was expected. This demonstrates that the diets of small-bodied fishes have changed to compensate for the alterations to the food web due to unrestricted ramping rates, and implies that ramping rates should be taken into consideration in the regulation of operating regimes on altered rivers.

Keywords Stomach content analysis · Ramping rate fluctuation · Regulated rivers · Food web

Introduction

The majority of the total power supply throughout Canada (63 %) is generated from hydroelectric facilities (Canadian Electricity Association 2009). Fully peaking storage facilities are considered the most damaging

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operational regime to river systems as water is released in accordance with electricity demand resulting in large hourly and daily downstream discharge fluctuations (Clarke et al. 2008). In lotic ecosystems, the loss of the natural flow regime has been identified as a major threat to riverine biota (Richter et al. 2003; Sabater 2008). Hydro-peaking operations greatly alter flow regimes, which modifies temperature patterns, interrupts geomorphological processes (e.g., sediment transport), reduces habitat diversity, causes organism-level physiological stress, and consequently reduces abundance, diversity and productivity of biota (Bunn and Arthington 2002; Sabater 2008).

One possible way of managing the flow of water through a peaking hydro dam is through restrictions on ramping rates (i.e., the rate of change of flow passing through the turbines in $m^3\ s^{-1}\ h^{-1}$). Unrestricted ramping rates allow the hydro dam operators to increase or decrease flows at an unlimited rate and at any period of the day to meet the demands in electricity (Smokorowski et al. 2009). Unrestricted ramping rates are thought to be more destructive to the downstream ecosystem than restricted ramping rates (Smokorowski 2010). With restricted ramping rates, peaking dams can still follow the demand in electricity but at a slower rate, reducing the magnitude of change, and lowering the facility efficiency (Murchie and Smokorowski 2004; Smokorowski 2010). The maintenance of a minimum flow in conjunction with unrestricted ramping rates has demonstrated important effects on river ecosystem productivity, including the invertebrate community below hydropower facilities (Hudson and Nichols 1986). Hydroelectric facilities that implement a minimum flow have been found to yield a significant improvement in invertebrate family richness, proportion of intolerant taxa (%EPT) and increase in dissolved oxygen concentrations, over peaking hydro dams without maintenance of minimum flow (Bednarek and Hart 2005).

In previous studies on two boreal rivers in central Canada, unrestricted ramping rates were found to have a negative effect on invertebrate communities (Smokorowski 2010). Comparisons of the abundance and diversity of invertebrate communities associated with both restricted and unrestricted ramping rates revealed that both abundance and diversity decreased after ramping rates were unrestricted (Smokorowski 2010). Stable isotope analysis is a powerful tool to study the transfer of mass ($\delta^{13}C$) and energy ($\delta^{13}N$) through the food web (Fry and Sherr 1984). Coupled with $\delta^{13}C$, $\delta^{13}N$ provides further insight on the trophic structure of the food web as the $\delta^{13}N$ values increase from a food source to a consumer (Marty et al. 2009). Carbon and nitrogen stable isotopes ($\delta^{13}C$ and $\delta^{13}N$) have also been compared between natural, restricted and unrestricted ramping rate flow regimes; Marty et al. (2009) found a significant decrease in the length of the food web due to unrestricted and higher ramping rate flow regimes. The decrease in the length of the food web was due to the increase in $\delta^{13}N$ of macroinvertebrates after unrestricted ramping rates were allowed on the altered river. The increase in $\delta^{13}N$ indicated a loss of baseline feeding macroinvertebrates and an increase in predatory macroinvertatabrates (Marty et al. 2009); however, the increase in $\delta^{13}N$ was not found in the higher trophic level (fish), as the nitrogen isotope signature in fish was found to be the same before and after restricted ramping rates. However, that study did not include any stomach content analysis. Stomach content analysis of benthophagous fishes is a useful strategy in taxonomic surveys because fishes exploit a wide variety of microhabitats and capture macroinvertebrates in areas that may be difficult to sample with conventional gear (Maroneze et al. 2011). In most cases, numerical method and occurrence method (see Loomis et al. 2011) would be sufficient to yield detailed understanding of feeding ecology.

The objective of this study was to help clarify the mechanism associated with previously observed food web alterations and how fish species' diets changed to compensate for shifts in invertebrate trophic level. Given that much of the previous work has occurred on two boreal rivers in Canada, it was intuitive to continue more mechanistic explorations on those systems. To do so, the stomach contents of small bodied, aquatic invertebrate feeding fish species collected during the Marty et al. (2009) study were analysed with a before-after-control-impact (BACI) sampling design to determine the possible effect of ramping rates. It was hypothesised that an unrestricted ramping rate flow regime would be associated with a change in the diets of fish species due to modifications of the invertebrate trophic level. It is predicted that 1) the fish species from the altered river after impact (i.e., unlimited ramping rates) will have an unchanged relative number of baseline trophic level species found in their diet, regardless of their suspected reduced abundance in the environment as indicated by Marty et al. (2009), 2) that there will be an increase in the abundance of invertebrates, and 3) that there will be a decrease in intolerant invertebrates and species diversity within the stomach contents.

Methods

Study site

The study was carried out in two rivers located on the boreal shield on the north-eastern shore of Lake Superior: the Magpie River (MR - altered or Impact river, 48º0′N, 84º7′W) and the Batchawana River (BR - unregulated Control river, 47º0′N, 84º3′W). The Steephill Falls hydroelectric dam on the Magpie River in Wawa, Ontario was commissioned by Great Lakes Power Limited in the late 1980s. The Ontario Ministry of Natural Resources predicted that the daily flow fluctuations might have a negative effect on the brook trout (*Salvelinus fontinalis*) population downstream of the facility (ESSA Technologies LTD 1999). Therefore, under Crown conditions, the facility operated as a 'modified peaking dam' with the implementation of ramping rate restrictions, which at the time was very rare in Ontario. The plant was restricted to a minimum flow of 7.5 $m^3 \cdot s^{-1}$. Ramping rates could not exceed $1 m^3s^{-1}\ h^{-1}$ increase or decrease in flow from October 10th to November 15th, and 2 $m^3s^{-1}\ h^{-1}$ from November 16th until spring freshet (early May). Also, from May until early October, the dam was restricted to an increase or decrease of 25 % of the previous hour's flow (Acres International 1994).

Three study sites were selected on each river (Fig. 1). The upper site (site M01) located on the MR was not influenced by flow regime changes as it is located upstream of the zone of influence of the Steephill Falls Dam. Both rivers have similar morphology with the main substrata of granitic cobble and areas of gravel and sand. The BR follows a natural hydrograph, where it typically experiences increased flow conditions during precipitation and run-off. The MR was found to be slightly more productive than the BR as indicated by total phosphorus of 7.4 μgL^{-1} versus 6.6 μgL^{-1}, respectively (Patterson and Smokorowski 2010).

The MR drains an area of about 1,930 km^2 with a historical (pre-dam) mean annual flow of 27 m^3s^{-1}, while the BR drains an area of 1,233 km^2 and has a mean annual flow of 22 m^3s^{-1} (Marty et al. 2009). Annual discharge changed from before to after ramping rate manipulations, with a decrease of 66 % in the control river and a decrease of 63 % in the altered river due to drought (Marty et al. 2009). Mean discharge throughout the study was higher at the altered sites (25.6 $m^3\ s^{-1}\ h^{-1}$) compared to the control sites (19.5 $m^3\ s^{-1}\ h^{-1}$). Seasonal variations were related to the spring freshet and consisted of higher discharge in the spring for both rivers. Restricted ramping rates occurred in 2003–2004 with a mean of 1.9 $m^3s^{-1}\ h^{-1,}$ while in 2005–2006 unrestricted ramping rates occurred on the MR with a mean of 3.5 $m^3s^{-1}\ h^{-1}$, with BR acting as a control (Marty et al. 2009). The mean rate of change and frequency of change in flow on the BR were significantly lower over all 4 years with ramping rates of about 0.7±2.7 $m^3s^{-1}\ h^{-1}$ (Marty et al. 2009).

Field methods

Backpack electrofishing (Smith-Root Model LR-24) was used to capture small-bodied fishes on both rivers. Electrofishing was conducted twice a year for all three study sites on both rivers, once each in May and August in all 4 years (2003–2004 restricted, and 2005–2006 unrestricted ramping rates). The transition to unrestricted ramping rates occurred in October 2004, thus samples in 2005 and 2006 were collected months after the change in operational regime. For each sample, the following common species were collected: slimy sculpin *(Cottus cognatus)*, brook stickleback *(Culaea inconstans*), white sucker *(Catostomus commersonii)*, brook trout *(Salvelinus fontinalis)*, longnose dace *(Rhinichthys cataractae)*, lake chub *(Couesius plumbeus)*, trout-perch *(Percopsis omiscomaycus)*, iowa darter *(Etheostoma exile)*, creek chub *(Semolitus atromaculatus)* and common shiner *(Luxilus cornutus)*. Ten individuals from each species were caught and placed in a water-filled cooler with an aerator to keep them alive for <1 h prior to euthanasia. All fish were euthanized using a percussive blow to the head. The whole digestive tract including esophagus, stomach and intestines where then removed and preserved in 70 % ethanol in a small vial (Marty et al. 2009).

Laboratory methods

A total of 1,253 small-bodied fish stomachs were dissected. The 2003 fishes stomachs had been dissected as part of a previous study and the results were included after a subsample was validated. With the aid of a dissecting microscope each stomach was opened using

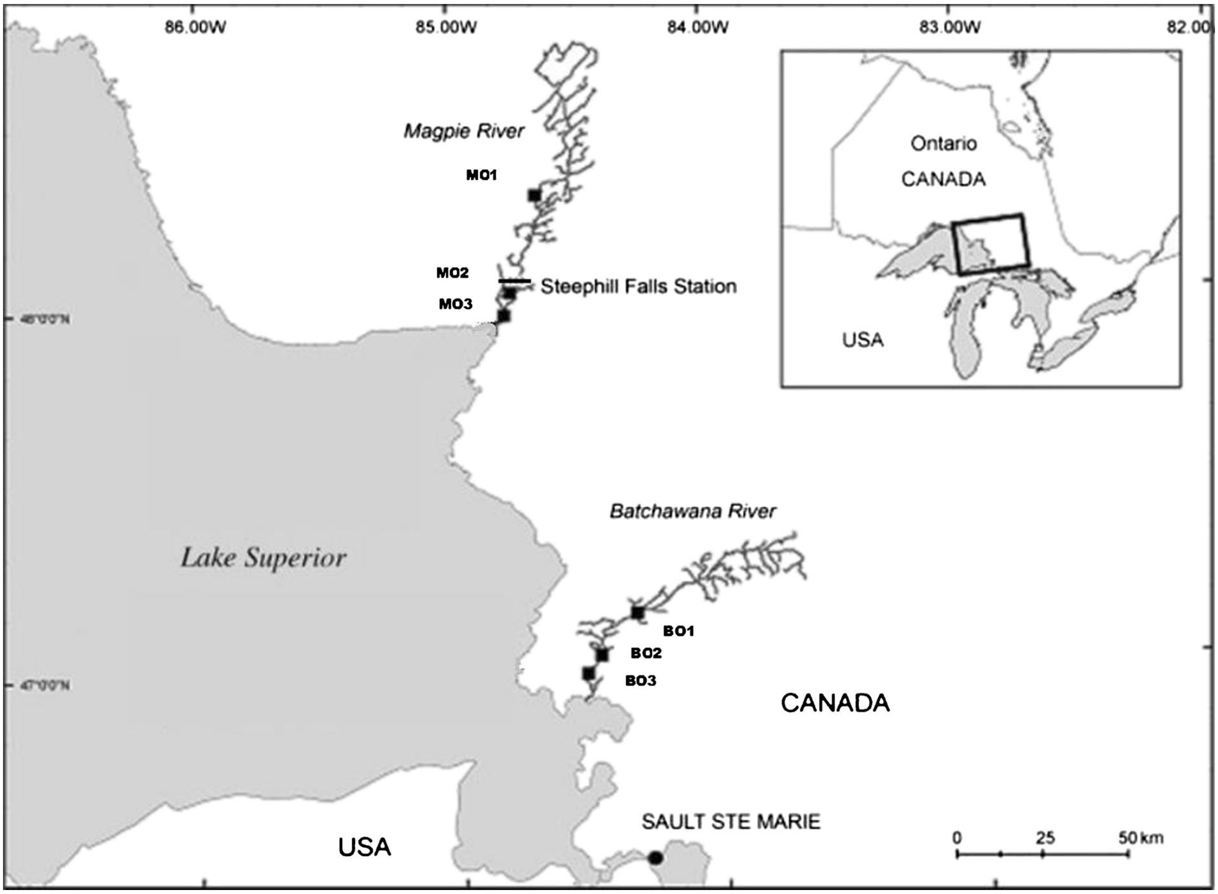

Fig. 1 Location of sampling sites on the MR and the BR marked as *solid squares* and placed in relation to Ontario on the inset map (altered from Marty et al. 2009)

a scalpel and all stomach contents were placed into a glass dish. The stomach contents were then examined under a microscope using a Fisher Scientific Stereomaster Zoom Microscope with an illuminated base (Fisher Scientific 12-562-157). Each organism found within the stomach content was identified to order and recorded. Any unidentifiable organisms (a small fraction overall) were recorded as such.

Statistical analysis

This BACI study collected data from multiple control and impact or altered sites, which were sampled before and after the change in ramping rates. A two-way analysis of variance (two-way ANOVA) was used to determine if there was a significant difference in variables before and after the disturbance (B), between control and altered impact sites (C) and their interaction (B×C). The study variables included abundance, stomach content taxa richness to order, ramping restrictions, river and year. For a few variables, transformation for normality was not possible due to the nature of the data. For these variables, a nonparametric Kruskal-Wallis one-way ANOVA test was performed.

The identified taxa found within the stomach content were separated into a number of metrics, including: 1) abundance 2) number of Ephemeroptera, Plecoptera, Trichoptera (EPT), and 3) diversity, calculated using probability of interspecific encounter (PIE). Abundance of intolerant taxa (EPT) was determined to analyze the effects of flow and ramping regime on sensitive organisms as the individuals in the orders of Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) are known to be more sensitive to changes in water quality compared to other orders of macroinvertebrates (Masese et al. 2009). A high abundance of EPT may indicate healthy water conditions, and a lower degree of impairment (Mackie 2004). Since no significant difference was found between fish species/body size and isotope signatures in the previous study by Marty et al. (2009), all fish species were pooled into one group for all indices and statistical analysis.

A BACI two-way ANOVA was used to analyze the abundance of invertebrates within fishes stomachs. All invertebrate indices were LN (x+1) transformed to down weight the influence of both dominant and rare taxa. Invertebrate order was used to calculate invertebrate diversity within the stomachs that contained contents using the PIE equation (Equation 1; Hurlebert 1971), that calculates the chance that two individuals will represent different families when randomly chosen (Smokorowski 2010):

$$PIE = \left[\frac{N}{N-1}\right]\left[1-\sum_{i}\left(\frac{Ni}{N}\right)^{2}\right]$$

There were no possible transformations to produce normality and homogeneity of variance for species diversity (PIE). Therefore, a Kruskal-Wallis one-way analysis of variance was used to validate the results found in the two-way ANOVA. The Kruskal-Wallis one-way ANOVA was used to determine if there was a difference in species diversity between river and year separately (Dytham 2003).

Invertebrate abundance, diversity and EPT within the stomach contents were averaged across all sites and plotted against year for each river. To simplify the comparison between the years of restricted vs. unrestricted ramping rates a BACI design was used in a two-way ANOVA to determine if there was a significant difference between treatments over time (Grafen and Hails 2009). In this BACI design, the sites on the BR plus the MR1 site were considered the “control” treatment, while the sites on the MR below the hydro dam were considered as the “impact” treatment. The years 2003–2004 were considered the “before” time as the hydro dam had restricted ramping rates, and the years 2005–2006 were considered the “after” time as the hydro dam had unlimited ramping rates.

For all statistical tests, *p*-values of less than 0.05 were considered significant. Specifically, for BACI analysis, the statistic of interest is the interaction term (treatment by time); if significant it implies that the change was a result of the “impact”, unlimited ramping.

Correspondence analysis was used to ordinate association among invertebrate taxa abundance found within the fishes stomachs. The correspondence analysis was done using BiPlot (using Excel add-in; McCune and Grace 2002), which provides information about the similarity between rivers based on the abundance of taxa consumed by fishes (Smokorowski et al. 2010).

The relative contribution of different types of taxa in the stomachs of the fishes between both rivers before and after unrestricted ramping rates was also tested. Two different classifications of taxa were used: baseline taxa, which included Cephalopoda, Gastropoda, Pelecypoda and Zooplankton, organisms known to have isotopic signatures related to that of primary producers; and macroinvertebrates. To conduct a proportional analysis, a Chi-square distribution was calculated in Excel 2010. The Chi-squared distribution for goodness of fit calculates the frequencies of observed to the frequencies of expected variable (Grafen and Hails 2009).

Results

A “river×year” (river×year, $F_{3,\ 1239}$=3.25, P=0.021, Table 1, Fig. 2) and “treatment×time” (B×C, $F_{1,\ 1243}$=4.035, P=0.045, Table 1, Fig. 2) 2-way ANOVA each showed significant interactions for invertebrate abundance. During restricted ramping rates in 2003 both rivers had similar abundance of invertebrates; however, after the impact (unrestricted ramping rates) in 2005 and 2006 the abundance of invertebrates found within the stomach content increased compared to before the impact (restricted ramping rates) in 2003 and 2004 for both rivers (year, $F_{3,\ 1239}$=10.52, P<0.001, Table 1, Fig. 2). Results also showed that, on average, the MR had a significantly greater abundance of invertebrates within the stomach content than the BR over all 4 years (river, $F_{1,\ 1239}$=27.94, P<0.001, Table 1, Fig. 2).

A “river×year” (river×year, $F_{3,\ 939}$=1.19, P=0.312, Table 1, Fig. 3) and “treatment×time” (B×C, $F_{1,\ 940}$=1.56, P=0.212, Table 1, Fig. 3) 2-way ANOVA both showed insignificant interactions in species diversity PIE. There was a significant difference in species diversity among years, with both rivers following the same increasing and decreasing trends over the 4 years (year, $F_{3,\ 936}$=12.79, P<0.001, Table 1, Fig. 3). There were no significant differences in species diversity PIE for the Time treatment (Before/After, $F_{1,\ 936}$=0.544, P=0.461, Table 1, Fig. 3). A nonparametric Kruskal-Wallis one-way ANOVA test was performed to confirm the results found in the two-way ANOVA. The species diversity between river and year were performed separately and

Table 1 River vs. year and before-after-control-impact results for abundance, species diversity (PIE), and abundance of intolerant taxa (EPT)

	Source of variation	S.S	*F*	*P*
Abundance	River	37.394	27.943	<0.0001
	Year	42.252	10.525	<0.0001
	River× Year	13.394	3.259	0.021
	Before/After	51.754	38.328	<0.0001
	Impact/Control	36.826	27.273	<0.0001
	B×C	5.449	4.035	0.045
PIE	River	0.289	2.968	0.085
	Year	3.735	12.791	<0.0001
	River× Year	0.348	1.191	0.312
	Before/After	0.055	0.544	0.461
	Impact/Control	0.009	0.084	0.771
	B×C	0.158	1.563	0.212
EPT	River	72.172	41.882	<0.0001
	Year	64.207	12.420	<0.0001
	River× Year	11.868	2.296	0.076
	Before/After	0.131	0.162	0.687
	Impact/Control	30.355	37.535	<0.0001
	B×C	1.922	2.376	0.123

found to follow the same trend as the 2-way ANOVA (results not shown).

A “river×year” (river×year, $F_{3,\ 1239}=2.296$, $P=0.076$, Table 1, Fig. 4) and “treatment×time” (B×C, $F_{1,\ 1239}=2.376$, $P=0.123$, Table 1, Fig. 4) 2-way ANOVA were both found to have insignificant interactions for EPT Index. The MR and BR followed the same decreasing (2004, 2006) and increasing (2005) trend over the 4 year period (Fig. 4); however there was a significant difference in EPT abundance among the 4 years (year, $F_{3,\ 1239}=12.420$, $P<0.001$, Table 1, Fig. 4), and a greater abundance of EPT on the MR (river, $F_{1,\ 1239}=41.882$, $P<0.001$, Table 1, Fig. 4). It should be noted that the difference between rivers was lower during unlimited ramping rates.

A biplot was created from the correspondence analysis showing the relationship among sites and invertebrate orders. The cumulative amount of variation explained by the first two axes of a correspondence analysis was 62 % (Fig. 5), with 40 % of the variability explained within the first axis and 22 % explained in the second. The MR and BR in 2003 are clustered together and separated from the other years with high abundance of Nematoda, Hydracarina and Plecoptera. The other 3 years (2004, 2005, 2006) BR grouped together and separated from BR 2003 along the first axis, with a high abundance of Odonata, Araneae, Zooplankton and Pelecypoda, while MR scattered across the two axes. Diptera, Ephemeroptera and Trichoptera clustered together and associated with MR 2006.

The relative contribution of different types of taxa within the stomachs of the fishes before and after unrestricted ramping rates was significantly different between rivers ($X^2=179.7$, DF=3, $P<0.001$). Both macroinvertebrates and baseline taxa had similar observed and expected values during restricted ramping rates between 2003 and 2004 on the MR, whereas baseline taxa abundance was significantly lower than expected on the BR. During unrestricted ramping rates, the macroinvertebrate taxa abundance was unchanged, while the baseline taxa had a significantly greater abundance than expected ($X^2=48.1$, DF=3, $P<0.001$, Fig. 6).

Discussion

The main focus of this study was to examine if and how fish species’ diets changed to compensate for shifts in the invertebrate trophic level due to hydroelectric

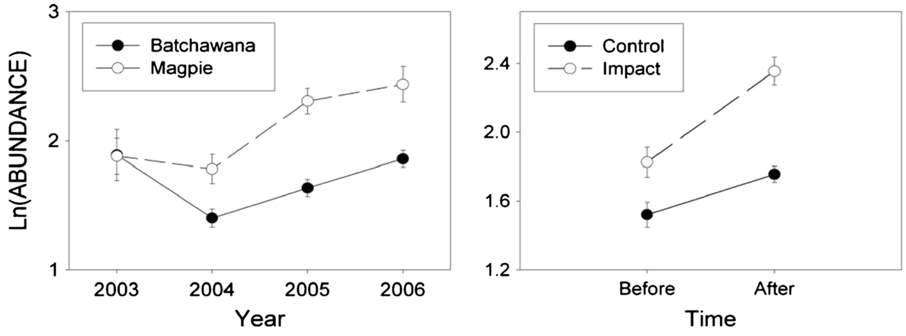

Fig. 2 Average abundance (LN +1 transformed)±standard error of invertebrates per fish stomach plotted as average across each river for each year, and as a before-after-control-impact plot

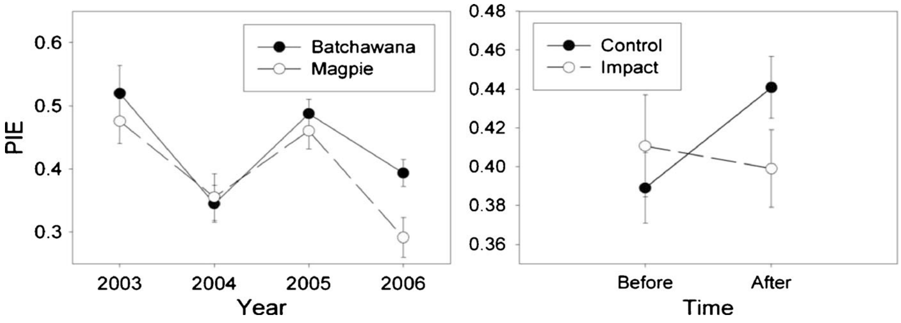

Fig. 3 Average diversity (PIE)± standard error of invertebrates per fish stomach plotted as average across each river for each year, and as a before-after-control-impact plot

operations at the Steephill Falls dam. The results show that an alteration in diets did occur as there was a significant increase in the overall abundance of invertebrates in the stomach contents within individuals from the MR after unrestricted ramping rates were implemented, relative to the control. Moreover, there was a significant increase in baseline taxa within fishes stomach content from the MR after unrestricted ramping rates were implemented, suggesting that the fish species were feeding more and consuming more baseline taxa to compensate for the alterations that occurred within the food web (see Marty et al. 2009). However, both species diversity and abundance of intolerant taxa in MR fishes stomachs followed the same trends as the control BR over all 4 years, showing no significant effect from the switch to unrestricted ramping.

Within the study by Marty et al. (2009) it was found that δ^{15}N for both baseline and macroinvertebrates on the MR was higher overall compared to the BR. The authors suggest that the alterations in δ^{15}N may be due to the difference in baseline signature between the rivers. Likewise, it was found that ramping rates were responsible for a significant decrease in $\Delta\ \delta^{15}$N, specifically unrestricted ramping rates were responsible for the reduction of the food chain length between marcoinvertebrates and fishes, equivalent of one trophic level (Marty et al. 2009). Given that a tropic level was shown to be lost between marcoinvertebrates and fishes, but the fishes signature remained unchanged, it was hypothesized that there would be no change in baseline taxa consumption despite the alteration in the food web (and thus prey availability). However, there was a significant difference in the relative contribution of different taxa within the fishes stomach content between both rivers before and after unrestricted ramping rates. More specifically, the abundance of baseline taxa significantly increased within the stomach content from the altered river after unrestricted ramping rates were implemented. Marty et al. (2009) also suggested that the influence of temperature dependent fractionation may have caused the alteration in δ^{15}N, with the difference in predator and prey δ^{13}C and δ^{15}N, decreasing and increasing, respectively, with decreased temperatures (Power et al. 2003). This temperature dependent fractionation may have occurred on the MR as the river received colder water from the base of the upstream reservoir as it passed through the hydro dam.

Abundance of invertebrates within the stomach contents of fishes were found to significantly increase in the MR after unrestricted ramping rates were implemented; this suggested that the fishes consumed a significantly greater amount of invertebrates. This result can be linked with the significant increase in baseline taxa found within the stomach contents of fishes. In a

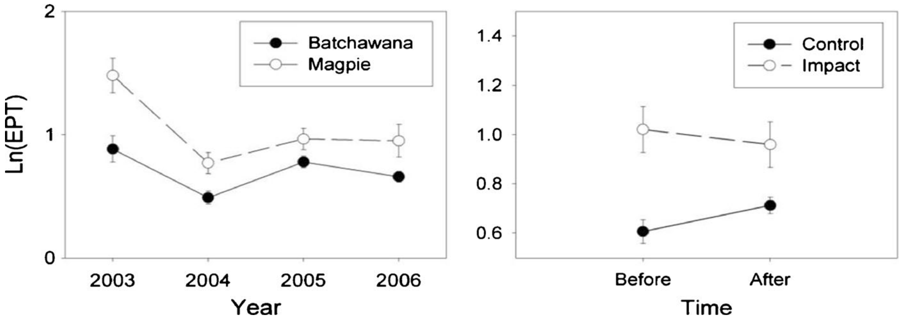

Fig. 4 Average EPT (LN +1transformed)±standard error per fish stomach plotted as average across each river for each year, and as a before-after-control-impact plot

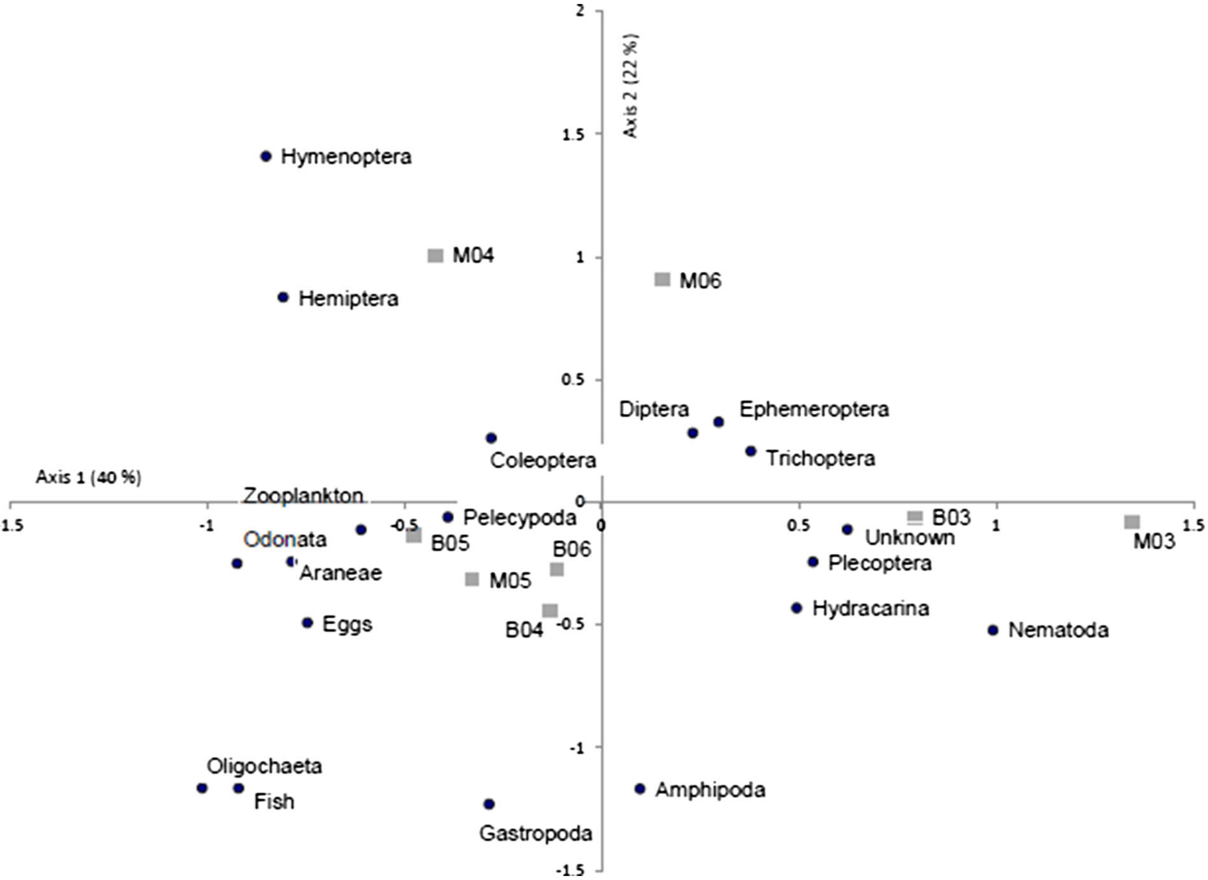

Fig. 5 Correspondence analysis projection of the 4 years per river (*M* Magpie, *B* Batchawana, 03=2003, 04=2004, 05=2005, 06=2006) and the abundance of major taxa illustrating the similarities and differences in community composition

study by Smokorowski (2010), macroinvertebrate abundance decreased in the altered river after unrestricted ramping rates were implemented. Therefore as a result of the decrease in macroinvertebrate abundance, the fishes on the MR had to increase their ingestion of baseline taxa. Baseline taxa were found to have lower $\delta^{15}N$ signatures than macroinvertebrates, classifying them in a lower trophic level than macroinvertebrates (Marty et al. 2009). The $\delta^{15}N$ of whole animals is generally ^{15}N-enriched relative to diet (Webb et al.

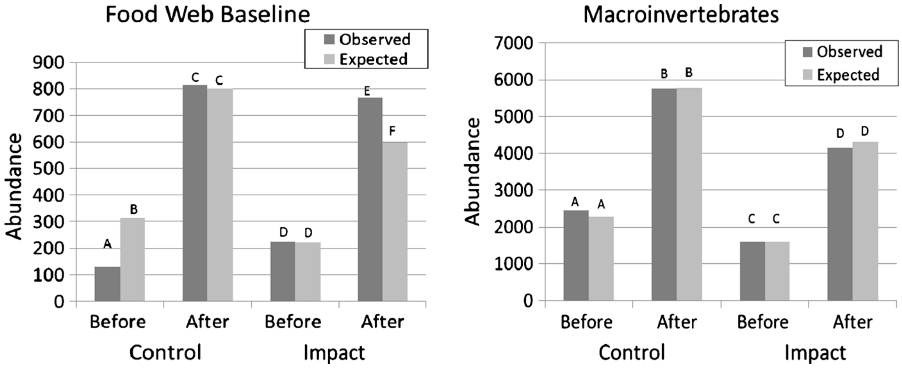

Fig. 6 Relative proportion of observed and expected taxa within the fish stomachs as a before-after-control-impact plot. All four site on the Batchawana River and site 1 on the Magpie River are the control system, sites 2 through 4 are the impacted system. Years 2003–2004 is before alteration occurred to the ramping rates and 2005–2006 is after ramping rate alterations were implemented

1998) with available energy decreasing with trophic level (Maxwell and Jennings 2006). The decrease in energy with trophic level is due to a decrease in dietary protein as smaller less protein-rich individuals are found increasingly in lower trophic levels (Webb et al. 1998). Therefore, fishes feeding on baseline taxa acquire less energy than individuals feeding on macroinvertebrates, and to compensate, fishes from the MR consumed a significantly greater amount of those individuals. Similar results were found in a study by Bowen et al. (1995), which examined the effect of dietary protein and energy on ingestion and growth of freshwater fishes. It was found that lower energy levels within each protein level were largely compensated for by increased ingestion (Bowen et al. 1995).

Optimal foraging focuses on what, when and where organisms obtain food, and when to switch food types and foraging patches to meet maximum energy gain (Harrel and Dibble 2001). The overall fitness and health of the fishes is a currency of optimal foraging theory and can be used to determine whether specimens are behaving in accordance with the predictions of optimal foraging theory by examining whether they occupy microhabitats that maximize their net rate of energy intake (Grossman et al. 2002). Optimal foraging may be a factor in the increased amount of baseline taxa found within the stomach contents of the fishes on the MR after unrestricted ramping rates were implemented. Due to the decrease in macroinvertebrates taxa found within the MR after unrestricted ramping rates (Smokorowski 2010), fishes may be maintaining optimal foraging by consuming a large abundance of baseline taxa from a single site and expending less energy than they would be searching for macroinvertebrates. Further analysis of the overall health and fitness of fishes in this system has the potential to clarify the effects of the alterations to the fishes diets.

Two predictions, that there would be a decrease in intolerant invertebrates and species diversity within the stomach contents, were not supported by the data. The MR followed the same trend as the BR for both intolerant invertebrates and species diversity, suggesting that the composition within the stomachs did not change significantly regardless of the significant alteration of intolerant invertebrates and species diversity found on the altered river after unrestricted ramping rates were implemented (Smokorowski 2010). It has been demonstrated that fishes species locally migrate within a river system based on the prey species presence, suggesting that the fishes may be migrating locally to find preferred taxa regardless of availability (Jackson et al. 2001).

Confounding factors may have played a role in the alteration of stomach contents, affecting the ability of this experiment to definitively implicate the change in ramping rates as the causative factor. The region experienced a 3-year drought starting in the fall of 2004 and continuing on through 2005 and 2006 (Smokorowski 2010). The drought resulted in above-average temperatures and lower-than-normal flows on all rivers in the area, including the BR. Temperature may be one of the most important limiting factors in determining the composition and abundance of invertebrate communities (Jackson et al. 2001). Higher temperatures may result in increased fecundity and food availability for invertebrates (Rader and Belish 1999; Wright et al. 2000), which may have influenced the results from this study.

The correspondence analysis showed that the variables river and year explained 62 % of the variability in the fishes diets. Between 2004 and 2006, the BR stomach contents data were clustered together and correlated with the orders Odonata, Araneae, Zooplankton and Pelecypoda. Odonata were found to be strongly associated with the BR by Patterson and Smokorowski (2010), who studied the effect of ramping rates on the drifting invertebrate community. MR stomach content data were scattered across both axes, with 2006 correlating with Ephemeroptera and Hemiptera. Ephemeroptera were strongly associated with the MR by Patterson and Smokorowski (2010), which suggested that these results follow the trends for invertebrate communities found previously for the MR and BR.

In conclusion, this study indicated that the shift in invertebrate tropic level due to unrestricted ramping rate fluctuations does impact higher trophic levels. The loss of a full trophic level between marcoinvertebrates and fishes resulted in consumption of an increased number of baseline species in order to obtain the required energy and dietary protein. The increased consumption may require an increased amount of energy expended which could impact the overall fitness of the individual. However, further studies are needed to investigate the overall effects on growth, fitness and health to determine if the alteration in the fishes diets is causing a negative effect, or is just a consequence of optimal foraging. If the alteration in fishes diets is causing a negative effect then ramping rates would need to be considered in the regulation of operating regimes to reduce these impacts. Further research is also needed to assess the effects of varying ramping rates on fluctuating flows on the MR. Throughout this study there were a number of confounding factors such as climate that may have played a role in the variation found within the stomach contents, affecting our ability to definitively implicate the change in ramping rates as the causative factor. Overall, this study suggests that environmental flow management practices should consider maintaining restricted flow regimes that follow a more natural regime, as unrestricted ramping rates are a source of ecosystem disturbance. These environmental constraints could benefit the riverine ecology.

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