

Experimental effects of reduced flow velocity on water quality and macroinvertebrate communities: implications for hydropower development in Bhutan

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The construction of flow diversion barriers from locally sourced cobbles in the Chamkhar Chhu to create reduced flow velocity in downstream habitats and maintain flow velocity in upstream habitats.

Abstract

Key to Bhutan's economic development strategy is the expansion of the country's hydropower projects, which requires the construction of a number of large dams. As dams affect the natural hydrological regime of rivers, the objective of this study was to assess these impacts on water quality and macroinvertebrate communities. Baseline physical and chemical properties of rivers in central Bhutan were gathered to provide spatial context for hydrological change associated with hydropower development.

Physico-chemical measures from central Bhutan rivers suggested that aquatic macroinvertebrate communities are not currently impacted¹ by poor water quality. An *in situ* experiment using flow diversion barriers in Chamkharchu at Jakar (Bumthang) was conducted to assess the short-term impacts of reduced water velocity on benthic macroinvertebrate communities to simulate

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the impacts of flow velocity changes associated with reaches downstream of hydropower facilities. We found benthic macroinvertebrate taxa abundance, richness and diversity were not significantly different between high and low flow velocity treatments, but community composition was significantly different between before and after the construction of flow diversion barriers, with reduced abundance of rheophilic (flow-dependent) taxa in treatments with reduced velocity. Current impacts of hydropower facilities are focused on the construction phase. This study has highlighted that the operation of hydropower facilities can also impact the ecological condition of rivers, and that these long-term impacts must be included in the decision making processes for hydropower development. Further investigation is warranted to determine how wide ranging these impacts will be throughout Bhutan.

Keywords: Rheophilic macroinvertebrates, river regulation, flow regime, impoundment, Chamkharchu, Bhutan

Introduction

The country of Bhutan, situated in the Eastern Himalayas on the southern edge of the Greater Himalayan Range, is endowed with immense freshwater resources (Dubey 1978). Fed by glacial melt and monsoonal precipitation, the rivers of Bhutan form the headwaters of the Brahmaputra River, and contribute water to millions of people (Xu *et al.* 2009; Immerzeel *et al.* 2011). These fresh water resources are generally considered pristine (Hartmann & Moog 2008) due to low population pressure and active conservation of watersheds (Ministry of Agriculture: Royal Government of Bhutan (MoA: RGoB, 2014). Increasingly however, these river systems are coming under pressure from climate change, population growth, urbanization and infrastructure associated with hydropower development.

Hydropower generation is currently the primary economic water use in Bhutan, and the generation of electricity both for domestic development and international export underpins the Bhutanese economy (Aquatat: Food and Agriculture Organisation of the United Nations (FAO) 2011). Much of the existing and planned hydropower development is termed 'run-of-river' and utilises natural flows and pressure gradients prevalent in Bhutan's steep and mountainous countryside to minimise impacts on flow regimes, riverine forest, cultivated land and displacement of settlements along riverbanks (Jager & Bevelhimer, 2007; FAO 2011). In reality, dams are often required to provide consistent discharge for power supply. For example, the Punatsangchu is termed a run-of river project designed to provide 5670.78 GWh of power annually, but incorporates a 136 m high dam to regulate flow (FAO 2011). Duration of impoundment in run-of-river schemes may be only in the order of days, but this does not eliminate the potential for impacts of regulation on downstream flow regimes, water quality and movement of biota.

The ecological effects of altered flow regimes downstream of hydropower facilities have been long established (Cushman 1985; Moog 1993). The impoundment of water and subsequent changes to flow velocity and natural flow regimes have a demonstrated potential to negatively affect the diversity and abundance of stream invertebrates that provide key trophic resources in river networks (Käiro *et al.* 2011; Table 3). However, the literature is sparse for both Himalayan rivers and run-of-river hydropower facilities. Invertebrate responses to flow regime shift vary depending on the magnitude, duration and seasonality of the change, the presence of other stressors and the characteristics of the affected system (Suren & Riis 2010, Brooks *et al.* 2011a,b). Altered flow regimes disrupt the transport of coarse and fine particulate organic matter on

which many invertebrates feed (Marchant & Hehir 2002; Takao *et al.* 2008), and alter the physical conditions provided by flow velocity for many rheophilic taxa. Macroinvertebrate responses to different flow velocities indicate that some species prefer particular habitat types (Brooks *et al.* 2011a), with water velocity a principal factor controlling faunal variation (Pardo & Armitage 1997) and the loss of species from reaches with reduced flow following impoundment for hydropower development (Dewson *et al.* 2007; Suren & Riis 2010). The impact of reduced flow velocity on benthic macroinvertebrate communities may be magnified under increased silt deposition and loss of specific habitat types such as gravel runs or rock rapids (Dewson *et al.* 2007; James *et al.* 2008). Short-term reductions in discharge have resulted in increased invertebrate density in remaining flow habitats, thereby increasing competition for resources (Dewson *et al.* 2007; James *et al.* 2008). In contrast, increasing discharge can expand habitat availability and therefore the productivity of lotic invertebrates (Englund & Malmqvist 1996).

Impacts of changes to water quality and the physical environment from hydropower infrastructure and operation include impediments to dispersal, migration and breeding of aquatic taxa, and the potential loss of food resources and changes to trophic networks (Pandit & Grumbine, 2012; Siergieiev *et al.* 2013), as well as altered sediment, organic matter and nutrient transport patterns (Räsänen *et al.* 2012; Boulton *et al.* 2014). Changes in water quality have been found to influence macroinvertebrate communities in conjunction with altered flow regimes (Lancaster *et al.* 2009). Studies suggest that water quality, particularly sedimentation, nutrient enrichment and reduced dissolved oxygen concentrations may be significant factors in how altered flow regimes affect long-term macroinvertebrate community composition, with populations of more sensitive species (e.g., mayflies and caddisflies) declining

while more tolerant species (e.g., aquatic worms, snails and chironomids) become dominant (Biggs & Stokseth, 1996) in rivers with altered flow regimes. Macroinvertebrate fauna appeared to be more resistant to the effects of changed flow regimes if water quality did not deteriorate (Durance & Omerod 2009; Lancaster *et al.* 2009). Therefore, the magnitude of change in macroinvertebrate communities will be influenced by the flow regime and water quality changes associated with presence and operational regime of the reservoir (Käiro *et al.* 2011).

This study aimed to replicate the reduced flow velocities that result from the damming of rivers to supply hydropower by constructing several small-scale experimental dams across an unregulated reach of the Chamkhar chu, central Bhutan. In addition, we characterized the water chemistry and flow velocity environments in a number of rivers across Bhutan to facilitate comparisons with the experimental site. We hypothesized that the reduction in flow velocity downstream of the small-scale dams would lead to a reduction in family-level abundance and richness, and a shift in macroinvertebrate community composition driven by a loss of rheophilic taxa associated with reduced flow velocity.

Methods

Bhutan and hydropower development

The rivers of Bhutan flow from the Himalayas in the north to Brahmaputra in the south, through ten main river basins (Beldring & Voksø 2011; Figure 1). The energy sector is the cornerstone of the Bhutanese economy and accounts for about 18% of the country's total revenue and about 20% of GDP (GNHC 2013). Between 2007-2012 construction began on four hydropower development projects, including Punatsangchu-I, Punatsangchu-II, Mangdechhu and the recently completed Dagachhu, with more projects planned. Globally, dam construction peaked in the 1970s (Malmqvist & Rundle

2002) and has since slowed down in developed countries, but the number of dams is increasing in developing countries (Pandit & Grumbine 2012; Kibret *et al.* 2015). India, for example, aims to double its current hydropower capacity. If all proposed 292 dams were built, the Indian Himalaya region would have one of the highest average dam densities in the world, with one dam for every 32 km of river channel (Pandit & Grumbine, 2012).

Bhutan has an estimated hydropower potential of 30,000 MW. Starting with the commissioning of the 336 MW Chukha Hydropower Power Plant in 1986, Bhutan's current hydropower capacity is 1,500 MW or about 5% of the total potential, with the goal to generate a minimum of 5,000 MW by 2020 (Kuensel 2015). Currently, construction of three hydropower projects ranging 770 to 1200 MW are ongoing and scheduled to be completed by 2020; another seven projects, to generate 10,000 MW of hydropower are planned to start

construction during the current plan period with construction time frames between 8 and 9 years (GNHC 2013).

Study region

The Chamkharchu is fed by the glaciers of Gangkar Punsum and the Monla Karchung ranges and some 557 glacial lakes in total, covering an area of 21.03 km² (Figure 1; Satterthwaite *et al.* 2007). The glaciers of the Gangkar Punsum (7570 masl) region are the source of the western branch, whereas the glaciers south of the Monla Karchung La range feed the two eastern branches of the Chamkhar (ICIMOD, 2015). The Chamkhar flows southwards through the Bumthang valley, which is dominated by blue pine forest (*Pinus wallichiana*) and has a subtropical highland climate. The mean annual rainfall in Jakar is approximately 1404 mm, of which 74% occurs during the monsoon season from June through September (Climate-Data.org, 2015; Department of Hydro Met Services

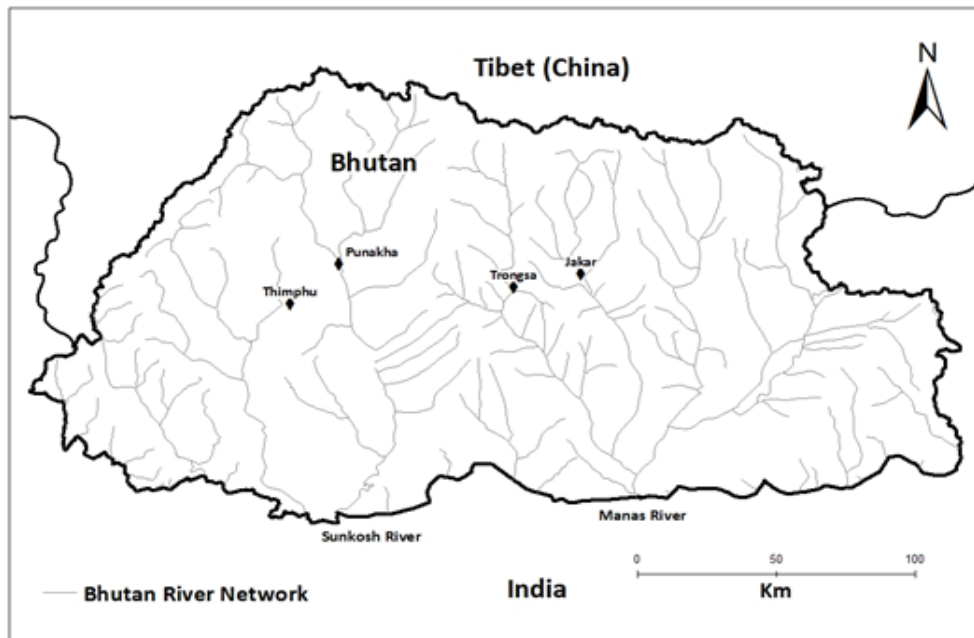


FIGURE 1 Location of major population centres, and study regions for physical and chemical features of rivers. Punakha = ToebiRong, Puna Tsang and Mo Chu; Trongsa = Thrupeang and MangdeChu; Jakar = ChamkharChu.

Bhutan). During this time, streams are subject to maximum water discharge due to heavy rainfall and snowmelt in the upper reaches (Bhatt *et al.* 2005).

The study site for the experimental dams was the Chamkharchu , approximately 2km downstream of the village of Jakar, within the

Bumthang district of Bhutan (E 278697, N 304769) at 2546 masl (Figure 1, Table 1). Five rivers across central Bhutan (Toebirongchu, Phochu, Mochu, Chamkharchu and Mangdechhu) in addition to the experimental sites were sampled for physical and chemical features from November 18th to 19th 2014 (Table 1).

TABLE 1 Location of study sites and physical features

River	Easting	Northing	Elevation (m)	River Width (m)	Disturbances
Chamkhar 1	278694	3048009	2556	30	Human occupation, point source pollution, agricultural runoff, exotic species, livestock access, road
Chamkhar 2	278719	3047942	2556	30	
Chamkhar 3	278737	3047896	2556	30	
Toebi Rong	783224	3047881	1257	10	Cattle, human construction other human impacts, introduced vegetation
Puna Tsang	783563	3050275	1207	38	Clearing, human impact-camping, livestock access
Mo	781811	3056438	1231	42	Human occupation, livestock, litter, road construction
Thuepang	253581	3044431	2088	9	Human occupation, point source run off and pollution, litter, livestock access, bank modification
Mangde	253141	3043872	1839	18	Bridge, road construction upstream

Experimental design and sampling

For the construction of experimental dams, the Chamkharchu was first sampled on 20th November 2014 (Day 1) and again on 25th November 2014 (Day 4). At the time of study, river discharge was an approximate 85th percentile flow, and had remained relatively constant in the previous three months (from ChamkharMET Class A station, Bhutan Hydro-meteorological network). Between sampling dates there was a single light snow and rainfall event higher in the catchment that did not impact river levels.

On Day 1 (pre), three sites were selected along a

150 m reach, approximately 70 m apart (Table 2) with similar depths (15-25cm) and flow velocities (0.13 – 0.71 m sec⁻¹). Semi-circular flow diversion barriers approximately 3 - 4m in length were constructed at each of the three sites with the aim of reducing downstream flow velocity without affecting the flow velocity immediately upstream or in adjacent habitats. Flow diversion barriers to mimic the effects of dams were made using locally sourced river rocks from the dry cobble/ boulder stretch adjacent to the river to minimize disturbance to the experimental sites (Figure 2).

Prior to the construction of the flow diversion



FIGURE 2 The construction of flow diversion barriers from locally sourced cobbles in the Chamkhar Chhu to create reduced flow velocity in downstream habitats and maintain flow velocity in upstream habitats.

barriers water chemistry, flow velocity and benthic macroinvertebrate communities were recorded at locations equivalent to each upstream and downstream experimental location. These spatially explicit data were used to facilitate comparisons with data from the same locations following the instillation of the flow diversion barriers. Water quality parameter of temperature ($^{\circ}\text{C}$), conductivity (μScm^{-1}), dissolved oxygen concentration (mgL^{-1}) and pH were recorded using a YSI 556 Multi-probe (Yellow Springs Instruments, Australia). Flow velocity was recorded in m sec^{-1} using the time taken for a standard flotation device to travel a measured distance downstream (Boulton *et al.* 2014). Water quality and flow velocity were also recorded in the five survey rivers using the methods outlined, with the addition of measurements in both slow (edge) and fast (channel) flow velocity habitats to establish the range of potential values.

Five randomly selected cobbles of approximately 20–25 cm diameter were removed from within each of the up stream and downstream

treatments prior to the construction of the flow diversion barriers. Cobbles were collected one-by-one, rinsed carefully in a bucket with river water to dislodge macroinvertebrates. Macroinvertebrates were then live-picked for 10 minutes and each family placed in a separate petri dish. Due to the requirements for not preserving macroinvertebrates for detailed taxonomic identification, all individuals were identified to family level (Gooderham & Tsyrlin 2002) in the field and their abundance recorded before they were released back into the river. Flow diversion barriers were left in place for 4 days, and macroinvertebrates sampled again at the end of the experiment using the methods outlined above.

Data analysis

For each sampling zone (upstream or downstream of the flow diversion barrier), richness and Shannon-Weiner Index (H') diversity were calculated for pre- and post-flow diversion barrier construction. Both richness and diversity were analysed using R statistical package (www.r-project.org) via

fixed factor analysis of variance (ANOVA), followed by planned comparisons (a priori contrasts) based on the hypotheses of this study. Similarities between macroinvertebrate community composition were analysed using the multivariate analysis package PRIMER (PRIMER-6, Plymouth Marine Laboratory, Plymouth, U.K.; Clarke & Warwick, 2001). To test the null hypotheses that there were no differences between locations upstream and downstream of flow diversion barriers, average differences within groups compared with differences between groups were calculated using analysis of similarities (ANOSIM). Similarities among locations were calculated using the Bray-Curtis similarity on $\log(x+1)$ transformed data. Non-metric multi-dimensional scaling (nMDS) ordination plots were used to graphically represent the patterns of community similarity between flow habitats and pre- and post-flow diversion barrier instillation. Individual taxa contribution to the observed differences among communities between up –and downstream locations were examined separately for each flow environment with the similarity percentage (SIMPER) contribution function in PRIMER.

Results

Water physico-chemistry

The water column physico-chemistry was consistent across all of the study rivers, and edge and channel habitats, with depth and flow velocity the only variables that differed substantially among rivers and habitats (Table 3). As expected for Himalayan streams, water temperature ranged from a chilly 6.2 in Chamkharchu 2556m to 15.4°C in Mo Chuat 1231m elevation. The pH of rivers was consistently alkaline, ranging from 7.3 in Chamkharchu to 8.2 in Mochu. Conductivity was consistently very low, peaking at $100\mu\text{Scm}^{-1}$ in Mochu, with dissolved oxygen concentrations at all sites and habitats exceeding 10mgL^{-1} . Flow velocity was consistently lower in edge habitats (0.1 to 0.5 msec^{-1}) compared with deeper channel habitats (0.86 to 2.5 msec^{-1}). The construction of the flow diversion barriers to mimic the impacts of dams successfully reduced the mean flow velocity of downstream habitats from 0.5 to 0.1 msec^{-1} and maintained upstream flow velocity at 0.5 to 0.6 msec^{-1} over the four day experimental period.

TABLE 2 Mean physical and chemical values for five rivers in central Bhutan, and upstream and downstream in the Chamkhar Chhu pre- and post- flow diversion barrier experiment.

	Toebi Rong			Puna Tsang			Mo			Thuepang			Mangde			Chamkhar		
	Edge	Channel	Edge	Channel	Edge	Channel	Edge	Channel	Edge	Channel	Edge	Channel	Edge	Channel	Edge	Channel	Pre	Post
Depth (m)	0.2	1.1	0.4	1.5	0.8	-	0.2	1.3	0.2	1.3	0.2	1.3	0.2	1.3	0.2	0.2	0.2	0.2
Velocity m sec ⁻¹	0.10	0.86	0.30	1.22	0.6	-	0.10	1.44	0.5	2.5	0.5	2.5	0.6	0.5	0.5	0.5	0.1	0.1
Temperature (°C)	13.9	13.7	13.6	13.2	-	15.4	9.7	9.9	8.7	8.7	9.3	6.2	9.5	6.3	9.5	6.3	9.5	6.3
Dissolved Oxygen mgL ⁻¹	9.7	9.4	11.5	10.7	-	12.6	11.9	10.6	11.3	11.7	10.7	11.1	11.0	12.0	11.0	12.0	11.0	12.0
pH	7.6	7.6	7.9	8.0	-	8.2	8.1	8.1	7.3	7.3	7.3	7.3	7.3	7.3	7.3	7.3	7.3	7.3
Conductivity (µScm ⁻¹)	64	63	90	88	-	100	30	26	73	72	63	64	64	64	64	64	64	64

Effect of flow diversion barriers on macroinvertebrate assemblages

Across all dates and treatments 2099 individual benthic macroinvertebrates were recorded during the experiment, 541 on day 1 compared with 553 on day 4 of the experiment in upstream treatments, and as predicted a reduction from 537 on day 1 to 468 on day 4 of the experiment in downstream treatments (Table 4). However, none of these changes in abundance was significant ($p = 0.05$, $n = 12$). Similarly, family-level richness ranged from 4 to 9, with no consistent response across the experimental treatments. The Dipteran Chironomidae was present at all sites and treatments and were the most numerically abundant taxa. The Ephemeropteran Leptophlebiidae, and Plecopterans Glossomatidae and Eustheniidae were dominant taxa throughout the study (Table 3).

TABLE 3 Review of macroinvertebrate Family-level responses to flow velocity, habitat preference and likely impact from flow regime change

Order	Family	Flow category (m sec ⁻¹)			Habitat preference	Likely impact of velocity change	Author
		<0.1	0.1- 0.6	>0.6			
	Hydropsychidae	x	x	x	Gravel runs/rock rapids; Present in high and low gradient riffles	Low	Brunke <i>et al.</i> (2001); Rabeni <i>et al.</i> (2002); Brooks <i>et al.</i> (2011a)
	Glossosomatidae	x	x	x	Gravel runs/rock rapids; Present in high and low gradient riffles	High	Poff and Ward (1992); Wellnitz <i>et al.</i> (2001); Brooks <i>et al.</i> (2011a)
	Hydroptilidae			x	Gravel runs/rock rapids	Low	Tall <i>et al.</i> (2006); Humphries <i>et al.</i> (1996); Brooks <i>et al.</i> (2011a)
	Leptoceridae	x	x		Edge and run habitats	High	Pardo and Armitage (1997); Humphries <i>et al.</i> (1996); Brooks <i>et al.</i> (2011a)
	Hydrobiosidae			x	Gravel runs/rock rapids; High and low gradient riffles	High	Collier <i>et al.</i> (1995)
Trichoptera	Conoesucidae		x	x	Gravel runs/rock rapids; High and low gradient riffles	Moderate	Jowett & Richardson (1990); Holomuzki & Biggs (2000)
	Neureclipsis	x	x			Low	Brunke <i>et al.</i> (2001); Hunken & Mutz (2007)

	Baetidae	x	x	Gravel and higher velocities; Avoids sand/mud/silt	High	Rabeni <i>et al.</i> (2002); Storey and Lynas (2007); Brooks <i>et al.</i> (2011a)
Ephemeroptera	Caenidae	x	x	High and low gradient riffles; Avoids sand/mud/silt	High	Rabeni <i>et al.</i> (2002); Storey & Lynas (2007); Brooks <i>et al.</i> (2011a)
	Leptophlebiidae	X	x	x	High	Jowett & Richardson, 1990 Holomuzki & Biggs, 2000
Order	Family	Flow category (m sec ⁻¹)		Habitat preference	Likely impact of velocity change	Author
		<0.1	0.1-0.6			
Odonata	Gomphidae	x		Macrophytes; Present in high-low gradient riffles	Low	Rabeni <i>et al.</i> (2002); Storey & Lynas (2007); Brooks <i>et al.</i> (2011a)
	Libellidae	x		Macrophytes; Present in edge waters	Low	Rabeni <i>et al.</i> (2002); Storey & Lynas (2007); Brooks <i>et al.</i> (2011)
	Corydalidae		x	High gradient riffles	High	Rabeni <i>et al.</i> (2002); Brooks <i>et al.</i> (2011a)
Megaloptera						
	Psephenidae	x	x	High and low gradient Riffles. Avoids sand/mud/silt	Moderate	Rabeni <i>et al.</i> (2002); Storey & Lynas (2007); Brooks <i>et al.</i> (2011a)
Coleoptera						
	Elmidae	x	x	Gravel riffles	High	Storey and Lynas (2007); Tall <i>et al.</i> (2006); Pardo and Armitage (1997); Brooks <i>et al.</i> (2011a)
Orthoptera						

	Hydrophilidae	x	x	Edge; Avoids sand/mud/silt	High	Storey and Lynas (2007); Brooks <i>et al.</i> (2011a)
Plecoptera	Gripopterygidae	x	x	High and low gradient riffles	Moderate	Humphries <i>et al.</i> (1996); Brooks <i>et al.</i> (2011a)
	Chironomidae	x	x	Mud/silt/sand/gravel; High and low gradient riffles	Low	Rabeni <i>et al.</i> (2002); Storey and Lynas (2007); Brooks <i>et al.</i> (2011a)
Diptera	Simuliidae		x	Gravel runs/rock rapids; High gradient riffles	Moderate	Fonseca & Hart (1996); Rabeni <i>et al.</i> (2002); Storey & Lynas (2007); Brooks <i>et al.</i> (2011a)
Gastropoda		x		Macrophytes	Moderate-High	Rabeni <i>et al.</i> (2002); Storey & Lynas (2007); Brooks <i>et al.</i> (2011a)
Oligochaeta			x	Mud/silt/sand; Low gradient riffles		Rabeni <i>et al.</i> (2002); (Pardo and Armitage (1997)

Family-level diversity of benthic macroinvertebrates was low in all treatments, ranging from 1.15 ± 0.17 in the upstream treatment to 0.90 ± 0.41 in the downstream treatment, both pre- and post-flow diversion barrier construction. Pairwise comparisons determined that there was no significant difference between the upstream and downstream treatment zones for both pre- and post-flow diversion barrier construction ($p = 0.096$, $n = 12$). Similarly, planned comparisons identified no significant difference ($p = 0.522$; $n = 12$) between pre- and post-construction in the upstream treatments as predicted, but also no significant difference ($p = 0.088$; $n = 15$) between pre- and post-construction in the downstream treatments which did not support the hypothesis of a reduction in family-level diversity with reduced flow velocity.

TABLE 4 Macroinvertebrate family-level abundance, richness and Shannon-Wiener diversity (H') in upstream and downstream habitats pre- and post- flow diversion barrier construction.

	Pre- flow diversion barrier						Post- flow diversion barrier					
	Upstream			Downstream			Upstream			Downstream		
	1	2	3	1	2	3	1	2	3	1	2	3
Acarina		1		1				1				
Chironomidae	186	135	44	40	206	74	157	104	71	100	19	52
Simuliidae			4	1								
Baetidae	1											
Leptophlebiidae	46	41	22	47	3	19	28	29	31	51	43	29
Glossomatidae	21	28	43	35	32	10	3	24	10	16	22	69
Eutheniidae	1	6	4	2	3	21	8	11	2	7	4	3
Notonemouridae			4				11		20	35	13	2
Dytiscidae	5			14								
Elmidae		6					11		7			
Psephenidae						1			21			
Hydrobirosidae				1		2	2	2				1
Leptoceridae	1		28	25					2			1
Richness	6	7	6	9	4	6	6	6	8	5	6	7
Abundance	174	218	149	166	244	127	218	171	164	209	102	157
Diversity (H')	0.93	1.03	0.85	1.25	0.45	1.17	0.96	0.98	1.30	1.19	1.23	1.03
Abundance (mean± s.d)	180.33	34.93		197.00	28.93		154.67	24.09		167.67	38.89	
Diversity (mean ± s.d)	0.94	0.09		1.15	0.17		1.13	0.14		0.90	0.41	

There were no significant differences in community composition between upstream and downstream treatments across both times ($p = 0.44$, $Global\ R = 0.037$), yet a significant difference was recorded between pre- and post- flow diversion barrier construction (Figure 3; $p = 0.01$, $Global\ R\ 0.389$). SIMPER analysis revealed that 61% of the variance in community composition dissimilarity between pre- and post- sampling was explained by the loss of rheophilic taxa such as Plecopteran Notonemouridae and Coleopteran Elmidae (riffle beetles), and reduction of the Ephemeropteran Leptoceridae in downstream treatments post- flow diversion barrier construction. This suggests that while macroinvertebrate diversity and richness recorded no significant response to reduced flow velocity, a reduction in the abundance of key rheophilic taxa resulted in a shift in community composition.

Discussion

Flowing water is a key characteristic of rivers and has a profound influence on aquatic fauna (Dewson *et.al* 2007). The flow of water exerts a physical force on taxa and influences water chemistry, nutrient and organic matter cycles, and habitat availability (Lessard & Hayes 2003; Bunn & Arthington 2002). The most important finding from this study was that a sudden reduction in water velocity directly downstream of the flow diversion barriers did not affect macroinvertebrate diversity and richness, but instead resulted in a shift in community composition, most notably a reduction in abundance of key rheophilic taxa that rely on specific higher flow velocities for food and habitat resources.

Macroinvertebrates have evolved life history traits in response to the natural flow regimes of rivers (Dewson *et al.* 2007). However, when these regimes are altered, predicting how taxa may respond can be difficult (Bunn &

Arthington 2002). For instance, the majority of studies have found that rivers with reduced flow velocity have lower densities, taxonomic richness and total biomass of benthic macroinvertebrates when compared to unregulated sites (Gowns & Gowns, 2001; Brooks *et al.* 2011a, b; Gillespie *et al.* in press). On the other hand, comparative studies have recorded an increase in macroinvertebrate density associated with decreased flows due to a shift in food resource availability (Wright & Symes, 1999). Generally, Chironomidae was the most abundant family both pre- and post- flow diversion barrier construction, which aligns with their description as the most dominant aquatic macroinvertebrate in glacial waters (Milner & Petts 1994; Hamerlík & Jacobsen, 2012). The dominance of Chironomidae compared with families commonly found in flowing streams such as Ephemeroptera, Plecoptera and Trichoptera (EPT) may result from the negative influence of increasing altitude and decreasing temperature that restrict their dominance (Beketov, 2008; Kruitbos *et al.*, 2012).

The rate and severity of flow reduction is a driver of macroinvertebrate abundance and composition as it affects changes to habitat availability, food resources and dispersal mechanisms (Dewson *et al.* 2007). Certain macroinvertebrates are more sensitive to these changes, such as those that initiate downstream drift when flow regime changes. Brewin and Ormond (1994) demonstrated the importance of drift as a dispersal mechanism for benthic macroinvertebrates in Nepalese streams, highlighting the potential impacts to long-term abundance of these taxa if longitudinal connectivity is reduced by the construction of large dams. Rheophilic taxa that have specific velocity requirements are also impacted by reduced flow velocity (Gowns & Gowns, 2001; Gowns *et.al.* 2009). Korte (2010) identified significant preferences for substrate type and

flow velocity for 50 taxa of Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Diptera, Odonata, Mollusca and Oligochaeta in the Hindu Kush-Himalaya region. The loss of rheophilic taxa such as Notonemouridae and Elmidae, and a reduction in Leptoceridae in the downstream treatments post-flow diversion barrier construction provides direct evidence for the potential impacts of altered flow regimes resulting from hydropower dam construction and operation. Equally, when flows are reduced, macroinvertebrates that would have otherwise been displaced by high flow or floods increase in abundance and may dominate the community, preventing the long-term recolonization of displaced taxa (Bednarek 2001).

Bioassessment methods for determining the ecological condition of rivers based on benthic macroinvertebrates are well-suited to assess water resource development and management in the Himalayas due to pronounced longitudinal pollution gradients (e.g. Sharma & Chowdhary 2011; Giri & Singh 2012), which are well reflected in biotic responses. Bioassessment tools for aquatic ecosystem health must include biogeographical factors (Ofenböck *et al.* 2010; Kruitbos *et al.* 2012) because of the inherent variability of benthic macroinvertebrate communities in space and time, the high variation in discharge in Himalayan glacial seasonal rivers (Bookhagen & Burbank 2010), and limited knowledge of aquatic ecosystems and invertebrate fauna in Bhutan (Korte *et al.* 2010). Despite the widespread lack of invertebrate-based assessment methods in the region, a number of studies have explored structural and functional aspects of benthic macroinvertebrates (e.g., Ormerod *et al.* 1994; Brewin *et al.* 2000). The ASSESS-HKH bioassessment protocol of Korte *et al.* (2010) was developed to assess the ecological condition of rivers in the lower mountains and lowlands of the Hindu Kush-Himalayan region

(Pakistan, India, Nepal, Bhutan and Bangladesh) using benthic invertebrates collected from 198 rivers in five different ecoregions and covering degradation gradients. Important for the context of the current study, Korte *et al.* (2010) identified habitat and flow velocity preferences as the dominant non-pollutant metrics that influenced the distribution of benthic macroinvertebrates in the HK-H region. Only 6 of the macroinvertebrate families collected in the current study are listed in the ASSESS HK-H table (Ofenböck *et al.* 2010), and therefore insufficient data were available to apply this assessment tool.

Macroinvertebrate richness was lower than might be expected when compared with other rivers assessed in the Bumthang region (Korte *et al.* 2010), and may be an artefact of undertaking the experiment in late autumn (November). However, Brewin *et al.* (2000) recorded little seasonal variation or direct response to monsoonal flooding in benthic macroinvertebrate communities in Himalayan streams, instead supporting the view that the ecological response might reflect an adjustment to a predictable flow pattern. Catchment land use was reported as a significant source of ecosystem instability, confounding the interpretation of seasonal effects. Decreased macroinvertebrate richness has been positively correlated to anthropogenic influences such as rubbish and effluent disposal in other parts of the Himalayas (Syrovatka *et al.* 2008), and specifically in rivers of Bhutan (Giri & Singh 2012). The low family-level richness and dominance of Chironomidae found in this study points to the possibility of water pollution, particularly the proximity of the experimental study site to the town of Jakar, although water quality assessments including nitrogen, phosphorus and suspended sediment concentrations are required to provide more information on the role of pollution on macroinvertebrate community structure.

The physical and chemical features of the six rivers sampled in this study were remarkably consistent despite their spatial separation and difference in elevation. Water temperature can regulate the broad-scale spatial distribution of macroinvertebrates and was higher than that proposed by Milner and Petts (1994) for glacial fed rivers. However, this may be explained by the presence of glacial lakes feeding rivers; for example, the lake Chubda Tsho (Komori 2008) lies high in the upper catchment of the Chamkharchu and may act as a modifier on temperature downstream (Milner & Petts 1994). Similarly, tributary streams can increase temperature, with the Chamkharchu having a number of permanent spring fed tributaries (Bookhagen & Burbank 2010) that may also modify water temperature. The presence of high velocity environments ($>1 \text{ m sec}^{-1}$) in all six of the rivers sampled in this study, and the clear response of benthic macroinvertebrate community composition to a reduction in flow velocity highlights the widespread potential for hydropower development to affect regional biodiversity. However the impacts of regulated flows on benthic macroinvertebrates differ according to the structural features, purpose and operation of the dam (Watts *et al.* 2010). Larger dams across a range of rivers are proposed as part of Bhutan's hydropower projects (Chhopel 2014). Much of the global literature that has focused on the construction and operation of hydropower dams has documented lower macroinvertebrate densities downstream of these larger structures (Moog 1993; De Jalon & Sanchez 1994; Martinez *et al.* 2013). It is possible to mitigate against the negative impacts of dams through a number of operational measures such as establishing minimum flows (Allan *et al.* 2009; Rolls *et al.* 2012) or implementing environmental flow regimes (Watts *et al.* 2009, Watts *et al.* 2010).

The short-term and spatially focussed nature of this experiment limits the broad-scale extrapolation of changes to benthic

macroinvertebrate community composition, but does highlight the potential for long-term change (see Dewson *et al.* 2007; James *et al.* 2008) and the opportunity to develop management interventions to minimise impacts. One of the three major goals of hydropower development in Bhutan is to 'provide adequate, safe and reliable electricity through sustainable and environmentally friendly development of hydropower potential' (Chhopel 2014). The discovery of the Himalayan relictual dragonfly *Epiophlebia laidlawi*, a beetle species *Hydraena karmai*, and the rheophilic taxa *Hydropsyche karmaii* in Bhutan highlight Bhutanese rivers as biodiversity hotspots in a relatively pristine landscape (Chhopel 2014). National water quality standards for Bhutanese streams were established in 1997 and require bi-annual water quality monitoring that will feed into the bioassessment of rivers (GNHC, 2013). Nonetheless, overcoming the core challenge of developing a robust monitoring program to assess the ecological condition of Bhutan's rivers requires increased knowledge of aquatic fauna and their response to altered water quality and quantity. Much of the focus on Bhutan's hydropower development has been on the impacts on riverine environments during the construction phase (Chhopel 2014). This study has highlighted that the operation of hydropower facilities can also impact the ecological condition of rivers, and that these long-term impacts must be included as part of using the best available science in hydropower development (Ryder *et al.* 2010). In the meantime, perhaps the Bhutanese belief of following 'the middle path' (*sensu* Chhopel 2014) may be the most viable solution, with caution applied to future hydropower developments while new information on their ecological impacts is gathered.

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