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Ecosystem engineering by beavers affects mayfly life histories

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SUMMARY

1. The North American beaver has been studied as a model ecosystem engineer for many decades. Previous studies have documented physical, chemical and biological impacts attributed to beaver engineering in both aquatic and terrestrial environments. This study focused on the effects of ecosystem engineering by beavers on life histories of a common mayfly and on the potential consequences for mayfly populations.

2. We studied 18 montane beaver ponds of varying size and shape in western Colorado near the Rocky Mountain Biological Laboratory. Our goal was to test whether variation in beaver pond morphology (pond size and shape) explains downstream changes in stream temperature, mayfly size and timing of emergence.

3. Downstream water temperatures varied predictably with pond morphology, being colder downstream of high-head dams and warmer downstream of low-head dams. Pond morphology was also a significant predictor of variation in the size of mature female *Baetis bicaudatus* (the most abundant mayfly), with larger females emerging downstream of high-head dams and smaller females downstream of low-head dams. The size of male *B. bicaudatus* was not significantly related to pond morphology or stream temperature. There was no relationship between pond morphology and variation in the timing of emergence of *Baetis* (males or females) between upstream and downstream reaches.

4. Our results have implications for the effects of beaver ponds on *Baetis* individual fitness because large *Baetis* females are more fecund. Therefore, predictable female size variation associated with beaver pond morphology makes it possible to model the effects of beaver activity on local contributions of *Baetis* to the regional pool of reproductive adults at the catchment scale. Additionally, predictable changes in the size of emerging mayflies may have important consequences for the magnitude of aquatic to terrestrial resource subsidies in beaver-modified systems.

Keywords: *Baetis bicaudatus*, beaver ponds, groundwater flow, life histories, streams

Introduction

The North American beaver (*Castor canadensis* Kuhl) has been studied as an ecosystem engineer of aquatic and terrestrial environments for decades. Their ability to alter ecological processes in streams and stream networks has been well documented (Rosell *et al.*, 2005; Anderson *et al.*, 2009). The ponds created by beaver activity are relatively short-lived compared to reservoirs created by human-constructed dams; hence, the riverine habitats created by beavers generally have more similarities to low gradient floodplain rivers (Naiman, Johnston & Kelley, 1988) or lentic systems (Hammerson, 1994; Anderson *et al.*, 2009) than to the low order streams that the dams impound (Jakes, Snodgrass & Burger, 2007). Therefore, engineering by

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beavers creates naturally occurring discontinuities of stream networks, thereby altering the continuity of river environments from that predicted by the River Continuum Concept (Vannote *et al.*, 1980). Those habitat changes also alter the productivity of the system by inserting high productivity pond habitats into lower productivity stream reaches (Anderson & Rosemond, 2007). Since headwater streams are known to affect rivers downstream (Gomi, Sidle & Richardson, 2002), the effects of beaver activity could extend well beyond local influences. Therefore, it is important to understand how ecosystem engineering by beavers fundamentally modifies stream networks.

Beaver dams were once ubiquitous across North American waterways (Naiman *et al.*, 1988; Butler, 1995). Despite an historical decline in beaver populations throughout North America in the 1800s, they are currently rebounding (Naiman *et al.*, 1988). Today, there are regions where as much as 40% of the overall stream length is affected by beaver dams (Hammerson, 1994). Similarly, European beaver (*Castor fiber* Linnaeus) populations are rapidly recovering after heavy exploitation (Rosell *et al.*, 2005). Furthermore, beavers are an invasive species in South America where their population growth is increasing at more than 20% per year (Lizarralde, Escobar & Deferrari, 2004). If these patterns of population growth continue, the influence of ecosystem engineering by beavers may inevitably extend across many temperate stream networks throughout the world.

Previous studies have reported abiotic and biotic differences between stream reaches upstream and downstream of beaver ponds. For example, beaver ponds may change groundwater flow patterns (White, 1990; Westbrook, Cooper & Baker, 2006), streambed substrate hydraulic conductivity (Genereux *et al.*, 2008), water temperatures (McRae & Edwards, 1994; Margolis, Castro & Raesly, 2001a; Margolis, Raesly & Shumway, 2001b; Maxted, McCready & Scarsbrook, 2005) and the timing of aquatic insect emergence (Rolauffs, Hering & Lohse, 2001). Higher water tables associated with beaver-altered landscapes have also been found to significantly affect riparian plant growth and species composition surrounding the pond (Wright, Jones & Flecker, 2002; Westbrook *et al.*, 2006). Furthermore, elevated water tables cause changes in pressure heads of ground water, which can result in greater groundwater upwelling downstream of beaver dams (White, 1990). Consequently, alteration in hydrology associated with pond-induced upwelling could cause cooler ground water to influence downstream water temperatures (White, 1990; Hunt, Strand & Walker, 2006). Those thermal modifications could affect aquatic insect development times and growth rates, thus altering life histories of insects in stream reaches downstream of beaver impoundments relative to their immediate upstream reaches (Ward & Stanford, 1983).

Given that stream insects often use water temperature as a cue for emergence (Sweeney & Vannote, 1978; Vannote & Sweeney, 1980; Ward & Stanford, 1982), changes in water temperatures associated with beaver-altered streams could also affect the phenology of those insects. However, emergence of some stream insects is triggered by a change in temperature rather than by cumulative degree-days (Ward & Stanford, 1979). Consequently, an abrupt shift towards lower temperatures resulting from upwelling into the stream could cause delayed insect emergence downstream of beaver ponds. In contrast, spillover from shallow ponds receiving more solar radiation may reduce the influence of upwelling on downstream water temperatures. Under this latter scenario, warmer water spilling over from shallow, low-head ponds could warm downstream reaches, resulting in opposite effects on insect development. Thus, expected effects on insect development downstream may vary depending on the size and shape of beaver ponds. Furthermore, accelerated development reduces the time for growth and can result in a smaller size at maturity when insects emerge from their aquatic habitats (Vannote & Sweeney, 1980). Relatively small changes in female size will affect individual fitness if fecundity is related to size at maturity (Peckarsky *et al.*, 1993).

The purpose of this study was to evaluate whether ecosystem engineering by the North American beaver altered the life history of animals inhabiting beaver-modified environments. Our approach was to investigate whether variation in beaver pond morphology was a predictor of differences in mayfly size and timing of emergence upstream and downstream of beaver ponds. We tested the hypothesis that reaches downstream of ponds engineered with high dams (high hydraulic head) relative to pond surface area would be cooler when compared to upstream reaches and ponds with low dams relative to surface area would warm waters downstream. We also tested

whether those changes in temperature were associated with variation in the size of mayflies emerging from downstream reaches in comparison with upstream reaches. Specifically, we predicted accelerated development and smaller size of insects emerging downstream of large surface area, low-head ponds and delayed development and larger sizes of insects emerging downstream of small surface area, high-head ponds.

Methods

Study sites

In the summers of 2007 and 2008, we studied a variety of beaver ponds in Colorado, near the Rocky Mountain Biological Laboratory, to evaluate their impacts on stream water temperatures, insect size and timing of emergence in tail waters downstream. Study sites (Table 1) ranged in elevation from 2800 to 3000 m in 2007 (n = 12) and from 2850 to 3150 m in 2008 (n = 10). Beaver ponds in 2007 were located in four different drainage basins (Coal Creek: 2 ponds; East Brush Creek: 3; Oh-Be-Joyful Creek: 3; and West Brush Creek: 4), while sites in 2008 were located in two drainage basins (Cement Creek: 6; and West Brush Creek: 4). Each site consisted of an upstream reach – beaver pond – downstream reach geomorphic pattern without any intervening tributaries. We chose this study site pattern to increase the probability of isolating the effects of a single pond on the downstream reach in comparison with a reference upstream reach. Thus, we collected data from upstream reaches far enough upstream of beaver ponds to avoid any influence of the pond itself. Hydraulic heights (measured as the distance from the water surface of pond to water surface of downstream reach) ranged from 0.28 to 1.77 m in 2007 and from 0.42 to 2.43 m in 2008. Surface areas of ponds ranged from 0.031 to 0.497 ha (2007) and 0.013 to 0.162 ha (2008) (Table 1). Pond lengths (linear distance from pond inlet to dam) were

Table 1 Pond site elevation, morphology characteristics and mean baseflow stream temperatures for upstream and downstream reaches of 2007 and 2008 study sites. Pond morphology ratio is the natural logarithm transformed ratio of dam height to pond surface area

Site	Year	Site elevation (m)	Hydraulic height (m)	Pond length (m)	Max pond width (m)	Surface area (ha)	Pond morphology ratio	Mean temperature (°C)	
								Up	Down
WBC1	2007	2911	1.77	26.9	39.8	0.074	3.2	10.7	10.7
WBC2	2007	2930	1.00	32.0	22.9	0.036	3.3	10.5	10.1
WBC4	2007	2924	0.75	26.6	31.3	0.046	2.8	10.4	10.3
WBC5	2007	2896	0.50	34.7	48.0	0.091	1.7	12.0	12.0
CC1	2007	2889	0.91	52.9	28.2	0.093	2.3	10.9	11.3
CC2	2007	2945	0.82	20.2	15.4	0.036	3.1	14.3	14.2
EBC1	2007	2847	1.00	53.5	88.0	0.187	1.7	11.1	11.5
EBC3	2007	2836	0.34	71.8	23.9	0.104	1.2	11.5	11.6
EBC4	2007	2836	0.28	21.7	16.9	0.031	2.2	11.8	11.7
OBJ1	2007	2911	1.23	47.7	57.6	0.182	1.9	13.7	13.7
OBJ2	2007	2944	1.19	91.0	116.6	0.497	0.9	13.6	13.8
OBJ3	2007	2955	1.22	49.9	63.0	0.144	2.1	12.1	12.3
WBC1	2008	2911	1.20	26.6	36.2	0.047	3.2	9.1	9.2
WBC2	2008	2930	0.75	19.8	7.6	0.0125	4.1	9.1	8.8
WBC4	2008	2924	0.81	33.9	11.5	0.013	4.1	8.9	8.7
WBC5	2008	2896	0.76	29.5	48.4	0.162	1.5	10.0	10.4
CMC1	2008	2893	0.46	30.7	10.3	0.025	2.9	8.7	8.7
CMC2	2008	2958	0.58	45.8	19.9	0.064	2.2	8.5	8.7
CMC3	2008	2994	0.42	23.1	19.1	0.031	2.6	8.7	8.6
CMC4	2008	3116	0.83	14.5	13.0	0.014	4.1	7.0	6.8
CMC5	2008	3120	2.43	48.6	10.1	0.037	4.2	6.7	6.9
CMC6	2008	3130	0.87	19.0	19.5	0.026	3.5	7.0	6.7

WBC indicates sites on West Brush Creek; CC indicates sites on Coal Creek; EBC indicates sites on East Brush Creek; OBJ indicates sites on Oh-Be-Joyful Creek; CMC indicates sites on Cement Creek.

generally short (Table 1), ranging from 20 to 90 m (2007) and 15 to 50 m (2008), supporting the assumption that natural longitudinal change within a stream would have been minimal in the absence of the beaver pond. Therefore, we attributed the observed differences between upstream and downstream reaches of a beaver pond to the presence of the pond. We measured of pond surface area and all linear distances using a Thales ProMark3 GPS unit with an *x*-*y* plane accuracy of ±1 cm and analysed the data using ArcMap 9.2 (ESRI, 2009). We measured vertical dam heights using a surveying auto level with a vertical accuracy of ±1 cm.

We did zig-zag substrate particle counts at seven sites studied in 2007 and compared particle sizes between upstream and downstream reaches. Substrate particle counts were not made in 2008. Additionally, we measured light insolation in upstream and downstream reaches during 2008 using Onset HOBO® Pendant Temperature/Light Data Loggers. We characterised each site by pond morphology. We used a principle components analysis to determine which pond dimensions (hydraulic height, pond surface area, maximum pond width and pond length) explained the largest variation among sites. On the basis of this analysis, we described pond morphology as the natural logarithm of the ratio of the beaver dam hydraulic height to pond surface area ln[hydraulic height (m):pond surface area (ha)]. This ratio was chosen because it incorporated both the variety of pond sizes and their relative depths. This ratio theoretically reflects variation in the potential influence of beaver ponds via groundwater inputs to downstream reaches; sites with low hydraulic heads and large surface areas should have less groundwater influence on water temperature downstream than sites with high hydraulic head and small surface areas. We selected sites spanning a wide range of pond morphologies to increase the probability of observing a relationship between pond size and shape and variation of downstream changes.

Stream temperature

We recorded stream water temperature upstream and downstream of beaver ponds at each site every 5 min using Onset HOBO® Pendant Temperature/Light Data Loggers with a resolution of ±0.1 °C. Although we installed the temperature loggers before baseflow was achieved in both 2007 and 2008, our analysis included only temperatures during the baseflow period for two reasons: (i) the greatest groundwater influence on temperature would be expected during baseflow; and (ii) the greatest influence on pond surface water temperature from solar insolation will occur at baseflow. We determined the baseflow period by observing daily discharge at a USGS gauging station (09112200) on the East River downstream of the confluence with Cement Creek) and downstream of all study streams. We calculated mean water temperatures for baseflow conditions downstream of all beaver dams in 2007 and 2008 and used each upstream reach as a reference. To analyse the effects of beaver pond morphology on stream temperatures, we subtracted the mean upstream from the mean downstream temperatures, which resulted in positive differences when the downstream reach was warmer than the upstream reach and negative differences when the downstream reach was cooler than the upstream reach. We used simple linear regression to test whether pond morphology predicted the observed differences between mean baseflow water temperatures upstream and downstream of beaver ponds for 2007 and 2008 independently.

Similarly, in 2008 we also recorded water temperature within each pond at the bottom, *c.* 10 cm from the surface and at mid-water. We recorded pond temperatures from 13 August to 11 September, and compared those temperatures to the downstream temperatures recorded over the same time period. To test whether pond morphology influenced downstream water temperatures, we subtracted the mean temperatures of each pond layer from the mean downstream temperature (e.g. downstream mean – pond bottom mean) and compared those differences to pond morphology using simple linear regression. This analysis also enabled us to observe which pond layer most closely reflected the downstream water temperatures, which provided a preliminary test of mechanisms explaining temperature variation downstream of beaver ponds.

Baetis bicaudatus size variation

To examine the effects of beaver ponds on aquatic insect development, we focused on the mayfly, *Baetis bicaudatus* Dodds (Baetidae), which is highly abundant and has been studied extensively in this region. Larval

development of *B. bicaudatus* is affected by stream temperatures (Harper & Peckarsky, 2006). During summer 2008, we collected mayflies with black wing pads (BWP) (life stage IV) weekly for 5 weeks (08 July–05 August) in both upstream and downstream reaches at all 10 sites. BWP stage *B. bicaudatus* are within 24 h of emerging from their aquatic habitat, have stopped eating (have empty guts) and therefore growing, and females have achieved full fecundity (Cowan & Peckarsky, 1990; Peckarsky *et al.*, 2001). Therefore, at this life stage mayflies are considered mature, and the influence of the aquatic environment on reproductive potential is complete.

We collected BWP mayflies with a D-net for 90 s. We sorted samples for BWP *B. bicaudatus* in the field and preserved them in 70% ethanol. In the laboratory, we measured head capsule widths (HCW) and determined sex using a dissecting microscope at 25× magnification and an ocular micrometer. We converted HCW to dry mass (DM) using the following regression equations: female $DM = 1.5845 \times HCW^{3.8302}$ ($r^2 = 0.9343$, $n = 448$) and male $DM = 0.8237 \times HCW^{3.1808}$ ($r^2 = 0.9283$, $n = 399$). We derived those equations from methods reported by Peckarsky *et al.* (2001).

We calculated mean DM of BWP female and male *B. bicaudatus* in both upstream and downstream reaches at each site. We used the difference between downstream DM minus upstream DM to determine the effect of the beaver pond on *B. bicaudatus* size at maturity. DM differences >0 indicated sites where mayflies matured at larger sizes downstream than upstream of beaver ponds, and differences <0 were obtained for sites where mayflies emerged at smaller sizes downstream than upstream. To correct for potential regional size differences between the two catchments (CMC and WBC) where specimens were collected, we conducted an analysis of covariance (ANCOVA) with catchment (fixed effect) and pond morphology (random effect) as the independent variables and downstream – upstream *B. bicaudatus* size difference as the dependent variable. We used restricted maximum likelihood to estimate the random factor in the mixed model. A non-significant catchment effect and no interaction between catchment and pond morphology indicated no regional size differences (ANCOVA; female and male: catchment effect $P > 0.4$, interaction $P > 0.4$). Therefore, we combined data from WBC and CMC and used simple linear regression to test whether beaver pond morphology predicted the observed variation in body size differences from upstream to downstream for mature male and female *B. bicaudatus*. To evaluate the relationship between temperature differences and *B. bicaudatus* size variation, we used a simple linear regression with temperature difference as the independent variable and size difference as the dependent variable. In all analyses, we natural logarithm transformed [$\ln(x)$] pond morphology ratios to meet normality assumptions; but it was not necessary to transform any other data. We conducted all statistical tests and transformations in *R* (R Development Core Team, 2008).

Timing of emergence of Baetis bicaudatus

In summer 2008, we compared timing of emergence of *B. bicaudatus* upstream and downstream of beaver ponds by evaluating abundance curves of BWP individuals at upstream and downstream reaches from weekly benthic samples. Since BWP larvae emerge within 24 h, they are a good alternative to using emergence traps for collecting emerging *B. bicaudatus* (Peckarsky *et al.*, 2001).

We used the test statistic (D) derived from two-sample Kolmogorov–Smirnov two-sided tests conducted in *R* (R Development Core Team, 2008) as an index to compare emergence timing of *Baetis* between reaches upstream and downstream of beaver dams. We assigned the test statistic (D) from each two-sample test a positive sign if downstream emergence was accelerated compared to upstream emergence and a negative sign if downstream emergence was delayed. We used simple linear regressions to test whether pond morphology predicted the differences in timing of emergence (range of D values) of *Baetis* larvae (females and males separately). With only five sampling dates for BWP *Baetis*, we fit a spline interpolation curve for each site, increasing the number of data points from 5 to 10 so that the Kolmogorov–Smirnov tests could be implemented. Such artificial inflation of the degrees of freedom does not affect the outcome of the analysis, because we did not base conclusions on significance tests; instead, we used the relative test statistic values to examine associations between pond morphology and the magnitude of differences between the timing of mayfly emergence upstream and downstream of beaver dams.

Results

Substrate particle sizes did not differ between upstream and downstream reaches (paired *t*-test; $t_{(6)} = -0.09$, $P = 0.9$). Additionally, light insolation was not significantly different between upstream and downstream reaches (paired *t*-test; $t_{(9)} = -0.87$, $P = 0.4$). Neither nutrient concentrations nor algal biomass varied consistently between upstream and downstream reaches (M. Fuller & B. Peckarsky, unpubl. data). Correlations between algal biomass and *Baetis* size were also not significant (M. Fuller & B. Peckarsky, unpubl. data).

Baseflow temperature and pond morphology

Hydrological conditions in the region of this study were very different between 2007 and 2008 (Fig. 1), which is reflected in differences in the annual hydrographs and in baseflow water temperatures. Mean baseflow stream water temperatures for 2007, a low flow year, ranged from 10.4 to 14.3 °C in upstream reaches and from 10.1 to 14.2 °C in downstream reaches ($n = 12$) (Table 1). In the year 2008, a year of very high snow pack, protracted period of thaw and extended high water, mean baseflow water temperatures were much colder, ranging from 6.7 to 10.0 °C in upstream reaches and from 6.7 to 10.4 °C in downstream reaches ($n = 10$). Pond morphology ratios ln[hydraulic height (m):pond surface area (ha)] of beaver ponds studied in 2007 ranged from 0.9 to 3.3 and from 1.5 to 4.2 for ponds studied in 2008 (Table 1). Despite the dramatic contrast in hydrology between years, the regressions between pond morphology and differences in mean baseflow water temperatures between upstream and downstream reaches were significant and negative in both years (2007: slope = −0.16, $r^2 = 0.37$, $F_{1,10} = 5.91$, $P = 0.035$; 2008: slope = −0.17, $r^2 = 0.42$, $F_{1,8} = 5.78$, $P = 0.043$) (Fig. 2). Stream reaches downstream of ponds with high morphology ratios (small surface area ponds with high-head dams) were cooler than upstream reference reaches, and stream reaches downstream of ponds with low-head dams and large surface areas (low morphology ratios) were warmer than upstream reaches.

Ponds never stratified during summer 2008, and mean pond morphology did not predict temperature differences between the mid-water and surface

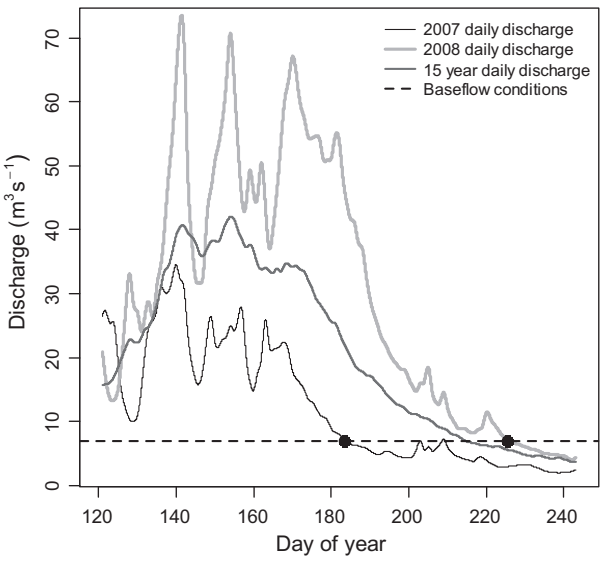

Fig. 1 Discharge from USGS gauging station (09112200) on the East River downstream of the confluence of Cement Creek in 2007, 2008 and a 15 year average (data from 1 May to 31 August). Dashed line at 7 m^3 s^{-1} indicates approximate baseflow conditions at the station and can be used to infer the timing of baseflow conditions in tributaries of the East River. Dots (•) on 2007 and 2008 hydrographs indicate the point in the hydrograph when baseflow temperatures began.

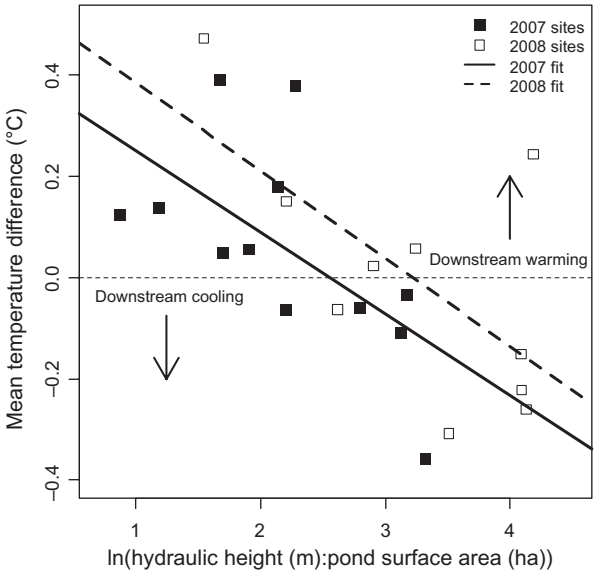

Fig. 2 The relationship between beaver pond morphology and the arithmetic differences in mean base flow temperatures between reaches downstream and upstream of beaver ponds. The *Y*-axis represents mean downstream minus mean upstream temperatures so that positive numbers indicate sites where beaver ponds warm the downstream reaches. Both 2007 (- - -, $y = -0.1608x + 0.4106$) and 2008 (—, $y = 0.1732x + 0.5569$) pond morphology significantly predicted temperature changes.

temperatures of the ponds and the downstream reaches. However, pond morphology was negatively related to the difference between the downstream mean temperature and the temperature at the bottom of the ponds (slope = −0.01, $r^2 = 0.62$, $F_{1,7} = 11.65$, $P = 0.01$). This relationship reveals that reaches downstream of low-head dams were warmer than the bottom of the ponds, and reaches downstream of high-head dams were colder than the bottom of the ponds, which suggests a greater groundwater influence downstream of high-head dams.

Mayfly size and pond morphology

In summer 2008, mean DM of BWP male *B. bicaudatus* ranged from 1.15 to 1.57 mg in upstream reaches and from 1.18 to 1.53 mg in downstream reaches (Table 2). Dry mass of female BWP *B. bicaudatus* ranged from 1.43 to 2.28 mg in upstream reaches and 1.51–2.48 mg in downstream reaches. Pond morphology significantly predicted DM differences of BWP *B. bicaudatus* females (downstream DM – upstream DM) (slope = 0.03, $r^2 = 0.46$, $F_{1,7} = 5.97$, $P = 0.045$) with a positive slope (Fig. 3). The ponds with high-head dams and smaller surface area produced larger female *B. bicaudatus* downstream than upstream. However, pond morphology did not significantly predict male DM differences (slope = 0.02, $r^2 = 0.15$, $F_{1,7} = 1.21$, $P = 0.3$), although the pattern of variation in male *Baetis* size was similar to that of females (Fig. 3). Evaluation of temperature differences as the mechanism of the observed size variation for female *B. bicaudatus* resulted in a significant regression (slope = −0.28, $r^2 = 0.62$, $F_{1,7} = 11.59$, $P = 0.01$) with larger females maturing in stream reaches with cooler temperatures and smaller individuals in warmer stream reaches. However, temperature differences were not significantly related to male *B. bicaudatus* size variation (slope = 0.04, $r^2 = 0.03$, $F_{1,7} = 0.2$, $P = 0.7$).

Emergence timing and pond morphology

Pond morphology did not significantly predict differences between timing of emergence of *B. bicaudatus* in reaches upstream compared to downstream of beaver ponds during summer 2008 (females: slope = −0.13, $r^2 = 0.08$, $F_{1,8} = 0.73$, $P = 0.4$; males: slope = 0.17, $r^2 = 0.14$, $F_{1,8} = 1.30$, $P = 0.3$).

Discussion

The results of this study suggest that ecosystem engineering by beavers predictably alters the life history of the mayfly *B. bicaudatus* by changing the temperature regime of streams. Specifically, the engineering of pond size and shape dictates the nature of the effect on *B. bicaudatus* life history. Ponds with small surface areas and high-head dams cool the baseflow temperatures of their downstream reaches resulting in *B. bicaudatus* that mature at relatively larger sizes than their counterparts in upstream reference reaches. In contrast, large surface area

Table 2 Mean dry mass and sample sizes for female and male black wing-pad *Baetis bicaudatus* collected in reaches upstream and downstream of beaver ponds in 2008

	Mean dry mass (mg)				Sample sizes			
	Upstream		Downstream		Upstream		Downstream	
Site	Female	Male	Female	Male	Female	Male	Female	Male
WBC1	1.97	1.39	1.83	1.37	23	28	41	30
WBC2	1.43	1.15	1.51	1.18	6	15	3	2
WBC4	1.55	1.19	1.67	1.23	30	35	28	16
WBC5	2.27	1.53	2.15	1.51	59	56	60	59
CMC1	2.12	1.39	2.07	1.33	43	51	44	22
CMC2	(2.02)	(1.36)	(2.48)	(1.44)	54	43	9	14
CMC3	1.79	1.34	1.76	1.31	79	75	127	106
CMC4	2.10	1.53	2.14	1.49	19	16	38	18
CMC5	2.14	1.49	2.10	1.53	35	24	19	16
CMC6	2.05	1.57	2.09	1.45	35	21	44	24

Site codes are the same as in Table 1. Values in parentheses were extreme outliers (high Cook's Distance values) and therefore not included in regression analyses (see Fig. 3).

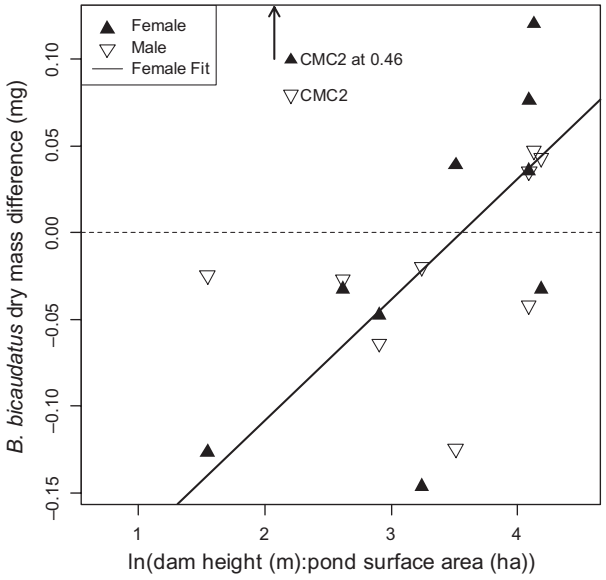

Fig. 3 Relationship between beaver pond morphology and the ratio of mean dry weights of male and female *Baetis bicaudatus* in reaches downstream compared to reaches upstream of beaver ponds. *B. bicaudatus* ratios >1 indicate sites where mayflies matured at larger sizes downstream of beaver ponds. A significant regression was observed for females (—, $y = 0.009571x + 0.9670$), but not for males. Labelled sites were not included in the regression analysis as a result of high Cook's Distance values suggesting high leverage and therefore outlier status.

ponds with low-head dams warm the baseflow temperatures of downstream reaches where mayflies emerge at sizes relatively smaller than in reference reaches upstream of ponds.

Beaver ponds clearly cause changes in stream hydrology and alter groundwater flow paths (White, 1990; Lowry & Beschta, 1994; Westbrook *et al.*, 2006), which are important determinants of stream water temperature regimes (Cadbury *et al.*, 2008). Previous studies mapping groundwater flow paths around beaver dams provide a plausible explanation for the effects of beaver pond morphology on mayfly development that deserves further exploration. Beaver ponds also alter stream bed hydraulic conductivity independently of pond morphology, which increases the potential for upwelling downstream of beaver dams (Genereux *et al.*, 2008). Those hydrological and physical alterations support the ground water–surface water interaction hypothesised in this study and potentially explain why we observed cooling downstream of high-head dams and warming downstream of low-head dams during baseflow conditions in 2 years with very different hydrological conditions (low and high water years) (Fig. 1). Further support for the importance of groundwater influence on downstream temperatures can be observed by comparing the bottom temperatures of beaver ponds to that of the downstream reaches. Downstream reaches were often colder than the bottoms of ponds, especially below high-head dams. Therefore, seepage through (or under) the dam from the pond could not explain the cooling of downstream reaches, consistent with the hypothesis that variation in the influence of groundwater upwelling explains the variation in water temperatures downstream of ponds of different morphology. Our data are consistent with the hypothesis that temperature variability downstream of beaver ponds reflects a balance between ground water–surface water interactions and heat transfer from the pond surface waters, especially in the warming downstream of low-head, shallow beaver ponds.

The temperature patterns revealed in this study could also provide information for managers considering beaver dam removals for creating better trout habitat. Beaver dam removals have been used as a common management practice designed to increase the interaction between ground water and surface water, with the ultimate goal of creating cold trout streams (McRae & Edwards, 1994). However, our study provides evidence that destroying high-head dams could be counterproductive by actually decreasing the interaction between ground water and surface water and thereby warming downstream reaches. Simple pond morphology measurements of the beaver ponds within trout habitat restoration projects could enable stream managers to optimise stream cooling by removing ponds systematically rather than removing all ponds within a catchment.

This study also has implications with regard to the impacts of beaver impoundments on the fitness of stream insects. We observed a significant increase in the size of mature female *B. bicaudatus* downstream of high-head ponds. Given that large *B. bicaudatus* females are more fecund (Peckarsky *et al.*, 1993) and that we can predict effects on the size of female *B. bicaudatus* from beaver pond morphology, we can also use patterns of beaver pond prevalence and morphology to predict local variation in mean individual fitness for *B. bicaudatus* females. It should then be possible to model the spatial variation of individual fitness of *B. bicaudatus* females for a given

population from known pond morphology for a catchment. This protocol could also be used to compare populations in neighbouring catchments and potentially explain some of the regional variation in female mayfly size and fecundity.

For example, *Baetis* females matured 6% larger downstream of one high-head dam in this study (morphology ratio = 4.1), and 7% smaller downstream of one low-head dam (morphology ratio = 1.5). Using published regressions for *Baetis* size–fecundity relationships (McPeek & Peckarsky, 1998), the effects of ecosystem engineering by beavers on the contribution of *Baetis* to the next generation could vary from +11 to −12% depending on the prevalence of beaver ponds of different morphologies. Thus, habitat alterations by beavers have the potential to substantially affect the regional pool of females available to disperse and oviposit throughout stream catchments. It should also be noted that *B. bicaudatus* female eggs do not vary in size, so female dry mass variations are directly related to the number of eggs produced (McPeek & Peckarsky, 1998).

Effects of pond morphology on male *B. bicaudatus* size were not significant, but did follow a trend similar to that of females. The lack of a significant relationship to pond morphology could be explained by differences between male and female growth, development and fitness optimisation, which is common in other insect species (Wiklund, Nylin & Forsberg, 1991; De Block & Stoks, 2003). For example, male *B. bicaudatus* do not have a large size advantage (Peckarsky *et al.*, 2002). Instead, the probability of mating is highest for intermediate sized male *B. bicaudatus* (Peckarsky *et al.*, 2002). Similarly, differences in fitness optimisation between males and females have been shown to result in different growth rates when exposed to similar environmental conditions in other species with sexual size dimorphism (Wiklund *et al.*, 1991; De Block & Stoks, 2003). Alternatively, a retrospective power analysis demonstrated low power (power = 0.18) to detect a significant effect of pond morphology on male size.

The timing of emergence of aquatic insects has been shown to vary predictably with environmental variables (Christman & Voshell, 1992; Harper & Peckarsky, 2006). For example, Harper & Peckarsky (2006) demonstrated experimentally that *B. bicaudatus* reared under higher temperature regimes (~2 °C on average) emerge earlier and at smaller sizes than those that have a longer development period. In this study, we did not observe significant differences in the timing of emergence between adjacent stream reaches upstream and downstream of beaver ponds despite the predictable effects of pond morphology on stream water temperatures during baseflow. While it is possible that such temperature differences are too small to cause phenological shifts in mayflies, we cannot rule out the possibility that weekly sampling was not frequent enough to capture more subtle differences in peak emergence times between stream reaches upstream and downstream of beaver ponds. Emergence timing differences of more than a few days are biologically significant for *B. bicaudatus*, because males live as adults for a maximum of 4 days and females even fewer (Vance, 1996; Peckarsky *et al.*, 2002).

Overall, the observed variation in mean body mass of female *B. bicaudatus* as a result of beaver activity and associated variation in the potential contribution of *Baetis* to the next generation could effectively alter the population sizes of future generations of this mayfly. Those changes in mayfly population sizes could also influence the contribution of emerging aquatic insects as a prey subsidy for terrestrial predators. Such resource subsidies from stream ecosystems have been shown to have important consequences for terrestrial food webs (Nakano & Murakami, 2001; Baxter, Fausch & Saunders, 2005). Thus, by modifying mayfly fecundity, ecosystem engineering by beavers could substantially alter the population dynamics of one of the most abundant species in these montane streams.

In conclusion, our results are consistent with the hypotheses that ecosystem engineering by beavers has a significant impact on the life histories of *Baetis* mayflies developing in their tail waters and that the nature of those effects can be predicted from pond morphology characteristics. Temperature variability in the downstream reaches of beaver ponds reflects a balance between two mechanisms: heat transfer to and from pond surface waters, and modification of ground water–surface water interactions. Further empirical tests of the conditions under which those alternative mechanisms predominate could be fruitful. Additionally, morphological variation among beaver ponds influences spatial variation within stream catchments of individual mayfly fitness and subsequent population growth, as well as variation in the contributions of emerging adults to resource

subsidies in the terrestrial environment. Finally, predictable patterns of variation among beaver ponds could enable forecasting of downstream impacts of ecosystem engineering by beavers on populations, communities and ecosystems in tail waters. As beaver populations continue to increase across Europe and North America and rapidly invade South America, understanding and predicting those alterations to stream ecosystems will be vital. Given that up to 40% of the length of streams in a catchment can be occupied by these ecosystem engineers (Hammerson, 1994), they are clearly a common geomorphic agent in streams that cannot be ignored in the landscape; their influences need to be incorporated into stream ecology theory.

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