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# Meta-analyses of the effects of river flow on fish movement and activity

Mark K. Taylor and Steven J. Cooke

**Abstract:** Estimating the timing and magnitude of fish movements relative to environmental factors can provide insight into why fishes behave as they do. To make broad-level inferences about fish movement in lotic environments, we conducted random-effects meta-analyses on the effects of river flow magnitude on (i) non-migratory movements, (ii) upstream migratory movements, (iii) downstream migratory movements, and (iv) fine-scale activity. We found a significant positive effect of river discharge on non-migratory movements ( $\bar{r} = 0.41$  (mean)  $\pm 0.07$  (SE),  $Z = 6.06$ ,  $p < 0.01$ ,  $k$  (sample size) = 27); fishes made larger and (or) more frequent movements during periods of elevated discharge. Furthermore, non-salmonids were more affected by river flow than salmonids. River discharge also had a significant positive effect on the rate, frequency, and probability of upstream migratory movements ( $\bar{r} = 0.23 \pm 0.10$ ,  $Z = 2.24$ ,  $p < 0.05$ ,  $k = 8$ ). However, the effect of discharge on the rate of downstream migratory movements ( $\bar{r} = -0.05 \pm 0.15$ ,  $Z = -0.35$ ,  $p > 0.05$ ,  $k = 5$ ) and fine-scale activity ( $\bar{r} = 0.01 \pm 0.11$ ,  $Z = 0.08$ ,  $p > 0.05$ ,  $k = 5$ ) were not significant. Heterogeneity of effect sizes was evident in all meta-analyses as well as inclusion and (or) publication bias. Collectively, our meta-analyses suggested that changes to a river's flow regime can modulate non-migratory fish behaviour, the consequences of which need to be explored in terms of habitat use and energy budgets. However, more studies are needed to examine potential effect modifiers and improve sample sizes overall.

*Key words:* river, flow regime, hydropower, telemetry, swimming activity, fish movement.

**Résumé :** L'estimation de la chronologie et de l'ordre de grandeur des mouvements des poissons en relation avec les facteurs du milieu fournissent des indices pour comprendre comment les poissons agissent comme ils le font. Afin d'établir des inférences à larges échelles à propos du mouvement des poissons dans des milieux lotiques, les auteurs ont conduit des métaanalyses à effets aléatoires concernant les effets de l'ampleur du flux des rivières sur (i) les mouvements non-migratoires, (ii) les mouvements migratoires vers l'amont, (iii) les mouvements migratoires vers l'aval et (iv) l'activité à échelle fine. Ils ont constaté un effet positif de la décharge des rivières sur les mouvements non migratoires ( $\bar{r} = 0,41$  (moyenne)  $\pm 0,07$  (SE),  $Z = 6,06$ ,  $p < 0,01$ ,  $k$  (dimension de l'échantillon) = 27); les poissons ont effectué des déplacements plus importants et plus fréquents lors de périodes de décharge plus abondantes. De plus, les non-salmonidés étaient plus affectés que les salmonidés. La décharge des rivières exerce aussi un effet positif significatif sur le taux/fréquence/probabilité des mouvements migratoires en amont ( $\bar{r} = 0,23 \pm 0,10$ ,  $Z = 2,24$ ,  $p < 0,05$ ,  $k = 8$ ). Cependant, l'effet de la décharge sur les taux de migration vers l'aval ( $\bar{r} = -0,05 \pm 0,15$ ,  $Z = -0,35$ ,  $p > 0,05$ ,  $k = 5$ ) et sur l'activité à échelle fine ( $\bar{r} = 0,01 \pm 0,11$ ,  $Z = 0,08$ ,  $p > 0,05$ ,  $k = 5$ ) n'était pas significatif. L'hétérogénéité des dimensions des effets était évidente dans toutes les métaanalyses incluant les biais des inclusions/publications. Collectivement, les métaanalyses des auteurs suggèrent que les changements de régime de flux d'une rivière peuvent moduler le comportement non migratoire des poissons, dont on doit explorer les conséquences en terme d'utilisation de l'habitat et de budgets énergétiques. Cependant, on doit conduire d'autres études pour examiner l'effet des modificateurs potentiels et améliorer les dimensions des échantillons en général.

*Mots-clés :* rivière, régime de flux, pouvoir hydroélectrique, télémétrie, activité natatoire, mouvement des poissons.

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## Introduction

There is growing recognition that alterations to river flow regimes threaten the biodiversity and ecosystem functions of rivers on a global scale (Nilsson et al. 2005). Transportation, water supply, flood control, agriculture, and power generation can profoundly alter natural flow regimes (Poff et al. 1997). Furthermore, climate change during the 21st century is expected to affect the magnitude and timing of low- and peak-flow events, especially in snowmelt dominated basins, producing hydrographs that are more similar to those of regulated rivers (Adam et al. 2009; Mantua et al. 2010). Given this, there is a need to develop a general quantitative understanding of aquatic ecosystem responses to various degrees of flow alteration to help support scientifically defensible flow standards that could be applied to rivers in the face of global environmental change (Poff and Zimmerman 2010).

Artificial increases in discharge are usually caused by “pulse flows” or “hydropeaking” in which water is retained in a reservoir and released as temporally variable water pulses downstream of a power station. However, river floods are an analogous event that increases river discharge, often very quickly, beyond its mean value and can also have detrimental effects on fish survival (e.g., Weyers et al. 2003; Xu et al. 2010; Young et al. 2010). While natural flow regimes are inherently variable (Poff et al. 1997), which has contributed to the evolution of organisms highly adapted to dynamic conditions (Giller and Malmqvist 1998), extreme flood events and anthropogenic flow alterations may be significant challenges for fish.

Despite literature documenting negative effects of unpredictable spates of water flow on river and stream fishes (e.g., Haxton and Findlay 2008), there is less research investigating mechanisms to explain these population or community scale changes. Movement studies are useful because properties of the physical environment (e.g., river velocity, temperature) modulate the distribution of fish, largely through their effect on fish swimming performance (Domenici and Kapour 2010). For example, pulse flows may impact community structure and survival when fish are forced downstream away from preferred habitat. Indeed, abrupt changes in stream discharge have been documented to cause “wash-out” in juvenile fishes (e.g., Heggenes and Traaen 1988; Vehanen et al. 2000), presumably because of their reduced swimming performance relative to large-bodied fishes. Out of concern for downstream forcing of adult fish, researchers have attempted to document their movements relative to river discharge. While some studies have found a significant effect of river flow on fish movement (e.g., Simpson and Mapleston 2002; Young et al. 2010), others have not (e.g., Scruton et al. 2005; Enders et al. 2008). Movement also enables migration between habitats used by different life-history stages. A number of studies have examined the effect of river flow on fish migrations and have found the timing to be correlated with both increases and decreases in the discharge hydrograph (e.g., Miller and Scarnecchia 2008; Almeida et al. 2002).

The precision of telemetry locations used to estimate fish movements is best suited for quantifying movement at a relatively coarse scale, and do not account for localized move-

ments (<1 m; Lucas and Baras 2000). Fish can expend energy swimming to hold station against a river current without actually displacing themselves (Gee 1983). Therefore, swimming activity — specifically referring to the fine scale movements associated with swimming — is also relevant to the fitness and survival of fishes (Boisclair and Leggett 1989). Researchers have tested the effects of river flow on fish activity (e.g., Cocherell et al. 2011) with interest in determining the mechanisms to explain reduced growth associated with altered flow regimes (e.g. Korman and Campana 2009).

Given the conflicting knowledge on the effect of river flow on fish movement, migration, and activity, we conducted meta-analyses on these topics. Our objective was to quantify the overall population effects and identify central trends across a multitude of studies to avoid the biases associated with narrative reviews. Meta-analyses are a more objective method of review (Schmidt 1992) using statistical techniques to synthesize assimilated independent studies while generating a measure of uncertainty for the average effect size. Originally used in medicine and epidemiology, meta-analyses are becoming increasingly used in natural sciences as part of evidence-based conservation (Pullin and Stewart 2006).

## Methods

### Data collection

We assembled relevant studies cited in our personal collections and then searched Web of Science database for studies that modeled the effect of some metric of river flow (e.g., river discharge or velocity) on fish non-migratory movements, upstream migratory movements, downstream migratory movements, and fine-scale activity. Specifically, our searches used “flow”, “discharge”, and “flood” to describe river hydrology and fish “movement”, “migration”, and “activity” to describe behaviour. The citations from the top ten relevant papers in each category were then reviewed for additional studies. The searches yielded 135 references on the appropriate topic. Many studies examined the environmental correlates of fish migration using fish captures at dams, ladders, weirs, and traps to quantify migration timing or dam passage (38). These studies were not used as it was unclear how river flow interacted with the fish passage structures to affect attraction or passage efficiency. Five movement studies that used mark and recapture techniques were also excluded as sample sizes (i.e., number of fish recaptured; often in the hundreds) were not compatible with sample sizes from electronic tagging studies (telemetry, PIT). Including mark and recapture studies would have biased results of our weighted meta-analysis (sample sizes were used to estimate variance associated with each effect size; see below). Ten studies specifically examined the downstream forcing of juveniles and fry by high water velocity (e.g., Heggenes and Traaen 1988; Vehanen et al. 2000). These studies were all conducted using artificial stream channels with some sort of downstream trap for counting “washed-out” individuals. Since these studies were not using free-ranging fish and did not actually quantify movement, we excluded them from the meta-analyses. Three studies examined the effect of changing vs. stable discharge on movement and activity. While these analyses were of interest to us, there were simply too few studies in this category to

be effectively meta-analyzed. This manuscript exclusively relied on electronic tagging studies (telemetry and PIT technologies) of free-ranging fish (78). However, many of these studies did not use quantitative methods or did not report enough detail in their statistics (33). For example, some manuscripts simply reported “no significant correlations were found”. Others reported  $F$  values and degrees of freedom (from which an effect size can be calculated), but did not indicate the direction of their non-significant effect (e.g., Berland et al. 2004; Cocherell et al. 2010). Three studies reported statistics on individual fish or reported an effect size for a multi-parameter model rather than partial correlations. Two studies reported AICs, but not effect sizes. Other researchers could not separate the effect of discharge from other factors that covaried with discharge such as temperature and season (5 studies). Finally, one study was excluded because of poor study design and one other because we were unable to understand the results.

Relevant studies were organized into four categories. The first category was the effect of river flow on non-migratory movements. These were resident fish movements that were not related to migration. This meta-analysis could not separate the effect of river flow between up- and downstream movements since most studies did not test for movement direction. Positive effects were those associated with relatively larger or more frequent movements. The second category was the effect of river flow on upstream migration. This analysis included both anadromous and potamodromous migrations, but only in the upstream direction (positive effects were in the upstream direction). The third category was downstream migratory movements of iteroparous species post-spawning (positive effects were in the downstream direction). Finally, we examined the effect of river flow on fine-scale movement (i.e., activity) which we defined as any external body movement associated with swimming. These activity studies were conducted using electromyogram (EMG) telemetry (see Cooke et al. 2004 for background on EMG telemetry) or fluctuations in radio signal strength (see Thiem et al. 2010 for background on signal strength fluctuations as a measure of activity). Positive effects were those associated with relatively higher activity.

The following data were extracted from each study: (1) author and year of publication, (2) study species, (3) the number of subjects, (4) units of river flow metric (discharge was used exclusively by all studies, although we would have accepted water velocity) and range of discharges tested, (5) predictors used in addition to river flow, (6) analysis time scale (e.g., hourly, daily, monthly or yearly), (7) whether the river flow regime was regulated or not, and (8) effect sizes. The distance moved between subsequent locations (during some specified time period) was used most often to calculate rates of movement (e.g., metres/day). However, some studies reported other movement metrics such as the number subjects moved, total distance of movements, probability of movement, and frequency of movement. Sometimes movements were estimated at one time period (e.g., daily), but analyzed at some other time scale (e.g., weekly or monthly). We selected Pearson’s correlation coefficient ( $r$ ) as an appropriate effect size (Hunter et al. 1982). Coefficients were obtained for each study, when possible, in the following ways: (i) direct reporting of  $r$ ,  $R^2$ , or partial correlation and (ii) other statisti-

cal values such as: means and standard deviations;  $F$  values and degrees of freedom; or  $P$ -values and sample sizes. These values were then converted to  $r$  using an online effect size calculator (<http://www.lyonsmorris.com/ma1/index.cfm>).  $P$ -values were assumed to be 2-tailed when not reported otherwise. Most authors reported multiple results from the same study when correlating river flow, fish movement, and activity. Using several effect sizes from a single study could potentially give rise to non-independence (Gates 2002). However, multiple effect sizes from the same manuscripts in these analyses were usually the result of multiple species or seasons. For those manuscripts, multiple effect sizes (e.g., different species; Brown et al. 2001) were assumed to be independent.

### Meta-analyses

Because effect sizes vary randomly from study to study, we used a random-effects model to account for both within-study variation and variability arising from differences among studies (Hedges and Vevea 1998). This method emphasises the need to correct for sources of error such as sampling error and reliability of measured variables by using the average correlation coefficient ( $\bar{r}$ ) in which untransformed correlations ( $r_i$ ) are weighted by the sample size ( $n_i$ ) on which they are based (eq. [1]). While the random-effects approach usually produces larger standard errors (and therefore, less-significant effects) than using fixed effects models, our objective was to make unconditional inferences that generalize beyond the studies in the meta-analyses (Field 2001). Standard error ( $SE_{\bar{r}}$ ) was calculated as the standard deviation ( $SD_r$ ) of the observed correlation coefficients (eq. [2]) divided by the square root of the number of studies ( $k$ ) being compared (eq. [3]; Schmidt and Hunter 1999). The significance of the mean effect size was obtained by calculating a  $Z$  score by dividing the mean effect size by the standard error of the mean (eq. [4]; Field 2001).

$$[1] \quad \bar{r} = \frac{\sum_{i=1}^k n_i r_i}{\sum_{i=1}^k n_i}$$

$$[2] \quad SD_r = \sqrt{\frac{\sum_{i=1}^k n_i (r_i - \bar{r})^2}{\sum_{i=1}^k n_i}}$$

$$[3] \quad SE_{\bar{r}} = \frac{SD_r}{\sqrt{k}}$$

$$[4] \quad Z = \frac{\bar{r}}{SE_{\bar{r}}}$$

### Assessment of bias and heterogeneity

Publication bias (i.e., “file drawer problem”) is a concern in meta-analyses: studies that show large effects may be more likely to be published than those that show no difference (Rosenthal 1979). Therefore, we calculated the number of studies averaging null results that must be filed away before the overall probability of a Type I error is brought to  $p = 0.05$  (i.e., the “fail-safe number”; eq. [5]; Rosenthal 1979). Bias was also assessed using funnel plots (Egger et

al. 1997), a graphical method in which the effect size and its associated measure of precision (i.e., sample size) is plotted. Studies with low precision should show a large scatter of effect sizes around the true values whereas larger studies should have an effect size closer to the true value (Gates 2002). Funnel symmetry was determined by regressing  $k$  and  $r_i$  and using the intercept as a measure of asymmetry (the greater the deviation from zero, the greater the asymmetry). Of course the statistical power of these tests depends on sample sizes (which are generally small in ecological meta-analyses, including this one). We therefore based evidence of asymmetry on  $p < 0.10$  (Egger et al. 1997). Deviance from this funnel pattern (i.e., asymmetry) may indicate bias in the studies in the meta-analysis (Gates 2002). Heterogeneity of effect sizes was assessed using the chi-square statistic ( $\chi^2$ ), calculated based on the sum of squared errors of the mean effect size (eq. [6]; Hunter and Schmidt 1990).

$$[5] \quad k_{fs} = \frac{k}{2.706} [k(\bar{Z}_k)^2 - 2.706]$$

$$[6] \quad \chi^2 = \sum_{i=1}^k \frac{(n_i - 1)(r_i - \bar{r})^2}{(1 - \bar{r}^2)^2}$$

## Results

### Is there an effect of river flow on non-migratory movements?

Effect sizes from a total of 27 individual tests (or models) were reported across 11 manuscripts (See Supplemental Table S1<sup>1</sup>). Of these 27 effect sizes, 20 were derived from regulated systems whereby hydropower infrastructure controlled river discharge. On average, the highest discharge events were 40 times (range = 2–332) the magnitude of corresponding low discharge events within each study. Almost all movements were estimated using distance between locations (average or sum) during some specified time period (i.e., rate of movement). One study used percentage of fish moving as their movement metric. Movements were analyzed at the monthly (4), weekly (8), daily (7), and sub-daily (8) scales (Table S1<sup>1</sup>). There was a significant positive effect of river flow on fish movement (no regard to direction of movement;  $\bar{r} = 0.41$  (mean)  $\pm$  0.07 (standard error),  $Z = 6.06$ ,  $p < 0.01$ ,  $k = 27$ ; Table 1), although heterogeneity of effect sizes was evident ( $\chi^2 = 113$ ,  $p < 0.05$ ). Eighteen additional studies with null effect would have to be published to reverse the effect ( $k_{fs} = 18$ ). Funnel plots suggested inclusion and (or) publication bias as Egger's test for funnel asymmetry was significant (intercept = 19.29; 95% confidence intervals (CI): 13.85–24.72;  $p < 0.001$ ; Fig. 1).

### Is there an effect of river flow on upstream migratory movements?

Effect sizes from a total of eight individual tests (or models) were reported across six manuscripts (See Table S2<sup>1</sup>). All studies, except one, were conducted in regulated systems whereby hydropower infrastructure controlled river discharge in at least part of the study area. On average, the highest dis-

charge events were 10 times (range = 3–31) the magnitude of corresponding low discharge events within each study. Six effect sizes were generated using distance between locations as their movement metric. One study used probability of being detected at a receiver and another study used the frequency of movements. Most effect sizes were generated from analyses at the daily (6) or weekly (1) temporal scale. Only one study examined sub-daily movements (See Table S2<sup>1</sup>). There was a significant positive effect of river flow on upstream fish migration ( $\bar{r} = 0.23 \pm 0.10$ ,  $Z = 2.24$ ,  $p < 0.05$ ,  $k = 8$ ; Table 1) and heterogeneity of effect sizes was evident ( $\chi^2 = 20$ ,  $p < 0.05$ ). The fail-safe number suggested that the effect was not robust ( $k_{fs} = 0$ ). Furthermore, funnel plots suggested inclusion and (or) publication bias as Egger's test for funnel asymmetry was significant (intercept = 34.20; 95% CI: 4.59–57.81;  $p = 0.03$ ; Fig. 1).

### Is there an effect of river flow on downstream migratory movements?

Effect sizes from a total of five individual tests (or models) were reported across four manuscripts (See Table S3<sup>1</sup>). All studies were conducted in regulated systems whereby hydropower infrastructure controlled river discharge in at least part of the study area. On average, the highest discharge events were 5 times (range = 4–8) the magnitude of corresponding low discharge events within each study. All five effect sizes were generated using distance between locations during a specified time period as their movement metric. Four studies generated effect sizes from analyses at the daily temporal scale. One manuscript reported downstream movements at the weekly scale. There was no significant effect of river flow on downstream fish migration ( $\bar{r} = -0.05 \pm 0.15$ ,  $Z = -0.35$ ,  $p > 0.05$ ,  $k = 5$ ; Table 1), possibly because of heterogeneous effect sizes ( $\chi^2 = 32$ ,  $p < 0.05$ ). Funnel plots also suggested inclusion and (or) publication bias as Egger's test for funnel asymmetry was significant (intercept = 50.52; 95% CI: -2.47–103.51;  $p = 0.06$ ; Fig. 1).

### Is there an effect of river flow on fish activity?

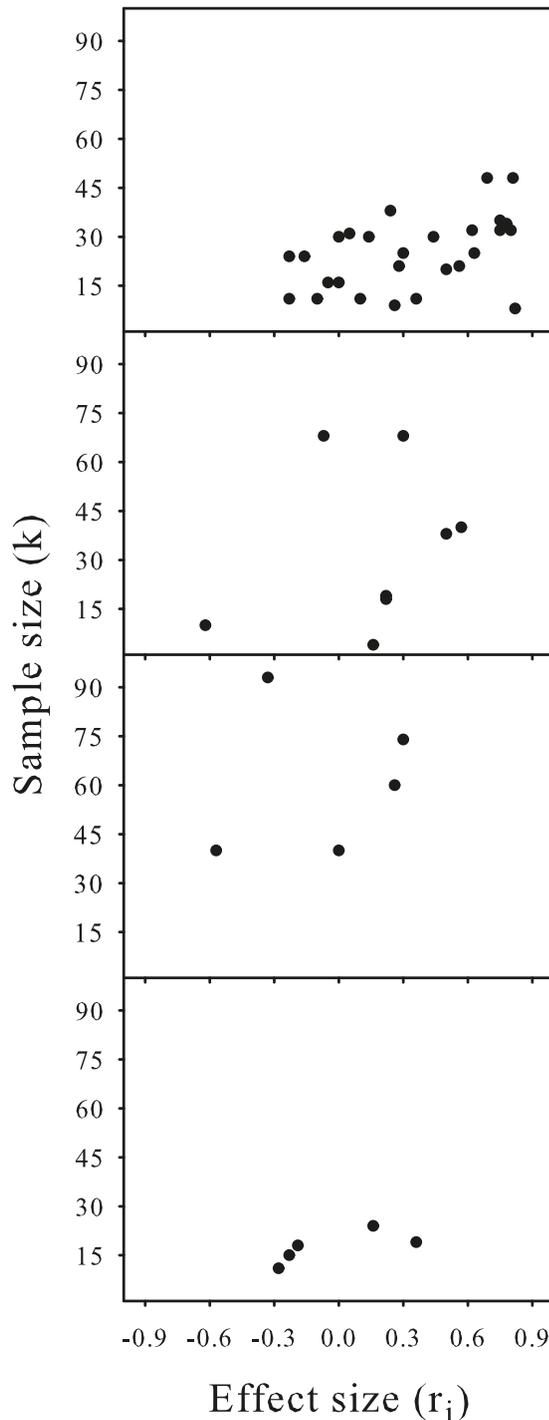
Effect sizes from a total of five individual tests (or models) were reported across four manuscripts (See Table S4<sup>1</sup>). All five effect sizes were derived from regulated systems whereby hydropower infrastructure controlled river discharge. On average, the highest discharge events were 7 times (range = 2–17) the magnitude of corresponding low discharge events within each study. Three effects sizes were generated using fluctuations in radio signal strength as their activity metric and two studies used electromyograms (Table S4<sup>1</sup>). Correlations between river discharge and fish activity were analyzed at the hourly scale, although two effect sizes estimated activity at the daily scale (Table S4<sup>1</sup>). There was no significant effect of river flow on swimming activity ( $\bar{r} = 0.01 \pm 0.11$ ,  $Z = 0.08$ ,  $p > 0.05$ ,  $k = 5$ ; Table 1). The chi-square statistic suggested homogeneity of effect sizes ( $\chi^2 = 5$ ,  $p > 0.05$ ); however, three effects were negative (reduced activity at relatively higher flows) and two effects were positive (heightened activity at relatively higher flows). Funnel plots suggested inclusion and (or) publication bias as Egger's test

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/a2012-009>.

**Table 1.** Estimated effect size ( $\bar{r}$ ), standard error (SE), Z score (Z),  $\chi^2$  test for heterogeneity ( $\chi^2$ ), number of effect sizes included in the meta-analysis ( $k$ ), number of manuscripts ( $N$ ), and fail safe  $N$  ( $k_{fs}$ ) for each meta-analysis.

Behaviour	Effect size ( $\bar{r}$ )	SE	Z	$\chi^2$	$k$	$N$	$k_{fs}$
1. Non-migratory movements	0.41	0.07	6.06	113	27	11	18
2. Upstream migratory movements	0.23	0.10	2.24	20	8	6	0
3. Downstream migratory movements	-0.05	0.15	-0.35	32	5	4	n/a
4. Activity	0.01	0.11	0.08	5	5	4	n/a

**Fig. 1.** Funnel plots for the effects of river discharge on (a) non-migratory movements, (b) upstream migratory movements, (c) downstream migratory movements, and (d) fine-scale activity.



for funnel asymmetry was significant (intercept = 20.49; 95% CI: 12.61–28.37;  $p < 0.001$ ; Fig. 1).

**Discussion**

**The effect of river flow on non-migratory movements**

We found an overall medium positive effect ( $r = 0.41$ ; effects  $>0.30$  are considered “medium” effects; Cohen 1992) of river flow on non-migratory movements. Although fish telemetry literature is often descriptive and without statistical models (e.g., Linnik et al. 1998; David and Closs 2002), the studies that did provide the appropriate statistical effects suggested that the overall population effect is positive; increased water flow may stimulate or promote fish movement. While our meta-analysis suggested that relatively high discharge is correlated with larger and (or) more frequent movements, extreme low discharge could also induce movement if habitat is being de-watered and fish move to avoid stranding (e.g., Armstrong et al. 1998). Some researchers qualitatively stated that no downstream forcing was evident (e.g., Bolland et al. 2008). However, the “flushing” effect observed in juveniles during high flows (e.g., Heggenes and Traaen 1988; Vehanen et al. 2000) could not be reported as movement direction was not usually tested quantitatively in the studies assessed by this meta-analysis. In the few studies that did examine directionality, direction was usually unpredictable (e.g., Simpson and Mapleston 2002). Some evidence suggested that lateral movements (i.e., to side channels and adjacent floodplains) are an effective behaviour to avoid elevated flows associated with main stream channels (e.g., Degrandchamp et al. 2008). Habitat heterogeneity and (or) size of the river may be an important factor that interacts with discharge; fish may be more likely to remain stationary during high flows when they have more refuge in the form of hydraulic retention areas (Simpson and Mapleston 2002; Scruton et al. 2005). Temperature could explain significant variation in movements in three manuscripts (Enders et al. 2008; Popoff and Neumann 2005; Young et al. 2010), but not in four other manuscripts (Clapp et al. 1990; Brown et al. 2001; Bolland et al. 2008; Degrandchamp et al. 2008), and was not tested in another three manuscripts (Simpson and Mapleston 2002; Scruton et al. 2005; Young and Isely 2007). Some studies did not explicitly test for an effect of temperature, but found seasonal differences in movement that may have been the result of temperature (e.g., Scruton et al. 2003). In addition, some researchers documented no response to elevated flow at the population level, but reported individual behaviours relative to discharge. Even when the population effect of discharge was statistically significant, large individual variation in movements was the norm in all studies.

### Is there an effect of river flow on upstream migratory movements?

We found an overall small positive effect ( $r = 0.23$ ; effects  $>0.10$  are considered “small” effects; Cohen 1992) of river flow on the rate, probability, and frequency of upstream migration. However, the mean effect was not robust ( $k_{fs} = 0$ ) and heterogeneity of individual effect sizes was evident. Miller and Scarnecchia (2008) found that paddlefish (*Polyodon spathula*) ascended the Missouri River during elevated discharge. Elevated discharges may have provided greater habitat area and cover from predators thus providing incentive to move. Despite the overall positive effect of discharge on upriver migratory movements, high discharge in the form of regulated releases or natural floods may also delay fish migrations when discharge reaches a certain threshold (Svendsen et al. 2004). For example, when discharge exceeded 72 m<sup>3</sup>/s in the River Mondego, Portugal, sea lamprey's (*Petromyzon marinus* L.) upstream groundspeed was compromised (Almeida et al. 2002). Large individual variation in the rate of upstream migratory movements was noted by almost all authors. Temperature was a significant predictor of migratory movement in three studies (Erkinaro et al. 1999; Svendsen et al. 2004; Paragamian and Wakkinen 2008), non-significant in one study (Miller and Scarnecchia 2008), and not tested in two studies (Almeida et al. 2002; Jeffres et al. 2006).

### Is there an effect of river flow on downstream migratory movements?

No significant effect of river flow on the rate of downstream migration was found. Four of five effect sizes in this meta-analysis were medium–large effects. However, two effects were negative and two effects were positive in direction, thus resulting in no significant effect when combined. For example, Aarestrup et al. (2002) found that the downstream migration speed of sea trout (*Salmo trutta*, L.) was positively correlated with discharge. In contrast, bull trout (*Salvelinus confluentus*) and paddlefish made faster and larger movements under relatively lower flow conditions (Monnot et al. 2008; Miller and Scarnecchia 2008). Only one study found no effect of discharge on downstream migratory movements (Atlantic salmon (*Salmo salar* L.); Aarestrup et al. 2002). Again, large individual variation in the rate of downstream migratory movements was noted by almost all authors. Temperature was a significant predictor of downstream movements in one study (brown trout (*Salmo salar* L.); Aarestrup et al. 2002), but not in three other studies (Aarestrup et al. 2002 (Atlantic salmon); Monnot et al. 2008; Miller and Scarnecchia 2008), and was not tested in one study (Dedual and Jowett 1999).

### The effect of river flow on fish activity

No significant effect of river flow on fish swimming activity was found. Similar to downstream migration, some individual effect sizes were negative and some were positive in direction, resulting in no significant effect when combined. Fish may become less active under relatively higher flows if the costs of foraging become too great. In contrast, fish may need to increase swimming speed to hold station at higher flows, but increased foraging in response to invertebrate drift has also been suggested as a possible mechanism (Cocherell

et al. 2011). The effects of river flow on fish activity are likely based on complex foraging decisions that reflect trade-offs between swimming cost, prey availability, prey accessibility, and the fish's internal energetic status (Huntingford et al. 1988; Metcalfe et al. 1999). Temperature could explain significance in activity in one manuscript (Robertson et al. 2004), was not significant in one other manuscript (Taylor et al. 2012), and was not tested in two manuscripts (Cocherell et al. 2011; Stickler et al. 2007). Due to the low number of studies we could not explicitly test for a seasonal interaction with discharge. However, some researchers reported that the effect of discharge on activity varied among seasons (Robertson et al. 2004).

### Assessment of bias and heterogeneity

Meta-analyses overcome some of the issues with narrative reviews, but they are not without problems. For example, bias in meta-analyses needs to be assessed (Gates 2002). Funnel plots and associated Egger tests suggested publication or inclusion bias in each of our four meta-analyses which may have biased our results. Furthermore, the homogeneity tests suggested that significant heterogeneity existed in each meta-analysis. There are many factors that may influence the effect size for any given study and it is important to identify these factors (Gates 2002). Therefore, we made post-hoc investigations into some possible sources of biological and methodological heterogeneity. For example, species-specific differences could potentially be a large source of heterogeneity as different guilds have different swimming capabilities, modes, and eco-morphological adaptations to deal with changes in flow (Videler 1993; Domenici 2003). For example, non-salmonids ( $k = 9$  effect sizes) were more affected by river flow, in regards to non-migratory movement, compared to salmonids ( $n = 18$ ) ( $t(25) = 2.66$ ,  $p = 0.01$ ). Effect sizes for non-migratory movements generated at the weekly or monthly scale ( $k = 8$ ) were higher compared to those at the daily or sub-daily scale ( $k = 18$ ;  $t(24) = 2.20$ ,  $p = 0.04$ ). A meta-regression (weighted by sample size) of the flow range ( $D_{max}/D_{min}$ , across each individual study period) and corresponding effect size within the non-migratory movement meta-analysis was used to examine additional potential effect modifiers. Flow ranges and effect sizes were log transformed to achieve normality. The effect of flow range was not significant ( $R^2 = 0.18$ ,  $\beta = 0.07$ , 95% CI: 0.00–0.15,  $p = 0.06$ ,  $k = 20$ ). Therefore, the relationship between river discharge and non-migratory movements was not modulated by the range of discharges tested within each study. In summary, some heterogeneity in effect sizes could be explained by our crude classification of species (salmonids vs. non-salmonids) and the time-scale of analysis (weekly/monthly scale versus daily/sub-daily) in non-migratory movements, but not the intensity of the intervention (range of flow conditions). Given the low sample sizes for upstream migratory movements, downstream migratory movements, and activity studies, we were not able to test for sources of heterogeneity.

Haxton and Findlay (2008) suggested that heterogeneity in the effects of water management on invertebrate and fish abundance should be investigated using a single integrated study designed specifically to explore sources of heterogeneity. To accomplish this for fish movement would require that multiple species with different swimming capabilities be

tagged simultaneously and tracked with a range of precision, at a variety of temporal scales, over multiple seasons, and across a range of flow manipulations. Ultimately, this would require that hydropower operators provide flow releases that are orthogonal (uncorrelated) with other pertinent variables such as temperature and day period. Many studies could not distinguish between the effect of discharge and temperature (e.g., Swanberg 1997; Geist et al. 2005) and were subsequently excluded from our meta-analyses despite meeting all the other criteria. As temperature can co-vary with discharge (Olden and Naiman 2010), much more effort is needed to separate these effects. Ultimately, this problem should be addressed in the study design phase of the project. Some statistical techniques are available to deal with collinearity, providing that collinearity is not too strong. We assumed that if collinearity was not discussed in a study, then it was not an issue and the effect of discharge was assumed to be a true effect. However, all fish movements studies need to report the magnitude of correlations amongst all predictors and their approach taken to ensure modelled effects are indeed true effects. Other variables that tend to correlate with discharge also need to be considered (e.g., turbidity; Miller and Scarnecchia 2008).

The meta-analyses presented here used exclusively electric tagging studies (telemetry and PIT technologies) to estimate fish movement and activity. Unfortunately, this excluded some excellent studies examining the effect of discharge on fish movement using other techniques (e.g., mark and recapture; Albanese et al. 2004). Recaptures via either electrofishing, weir counts, or dam counts typically number in the hundreds and are therefore not directly comparable to sample sizes used in telemetry. Very few non-migratory movement papers actually examined directionality of movements and we encourage researchers to do so when possible. Activity studies were exclusively performed on salmonids, which could bias the overall population effect considering that salmonids are considered to be quite strong swimmers (Beamish 1978).

While our meta-analyses have not defined an exclusive set of movement rules for all species, our objectives were to make broad-level inferences about fish movement from multiple independent studies. This provides fundamental insight into the constraints imposed on fish by their environment. In addition, from an applied perspective our findings should improve the ability to anticipate the immediate and cumulative effects of water management practices. Indeed, there is growing recognition that river flow (extreme low and peak flows) can affect growth (e.g., Korman and Campana 2009), abundance (e.g., Liebig et al. 1999), and mortality (e.g., Xu et al. 2010; Young et al. 2010) in fishes. Yet, there is less known about underlying mechanisms to explain these effects. Our analyses show that changes in a river's flow regime do show the potential to modulate a fishes energy budget as some research has suggested that activity metabolism (the portion of the energy budget dedicated to fish movement and station-holding) represents one of the most important determinants of among-population variability in fish growth rates (Boisclair and Leggett 1989; Boisclair and Sirois 1993; Aubin-Horth et al. 1999). For example, Korman and Campana (2009) found higher growth rates of rainbow trout (*Oncorhynchus mykiss*) on days when hydropeaking in the Colo-

rado River was reduced, although no single study has linked flow regime to activity and growth rate. Understanding fish movement in response to changes in flow regime may help explain long-term changes in the presence or absence of certain species from a river if the energetic costs of foraging outweigh the energetic gains from consumption. Furthermore, although we did not find direct evidence of downstream forcing of fishes in response to flow, this would also be a potential mechanism that reduces habitat availability and therefore explains population and community scale changes.

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