

# Non-random dispersal in sympatric stream fishes: Influences of natural disturbance and body size

Akira Terui<sup>1</sup>  | Seoghyun Kim<sup>1,2,3</sup>  | Kasey C. Pregler<sup>2,3</sup>  | Yoichiro Kanno<sup>2,3,4</sup> 

<sup>1</sup>Department of Biology, University of North Carolina at Greensboro, Greensboro, NC, U.S.A.

<sup>2</sup>Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, U.S.A.

<sup>3</sup>Department of Forestry and Environmental Conservation, Clemson University, Clemson, SC, U.S.A.

<sup>4</sup>Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, U.S.A.

## Correspondence

Yoichiro Kanno, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO, U.S.A.

Email: Yoichiro.Kanno@colostate.edu

## Abstract

1. Although the prevailing paradigms in spatial ecology have treated dispersal as a stochastic process, there is an increasing awareness that spatial processes are non-random such that individual characteristics and ecological contexts influence dispersal. Natural disturbance, such as river flooding, is known to stimulate dispersal behaviour, but its interactive effects with individual-level characteristics (e.g. body size) of potential dispersers remain elusive. It is critical to fill this knowledge gap because anthropogenic impacts (including climate change) alter both disturbance regimes and population structures.
2. Here, we examined how extreme high flows and individual body size combined to influence dispersal of three fishes (creek chub *Semotilus atromaculatus*, bluehead chub *Nocomis leptocephalus*, and striped jumprock *Moxostoma rupicartes*) in two streams (740 and 520 m long) in South Carolina, U.S.A. We focused on extreme high flows as a natural disturbance, whereas body size was used as an individual-level characteristic of dispersers. A total of 5,604 individuals were uniquely marked in the two streams over a >2-year study period, during which sampling occurred every 2 months.
3. The intensive capture–recapture study revealed differential effects of disturbance and body size among sympatric stream fishes. Extreme high flows increased dispersal of striped jumprock and creek chub, whereas body size influenced dispersal of striped jumprock with larger individuals traveling longer distances. Bluehead chub showed a complex dispersal response. That is, size-dependence in dispersal emerged only during high-flow periods.
4. The results of this study build upon previous efforts by providing field-based evidence of how disturbance and individual characteristics (body size) combine to drive non-random dispersal and how it varies among sympatric species. This finding is important because metapopulations that are maintained by different non-random dispersal (i.e. externally or internally driven) may show varied sensitivities to human-induced environmental changes.

## KEYWORDS

aquatic system, condition dependency, context dependency, disturbance, river

## 1 | INTRODUCTION

Dispersal, defined as any movement between habitat patches with potential effects on gene flow (Bowler & Benton, 2005; Comte & Olden, 2018b), is a fundamental process that drives species distribution (Kadoya & Inoue, 2015), population dynamics (Lowe, 2003; Shaw et al., 2014) and disease spread (Hess, 1996; Terui et al., 2017). The prevailing paradigms in spatial ecology, such as metapopulation and metacommunity theories, have long treated dispersal as a stochastic process that is independent of ecological contexts (Brown et al., 2011; Hanski, 1999; Leibold et al., 2004). In the meantime, behavioural and evolutionary ecologists have long recognised that dispersal is a flexible trait, such that individual-level characteristics and ecological contexts can influence dispersal (Clobert et al., 2012). Non-randomness in dispersal emerges because the decision to leave a current habitat is ultimately the consequence of balancing fitness costs and benefits. Benefits and costs of dispersal vary among individuals and contexts (Bonte et al., 2012), and dispersal will be favoured only if the expected benefits outweigh the costs (Bonte et al., 2014; De Bona et al., 2019; Terui et al., 2017). Recent theoretical evidence suggests that non-random dispersal can drastically alter the dynamics of spatially structured systems with important implications for ecosystem management (Fronhofer et al., 2017, 2018; Terui et al., 2017). Therefore, understanding the causes of non-random dispersal represents a critical topic in ecology.

Natural disturbance, such as river flooding, is an event that has disproportionate impacts on various ecological processes including dispersal (Fronhofer et al., 2014; Lytle & Poff, 2004; Poethke et al., 2003; Thom & Seidl, 2016; Tonkin et al., 2018). In the long term, disturbance may drive the population-level evolutionary response of increased dispersal as it creates opportunities for dispersers to become founders by vacating local habitats (Denno et al., 1996; Fronhofer et al., 2014; Poethke et al., 2003). In the same vein, it seems logical to expect that disturbance stimulates non-random behaviours to explore new habitats because it reshuffles distributions of trophic (e.g. prey items) and/or non-trophic resources (e.g. microhabitats). Indeed, a handful of studies found increased dispersal after natural or manipulated disturbance events (Bates et al., 2006; Gilliam & Fraser, 2001; Tournier et al., 2017). Thus, natural disturbance may also represent a key signal that initiates non-random dispersal in the short term.

Behavioural dispersal responses to natural disturbance may be complex since the cost-benefit balance of dispersal may depend on the possession of particular species traits at the individual level (Clobert et al., 2012). For example, larger individuals may benefit more from post-disturbance dispersal if they are better able to cope with dispersal costs due to higher locomotive capacity (Debeffe et al., 2012; Ojanguren & Braña, 2003; Terui et al., 2017). Further complexity may arise if we wish to compare dispersal patterns of multiple species as species differ in their ecological niche, such as habitat requirements and mean dispersal ability. Nevertheless, the potential interaction between natural disturbance and

individual-level characteristics is rarely explored in the wild perhaps because of the unpredictable nature of natural disturbance (but see Gilliam & Fraser, 2001 for an exceptional example). It is critical to fill this knowledge gap because anthropogenic impacts (including global climate change) concurrently modify disturbance regimes and population structure of organisms (e.g. body size distribution; Asadieh & Krakauer, 2017; Caruso et al., 2014; Sheridan & Bickford, 2011). Therefore, there is a clear need to deepen our understanding of how dispersal responses to disturbance are related to individual-level characteristics and how species vary.

Streams are highly dynamic such that stream organisms are recurrently exposed to disturbance events, such as floods. Therefore, streams are an ideal system to study how organisms respond to natural disturbance through dispersal. In particular, stream fishes provide a unique opportunity to examine dispersal in the field. Movement of stream fishes is typically restricted to several tens of meters, forming fine-scale habitat units in which local intra- and interspecific interactions may occur (Radinger & Wolter, 2014; Rodríguez, 2002; Terui et al., 2014). These local habitats are connected through movement of a subset of individuals in a population that travel varying distances (Fausch et al., 2002; Radinger & Wolter, 2014; Skalski & Gilliam, 2000; Terui et al., 2014). Movement of stream fishes that drives spatial ecological interactions manifests itself at relatively small spatial scales where direct observations of movement are practically possible using traditional mark-recapture methods.

Here, using a >2-year mark-recapture dataset with a 2-month sampling interval, we examined how natural disturbance interacts with an individual-level characteristic to influence dispersal of three sympatric fishes in two streams in South Carolina, U.S.A. The south-eastern U.S.A. harbours high diversity of freshwater fish (Warren et al., 2000) and several species often occur even in small streams, where high recapture rates of fish are readily feasible. In this study, we focused on extreme high flows as natural disturbance because it is well known to restructure aquatic habitats by modification of channel morphology and transport of sediment and woody debris (Death et al., 2015; Nakamura et al., 2000). In addition, stream fishes respond innately to changes in stream flows, and abrupt rates of changes in stream flows associated with peak flows trigger dispersal (Harvey-Lavoie et al., 2016; Nunn et al., 2010). Meanwhile, body size was used as an individual-level characteristic as fish dispersal capability is strongly correlated with body size (Comte & Olden, 2018a; Gilliam & Fraser, 2001; Ojanguren & Braña, 2003; Radinger & Wolter, 2014; Terui et al., 2017). Specifically, we tested the following predictions using three fish species predominant in the study streams (creek chub *Semotilus atromaculatus*, bluehead chub *Nocomis leptocephalus*, and striped jumprock *Moxostoma rupicartes*): (1) extreme high flows trigger dispersal of stream fishes; (2) larger individuals disperse longer distances; and (3) high flows and body size interact to influence dispersal. We postulated that the outcome of these predictions may depend on species given ecological differences of the study species (see Section 2).

## 2 | METHODS

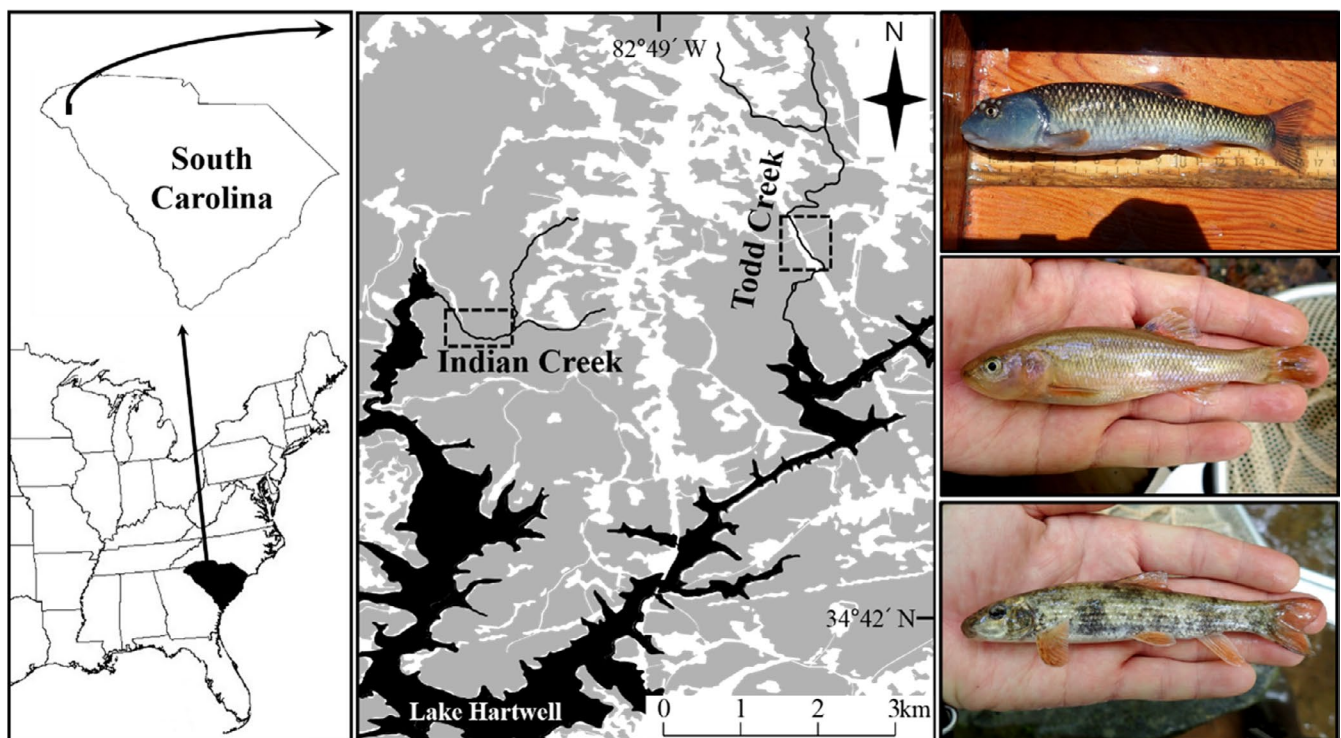
### 2.1 | Study sites

This study took place at Indian (34°44'32"N, 82°51'05"W) and Todd (34°45'15"N, 82°48'56"W) creeks in the Clemson University Experimental Forest in the upper Piedmont region of South Carolina, U.S.A. (Figure 1). Both streams were located within the same catchment and were approximately 3.4 km apart in Euclidean distance from one another. Both were second-order perennial streams, and a man-made reservoir (Lake Hartwell) downstream of the study streams made them isolated habitats for stream fishes (Figure 1). In addition, impassable waterfalls (c.a. 10 m high) existed approximately 150 m downstream of the study area in Todd Creek. Indian Creek (mean wetted width = 2.6 m; range = 1.4–4.7 m) had a well forested riparian zone and Todd Creek (mean wetted width = 3.3 m; range = 1.0–5.6 m) had an open canopy located in a power-line corridor (Table 1; Figure 1). Both streams were characterised by a series of riffle-pool sequences. Indian Creek was mainly composed of fine to medium substrates and Todd Creek of medium to large substrates (Table 1). In the study area, high flows occur due to rain, including those caused by hurricanes.

### 2.2 | Study species

We studied three species common to both streams; two cyprinids (creek chub and bluehead chub) and one catostomid (striped jumprock).

All three species can be found in pool and run habitats of small to mid-sized streams, and they exhibit a resident (non-migratory) life history in our isolated habitats. The species possess ecologically distinguishable characteristics that may affect dispersal of each species uniquely. Striped jumprock have the most fusiform and streamlined body shape suited for swimming and dispersal among the study species (Figure 1). Adult body size of striped jumprock is typically larger than the other two species, a pattern similarly observed in Indian and Todd creeks (see Section 3). Creek chub is the most headwater species among the study species, and often occupy small streams in which striped jumprock or bluehead chub does not occur in the study region (Rohde et al., 2009). Creek chub is also the most tolerant of environmental degradation among study species, eat a variety of food resources (i.e. insectivores–carnivores), and are not selective of substrate size of their habitat and are often abundant in homogeneously rock- or sand-dominated streams (Bramblett et al., 2005; McCormick et al., 2001). These opportunistic traits make them a habitat generalist that exploits a wide range of habitats including temporally dynamic habitats (e.g. headwater streams, dryland streams) undergoing a cycle of channel drying and re-wetting, in which recolonisation is a key process for populations to persist. Finally, bluehead chub is morphologically similar to creek chub, but has more specialised habitat requirements (i.e. silt-free or *clean* pebble and gravel substrate; Rohde et al., 2009). Their requirement for substrate size is noteworthy because adult males (>100 mm total length) construct their nests by moving mouth-gape-sized substrate in spring and its availability is important for reproduction (Bolton et al., 2015).



**FIGURE 1** Locations of study streams (dotted rectangles) in the upper Savannah River basin in South Carolina, U.S.A. Waterways (lakes and streams) are shown in black and forested areas are grey. Photos show study species from the top to the bottom; bluehead chub (*Nocomis leptocephalus*), creek chub (*Semotilus atromaculatus*), and striped jumprock (*Moxostoma rupicartes*). Photo credit: S. Kim

Variables	Stream	
	Indian	Todd
Daily mean water temperature (°C)	15.1 (1.4–23.6)	15.8 (0.8–25.7)
Mean wetted width (m)	2.6 (1.4–4.7)	3.3 (1.0–5.6)
Mean depth (cm)	13.2 (6.6–29.8)	24.3 (13.3–43.3)
Substrate		
Coarse (%)	6.9 (0.0–55.5)	44.4 (0.0–100.0)
Medium (%)	41.1 (0.0–77.8)	37.2 (0.0–100.0)
Fine (%)	52.0 (0.0–100.0)	18.4 (0.0–77.8)
Meso-habitat type		
Pool (m <sup>2</sup> )	19.8 (0.0–81.6)	27.3 (0.0–104.0)
Run (m <sup>2</sup> )	14.4 (0.0–53.9)	23.0 (0.0–46.9)
Riffle (m <sup>2</sup> )	20.5 (0–56.4)	22.2 (0.0–58.4)

Note: Mean (range) values are shown. Substrate: coarse includes boulder (256–512 mm) and bedrock (>512 mm), medium included pebble (16–64 mm) and cobble (64–256 mm), and fine includes silt (<0.01 mm), sand (0.1–2 mm), and gravel (2–16 mm).

### 2.3 | Field sampling

Mark-recapture sampling was conducted at two creeks from January 2016 to March 2018 at an interval of 2 months (mean of 60.9 days [range = 45–75] in both creeks). Study area was 520 m in length in Todd Creek and 740 m in Indian Creek. The length differed by creek due to variation in fish density, and the study area in Indian Creek was longer to increase sample size given lower fish densities. Permanent 20-m sections were established in a spatially continuous manner in each creek and the sections were sampled in an upstream direction on each occasion by backpack electrofishing units (Smith Root Model LR-24; and Halltech Aquatic Research Inc. Model HT-2000) using a two-pass depletion approach. Electrofishing was operated with 300–400 V and 30–60 Hz with DC or pulsed-DC settings. Once captured, fish were held in a bucket separated by section and pass until processing.

All captured fish were identified to species and measured for total length (mm). Fish 50 mm or greater in total length were tagged with 8-mm passive integrated transponder (PIT) tags (Oregon RFID; Biomark). Detailed PIT tag incision protocols are described in Cary et al. (2017), who showed high survival and tag retention rates (99%–100%) immediately following the incision procedure for our study species. Fish were scanned with a PIT tag reader (Avid PowerTracker 7) to identify previously tagged individuals (recaptures) and fish without a tag were implanted with a PIT tag before they were returned to the section of capture alive.

To monitor environmental variation over time, temperature, and water level loggers (HOBO Onset Computer Corp, Model U20L-004) were deployed in each stream to measure water temperature and level hourly (Figure S1). Habitat was measured during baseflow conditions in the autumn of 2017 (18–27 October) to characterise its spatial variation within each stream (Table 1). We estimated mean wetted width, mean depth, and substrate composition based on measurements taken at three transects per section.

**TABLE 1** Habitat characteristics of study streams. Mean (range) are shown. Water temperature was recorded hourly between January 2016 and March 2018. Other variables were measured in the base flow condition on October 18–27, 2017, and values represent mean (range) across 20-m sections

In each transect, variables were measured evenly at three points across the wetted width. Substrate was visually estimated at each point and the dominant substrate was recorded. Silt (<0.01 mm), sand (0.1–2 mm), and gravel (2–16 mm) were categorised into the fine substrate. Medium substrate was composed of pebble (16–64 mm) and cobble (64–256 mm). Coarse substrate consisted of boulder (256–512 mm) and bedrock (>512 mm). We also visually identified meso-habitat type (i.e. riffle, run, or pool). A total longitudinal length of meso-habitat types was measured in each section and was multiplied by mean wetted width to calculate the size of habitat type (m<sup>2</sup>).

### 2.4 | Dispersal model coupled with observation process

Our aim was to examine the effects of external and internal factors on dispersal distances (20-m resolution) over 2-month sampling intervals, accounting for imperfect detection of cryptic aquatic species. We define dispersal broadly as any movement across space (Bowler & Benton, 2005) and use dispersal distance as a continuous measure of dispersal because stream habitats are spatially contiguous. We employed the Laplace (double exponential) kernel, which has been proven to provide adequate fits to dispersal data in various fishes (Pépin et al., 2012; Rodríguez, 2002; Terui et al., 2017). Specifically, we described recapture location  $x_i$  (measured as the distance from the centre of a recapture section to the downstream end of the whole study stretch) as a random Laplace variable with mean dispersal distance  $\delta_i$  and capture (release) location  $\alpha_i$  for fish individual replicate  $i$ , which includes multiple recaptures of the same individuals at different sampling period  $t$ :

$$x_i | \delta_i, \alpha_i \sim \text{Laplace}(\delta_i, \alpha_i) \quad (1)$$

The Laplace density function  $f_L$  has a symmetrical exponential decay to either side of the origin, defined as the following probability density function:

$$f_L(x_i, \delta_i, \alpha_i) = \frac{1}{2\delta_i} \exp\left(-\frac{1}{\delta_i} |x_i - \alpha_i|\right) \quad (2)$$

The term  $x_i - \alpha_i$  represents the dispersal distance in which positive and negative values represent up- and downstream movement, respectively. It is important to note that the Laplace model is robust to outliers, typical of dispersal data (Nathan et al., 2012; Terui et al., 2017), because the expected variance ( $2\delta^2$ ) nonlinearly increases with increasing mean dispersal distance ( $\delta$ ).

We related the mean dispersal distance to predictors with a log-link function:

$$\ln \delta_i = \beta_1 + \beta_2 \text{Flow}_{t[i],s[i]} + \beta_3 \text{Size}_i + \beta_4 \text{Flow}_{t[i],s[i]} \cdot \text{Size}_i + \beta_5 \text{Temp}_{t[i],s[i]} + \beta_6 \text{Stream}_i + \ln(\text{Interval}_i/60) \quad (3)$$

where  $\beta_1$  is an intercept and  $\beta_2 - \beta_6$  are standardised regression coefficients of high flows ( $\text{Flow}_{t[i],s[i]}$ ), body size at a capture occasion ( $\text{Size}_i$ ), interaction between high flows and body size, water temperature ( $\text{Temp}_{t[i],s[i]}$ ), and stream identity ( $\text{Stream}_i$ ), respectively.

The flow variable ( $\text{Flow}_{t[i],s[i]}$ ) is binary and refers to occurrence of high flows in each sampling period  $t$  for stream  $s$ . We coded the variable as 1 if there was occurrence of daily mean flows exceeding the 99th percentile of daily water levels observed during the whole study period. The 99th percentile of water level, which is high enough to transport sediment and woody debris and reshuffle riffle–pool sequences in the study streams (personal observation), was defined in each stream separately. We also developed models with the median of standardised water levels (standardised by subtracting the minimum water level for each stream) instead of the occurrence of high flows. Prior to the main analysis, we compared the widely applicable information criterion (Watanabe, 2010) of the two models. The models with the occurrence of high flows performed better than those with the median water level for all species except striped jumprock (Table S2), whose results were qualitatively similar between the two models (see Table S4 in Supporting Information). Thus, we report and discuss the results with the occurrence of high flows in the main text.

Body size ( $\text{Size}_i$ ) is the total length of each fish individual at the time of capture and release. Water temperature ( $\text{Temp}_{t[i],s[i]}$ ), calculated as the mean of each sampling period  $t$  for stream  $s$ , was incorporated into the model as a control variable to account for temperature effects or seasonality of fish movement patterns. Although it is possible that water temperature has ecological effects on dispersal of stream fishes, we have included this variable as a *control* because temperature and seasonality effects were strongly correlated and were difficult to provide ecological interpretation. Stream ( $\text{Stream}_i$ ) is the dummy binary variable that specifies stream identity (Todd = 1, Indian = 0) and was included to control for the stream effect. The offset term,  $\ln(\text{Interval}_i/60)$ , was included to align sampling intervals among fish individuals and sampling periods;

thus, the regression coefficients can be interpreted as the effects on dispersal distance of a 60-day recapture interval. Continuous explanatory variables were standardised (mean = 0,  $SD = 0.5$ ) so that estimated coefficients are comparable between continuous and binary variables.

To incorporate sampling designs into the parameter inference of dispersal kernels, we used a dispersal model that integrates observation processes (Terui, 2020). This framework accounts for: (1) imperfect detectability, (2) survival; and (3) permanent emigration from the study area. The binary variable of capture history  $Y_i$  ( $Y_i = 1$  if recaptured, otherwise 0) was modelled based on a Bernoulli distribution:

$$Y_i \sim \text{Bernoulli}(\xi_{t[i]} \gamma_{t[i]} z_i) \quad (4)$$

where  $\xi_{t[i]}$  is the probability of capture by two-pass electrofishing (detectability) for sampling period  $t$  and  $\gamma_{t[i]}$  is the survival probability during a single capture–recapture interval. The parameter  $z_i$  is a latent variable indicating whether fish individual  $i$  stays in the study stretch (stay = 1, otherwise 0) during the sampling period  $t$ . For recaptured individuals,  $z_i = 1$  as we know those were present in the study stretch at the time of recapture. For unrecaptured individuals,  $z_i$  is determined by the value of  $x_i$  randomly drawn from the Laplace distribution (Equation 1):

$$z_i = \begin{cases} 1 & \text{if } 0 \leq x_i \leq L \\ 0 & \text{if } x_i < 0 \text{ or } x_i > L \end{cases} \quad (5)$$

where  $L$  is the length of the study stretch (520 m for Todd Creek, 740 m for Indian Creek). Therefore, the latent variable  $z_i$  is a realisation of a random variable drawn from a Bernoulli distribution with the probability of staying in the study stretch  $D_i = \int_0^L f_L(x_i, \delta_i, \alpha_i) dx_i$ . As such, dispersal parameters ( $\beta$ ) in this model are corrected for permanent emigration from the study stretch as Equation 5 accounts for individuals that left the study stretch (Terui, 2020; Terui et al., 2017).

In this study, our focus was to estimate the effects of linear predictors ( $\beta$ ) on dispersal distance. Thus,  $\xi_{t[i]}$  and  $\gamma_{t[i]}$  were summarised into a single parameter  $\phi_{t[i]}$  ( $=\xi_{t[i]} \gamma_{t[i]}$ ) to reduce statistical uncertainty in estimating the rest of parameters:

$$Y_i \sim \text{Bernoulli}(\phi_{t[i]} z_i) \quad (6a)$$

$$\text{logit} \phi_t \sim \text{Normal}(\text{logit } \mu_\phi, \sigma_\phi^2) \quad (6b)$$

where  $\text{logit } \mu_\phi$  and  $\sigma_\phi^2$  is the average and variance of period-specific recapture probability  $\phi_t$  on a logit scale.

The model was fit to the data for each species separately using JAGS 4.3.0 (Plummer, 2003) and the R package *runjags* (Denwood, 2016). Vague priors were assigned to the parameters: normal distributions for  $\beta$  and  $\text{logit } \mu_\phi$  (mean = 0, variance =  $10^2$ ) and a half-Cauchy distribution (location = 0, scale = 2.5) for  $\sigma_\phi$ . Three



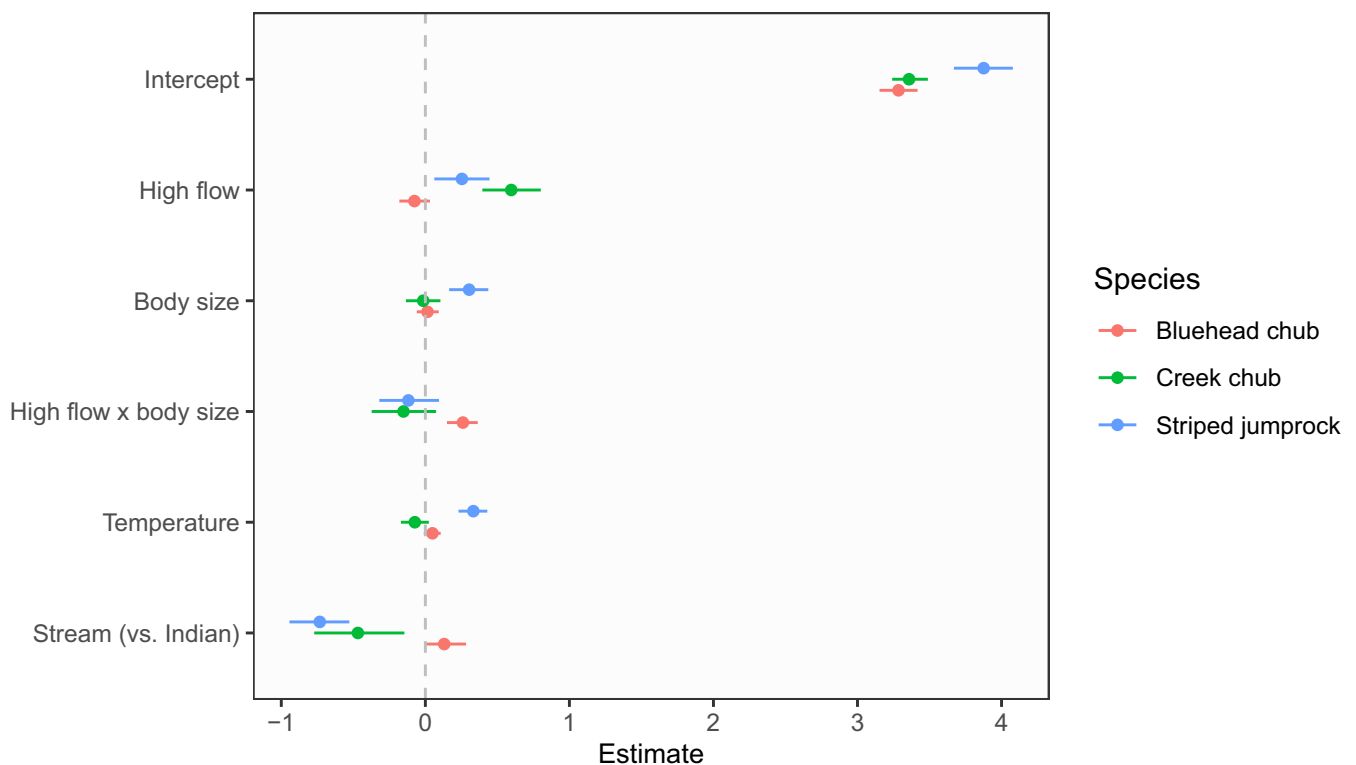
Markov chain Monte Carlo chains were run with 12,000 iterations with a 4,000 burn-in period, with 500 samples per chain retained (i.e. 16 thinning) and used to calculate posterior probabilities. Model convergence was checked by comparing the estimated variances between and within chains for each parameter, which is referred to as the potential scale reduction factor ( $\hat{R}$ ). We ensured that the  $\hat{R}$  value was less than 1.1 for all parameters to assume model convergence (Gelman & Hill, 2007). All statistical analyses were conducted with R ver. 4.0.2 (R Core Team, 2020).

### 3 | RESULTS

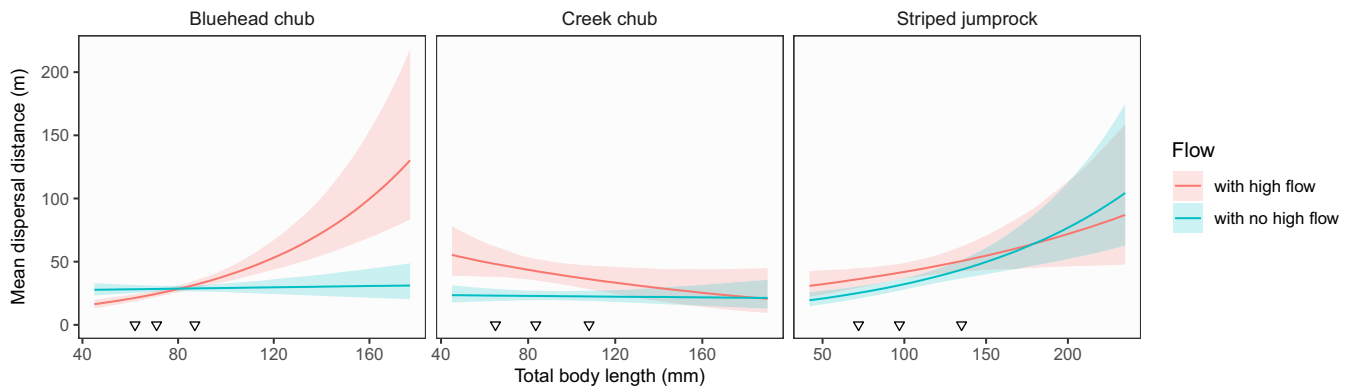
Environmental conditions in the study streams were summarised in Table 1. In total, we tagged 3,832, 893 and 879 unique individuals of bluehead chub, creek chub and striped jumprock across the whole study period (Table S1). The total number of released individuals (i.e. *individual replicates* including those released multiple times) were 6,071 (bluehead chub), 1,720 (creek chub) and 1,806 (striped jumprock) with corresponding recaptures of 1,386, 492 and 539 individuals (Table S1). Mean initial body size (body size at release) was largest for striped jumprock (mean  $\pm$  SD = 104.2  $\pm$  34.9 mm, coefficient of variation [CV] = 0.34,  $n$  = 1,806), followed by creek chub (87.7  $\pm$  24.7 mm, CV = 0.28,  $n$  = 1,720) and bluehead chub (75.6  $\pm$  17.4 mm, CV = 0.23,  $n$  = 6,071). Coefficient of variation of body size was also largest for striped jumprock, indicating that their body size varied most widely among the three study species. Mean recapture probability  $\mu_\phi$  was

0.22, 0.28 and 0.31 for bluehead chub, creek chub, and striped jumprock, respectively (Table S3). Five out of 13 periods experienced at least one high flow event exceeding the 99th percentile of daily water levels in each stream (Figure S1). The number of individual replicates that were exposed to the high flow events was 2,402 for bluehead chub, 613 for creek chub, and 735 for striped jumprock. We did not observe biases in movement directions even during high flows (see Figure S2–S4 for raw data), implying that the observed displacement reflected the active movement of fish. Individual fish that were recaptured multiple times showed high degrees of site fidelity and rarely returned to their original section once they dispersed (Figure S5).

Our model revealed that high flows and body size had varied effects on dispersal of different fish species (Figure 2; Table S3). The high flow (occurrence of flow events that exceeded the 99th percentile of daily water levels during the whole study period) and body size interacted significantly to influence dispersal of bluehead chub (Figure 2). Specifically, size-dependent dispersal emerged only when high flows occurred (Figure 3; see also Figure S6 for dispersal kernels). Thus, bluehead chub reacted differently to high flows according to their body size. The estimated proportion of individuals that stayed in the original 20-m section (hereafter, *stayers*) was 0.33 with high flows versus 0.30 without them. It should be borne in mind that the interactive effect was no longer significant when we used the median flow as a substitute of the high flow (Table S4). Although the model performance was better when using the high flow (Table S2), this result implies bluehead chub might respond differently to seasonal variation in averaged flow conditions.



**FIGURE 2** Parameter estimates of the Bayesian dispersal model. Median estimates (points) and the associated 95% credible intervals (error bars) were reported. Colours distinguish species



**FIGURE 3** Estimated mean dispersal distance in relation to body size and high flows. Panels distinguish species, while colours represent the presence–absence of high flows (flow events exceeding the 99th percentile of daily water levels). Shades indicate 95% credible intervals of estimated mean dispersal distance. Triangles indicate 20, 50, and 80th percentiles of total body length. See Figure S6 for dispersal kernels

Meanwhile, creek chub responded to occurrence of high flows by increasing dispersal distance with little influence of body size (Figure 2; Table S3). For example, medium-sized creek chub (50th percentile = 84 mm) dispersed on average  $42.9 \pm 4.3$  m during 2-month intervals with high flows versus  $22.9 \pm 1.9$  m without them. This pattern was consistent among individuals with different body size (Figure 3; see also Figure S6 for dispersal kernels) and no significant influence of an interaction term was found for creek chub (Figure 2). Reflecting these patterns, the estimated proportion of stayers was lower during periods with high flows (0.21) compared with those without them (0.36).

Striped jumprock increased dispersal distance as body size increased and became more dispersive when high-flow events occurred (Figure 2; Table S3). Average dispersal distance of small-sized striped jumprock (20th percentile = 72 mm) was  $36.4 \pm 4.0$  m with high flows versus  $25.3 \pm 2.5$  m without them, while large-sized individuals (80th percentile = 135 mm) showed average dispersal distance of  $51.0 \pm 5.2$  m with high flows versus  $43.8 \pm 3.9$  m without them. Again, we did not find a significant interaction of high flows and body size for striped jumprock (Figure 2), i.e. reactions to high flows were not dependent on their body size (Figure 3; Figure S6). The estimated proportion of stayers ranged from 0.21 (with high flows) to 0.27 (without high flows).

Water temperature had some influences on dispersal of bluehead chub and striped jumprock (Figure 2; Table S3). These effects may reflect either seasonality or pure effects of water temperature. However, since these two factors are correlated strongly, it is difficult to tease two factors apart in our model and interpret these results ecologically. Also, study species showed different dispersal distance between study streams (Figures 2 and 3; Table S3), probably capturing environmental differences that cannot be inferred from modelled explanatory variables.

## 4 | DISCUSSION

Ample evidence indicates that non-random dispersal results from individual decisions balancing fitness benefits and costs,

which are influenced by environmental factors (e.g. disturbance) and individual-level characteristics (Cote et al., 2013; De Bona et al., 2019; Fronhofer et al., 2018; Terui et al., 2017). However, little is known about how natural disturbance and individual-level characteristics combine to influence dispersal in the wild (but see Gilliam & Fraser, 2001). Here, using a large mark–recapture dataset, we identified important effects of extreme high flows and body size on stream fish dispersal. The effects of high flows and body size interacted differently among sympatric species, suggesting that these species maintain spatial processes through different non-random dispersal patterns. It is important to note that subtle differences in average dispersal distance are ecologically significant as variance of a Laplace distribution increases non-linearly (variance =  $2\delta^2$ ). For example, a 10-m increase in average movement distance  $\delta$  translates into 200-times greater variance of dispersal distance, leading to a higher possibility of long-distance dispersal that transcends multiple local habitats in our study streams. To our knowledge, this study is among the first to provide field-based evidence for differential interactive effects of natural disturbance and individual-level factors on dispersal of aquatic species.

All species increased dispersal distances in response to extreme high flows, although interactive effects with body size were found in bluehead chub. There are at least two possible explanations. Firstly, individual fish might be simply swept downstream by high flows. However, we did not see downstream-biased dispersal during high flows. Therefore, any form of passive dispersal is an unlikely explanation for the observed patterns. The second explanation is that our results reflect spatial tracking of temporarily dynamic resources. It is well known that flood disturbance significantly alters aquatic habitats through redistribution of substrate and reformulation of channel geomorphology (Behn & Baxter, 2019; Death et al., 2015; Larson et al., 2018; Nakamura et al., 2000; Robertson et al., 2015). Our previous study documented that high flows, even those of smaller magnitudes than defined and modelled in this study, mobilised and redistributed nest substrate of bluehead chub during the reproductive period (Kim et al., 2020). Furthermore, extreme high flows dug new pools in some locations and filled existing pools elsewhere in

our streams (personal observation). Therefore, it is conceivable that individuals may emigrate from the previously suitable, but no longer beneficial habitat to seek new habitats after disturbance. Although our data cannot provide a conclusive explanation for why fish moved more during high flow periods, a mechanistic understanding would be particularly useful when inferring metacommunity assembly processes. We encourage researchers to address this issue in future studies.

Body size effects, which were found in striped jumprock (i.e. irrespective of flow conditions) and bluehead chub (conditional on the occurrence of high flows), may reflect the fact that larger individuals can cope better with dispersal costs due to their high dispersal capability (Comte & Olden, 2018a; Debeffe et al., 2012; Gilliam & Fraser, 2001; Radinger & Wolter, 2014; Terui et al., 2017). Body size regulation of dispersal is found in both intra- (Gatz & Adams, 1994; Gilliam & Fraser, 2001; Terui et al., 2017) and interspecific comparisons of freshwater fishes (Comte & Olden, 2018a; Radinger & Wolter, 2014) as well as other organisms (Debeffe et al., 2012; Ness et al., 2004; Sekar, 2012). This result is understandable because energetic advantages may allow larger individuals to travel longer distances (Ojanguren & Braña, 2003). Such advantages may be particularly evident in striped jumprock because of their fusiform body shape suitable for swimming. Besides, body size varied more widely among individuals of this species than those of the other two species, providing an additional explanation for the strong regulation of dispersal by body size in striped jumprock. However, the lack of body size effects on dispersal distance of creek chub—a pattern also found in other streams (Skalski & Gilliam, 2000; Walker & Adams, 2016)—highlights the complexity of dispersal in the wild. Since creek chub also inhabit highly unstable habitats (e.g. large pools in intermittent streams; Walker & Adams, 2016), it is possible that immediate relocation after disturbance is more critical than size-related dispersal costs. Our results support this hypothesis as creek chub responded most strongly to the occurrence of high flows.

The dispersal response of bluehead chub to high flows was complicated: the positive size dependence in dispersal emerged only during high flow periods. This may stem from a combination of size-dependent costs of dispersal and the unique ecology of the species. It is possible that size-dependent costs of dispersal manifest only under high flow conditions, in which smaller individuals with limited swimming abilities may suffer from turbulent hydrologic conditions. The reproductive ecology of the species may provide additional insight into why larger individuals moved during/after high flows. Male bluehead chub move thousands of pebbles by mouth to construct their nests during spring (Kim & Kanno, 2020; Wallin, 1989), and their nests are often spatially clustered due partly to limited availability of suitable substrate (Bolton et al., 2015). This unique reproductive ecology might motivate large mature and maturing individuals to disperse under high-flow conditions as their preferred substrates may be mobilised. Indeed, high-flow events occurred before or during the spawning season of bluehead chub (January–May).

Interestingly, even during high-flow periods, a significant portion of fish remained in the local habitat, corroborating the restricted

movement paradigm in resident stream fishes (Gowan et al., 1994; Rodríguez, 2002). Dispersal costs, such as increased mortality during relocation, are generally high (Bonte et al., 2012). Therefore, it is reasonable for some individuals to stay in the local habitat given the inherent risks associated with dispersal. Alternatively, it is possible that stayers benefit from reduced competition when other fishes move away. However, the magnitude and mechanisms of intra- and interspecific competition are poorly characterised for our study species. In addition, the spatial grain of our data (i.e. every 20 m) did not match with the finer scale at which behavioural encounters occur, which prevented us from drawing mechanistic inferences about density-dependent dispersal that are reported in other animals (De Bona et al., 2019; French & Travis, 2001). These mechanisms could act in concert in the wild, and the relative importance of these mechanisms may vary in accordance with species-specific dispersal costs and the strength of competition.

The limited spatial coverage of our mark–recapture study could influence dispersal parameter inference because we did not observe the dispersal distance of individuals that had left the study area. However, like recent spatial-capture–recapture models (e.g. Ergon & Gardner, 2014; Honeycutt et al., 2019), our statistical approach incorporated survival and imperfect observation processes into the model (including limited spatial coverage of observations), thereby accounting for permanent emigration of individuals (Terui et al., 2017). As a result, this approach—a variant of spatial Cormack–Jolly–Seber models (Schaub & Royle, 2014)—has been shown to provide substantially improved estimates of dispersal parameters (Terui, 2020). Therefore, our statistical inference of dispersal parameters should be robust. Another potential problem is that measured movement might reflect ecological processes other than dispersal, such as foraging behaviour. However, a majority of the individuals show high degrees of site fidelity at the scale of our sampling (i.e. a 20-m section) and rarely returned to their original section once they moved out. Therefore, the observed movement patterns probably reflect dispersal processes of the study species.

There is an increasing awareness that non-random dispersal has far-reaching impacts on spatially structured systems, ranging from metapopulations to metacommunities to meta food webs (Fronhofer et al., 2017, 2018; Little et al., 2019; Terui et al., 2017). The results of this study build upon these efforts by providing field-based evidence of how external (i.e. disturbance) and internal factors (i.e. body size) drive non-random dispersal and how it varies among sympatric species. This finding is important because metapopulations that are maintained by different non-random dispersal may show varied sensitivities to human-induced environmental changes. For example, hydrological alterations (e.g. water abstraction) that reduce the magnitude of high flows (Bunn & Arthington, 2002) may have greater impacts on species with externally driven dispersal processes. In contrast, human harvest that selectively exploits the largest or boldest individuals of a species via fishing (Biro & Post, 2008; Vainikka et al., 2016) may strongly influence species that show strong body size regulation of dispersal. Climate change, which concurrently changes hydrological regimes (Asadieh & Krakauer, 2017)



and population structure (Caruso et al., 2014), may have complex influences on metapopulation dynamics of species depending on their relative sensitivity to external and internal factors. A mechanistic understanding of why non-random dispersal is driven by different factors among species may provide the means to generalise our findings. Despite challenges in investigating dispersal in the wild, such an insight should pave the way towards spatial biodiversity forecasting during rapid environmental changes.

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## CONFLICT OF INTEREST

None declared.

## AUTHOR CONTRIBUTIONS

A.T. and Y.K. conceived the idea; K.C.P., S.K., and Y.K. performed field work; A.T. performed statistical analysis and drafted the manuscript; All authors contributed to revision and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data and scripts are made available at <https://doi.org/10.5281/zenodo.5071276>.

## ORCID

Akira Terui  <https://orcid.org/0000-0003-3774-2844>

Seoghyun Kim  <https://orcid.org/0000-0003-3273-0596>

Kasey C. Pregler  <https://orcid.org/0000-0002-0664-9594>

Yoichiro Kanno  <https://orcid.org/0000-0001-8452-5100>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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