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Seasonal Movement of Redside Dace (*Clinostomus elongatus*) in Relation to Abiotic and Biotic Factors

D. Andrew R. Drake[1] and Mark S. Poesch[2]

[1]Fisheries and Oceans Canada
Great Lakes Laboratory for Fisheries and Aquatic Sciences
867 Lakeshore Rd.
Burlington ON L7S 1A1 Canada

[2]Department of Renewable Resources
University of Alberta
751 General Services Building
Edmonton, AB T6G 2H1 Canada

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Most animal populations are composed of stationary and mobile individuals, which can influence metapopulation structure and the spatial distribution of mortality. We investigated the incidence of stationarity and mobility in two relatively stable populations of Redside Dace (*Clinostomus elongatus*) in the Rouge River drainage in Ontario, Canada. Multiple linear regression was used to determine if stationarity and mobility were related to stream flow attributes (mean and 90th percentile of daily discharge; stream flow flashiness). For the mobile fraction of the population, spatial interaction models were used to determine the abiotic variables (aquatic habitat) and biotic variables (species-level catch-per-unit-effort (CPUE) of the fish assemblage) associated with movement. Results indicated a high level of movement synchrony among populations (Berczy Creek and Leslie tributary), with generally similar stationarity and movement bias depending on season. Stationarity ranged from a high of 74% and 67% (spring 2007, Berczy and Leslie, respectively) to a low of 0% and 7% (October – early May and early – late May, Berczy; October – early May, Leslie). Stationarity was only weakly negatively related to stream flow attributes (mean and 90th percentile of daily discharge), while movement bias was weakly positively and negatively related to stream flow. At the reach level, spatial interaction models indicated that distance and biotic factors (CPUE of Creek Chub [*Semotilus atromaculatus*], Common Shiner [*Luxilus cornutus*], and White Sucker [*Catostomus commersonii*]) were important predictors of the probability of moving to a reach, as were aquatic habitat variables (standard deviation of reach volume [positive], mean and standard deviation of stream depth [positive], and mean reach width [negative]). Results indicate that factors operating at different spatial and temporal scales (stream flow, species CPUE, reach-level habitat) influence stationarity and mobility of Redside Dace, yet a substantial amount of movement variation remains unexplained by environmental factors. Future work is needed to resolve the implications of stationarity and mobility on individual and population-level mortality so that projections of extinction risk can be refined.

INTRODUCTION

Relatively little is known about the movement of stream fishes, including small cyprinids such as Redside Dace (*Clinostomus elongatus*). Because movement involves tradeoffs to maximize fitness (e.g., obtaining food resources, accessing reproductive habitat, minimizing predation risk), movement of individuals should be driven by species- and site-specific factors as they relate to life history requirements and the habitat matrix available to a population (Fahrig 2001). There is growing evidence that most animals, including freshwater fishes, exhibit two distinct movement states (e.g., Smithson and Johnston 1999; see Radinger and Wolter 2014 for review). Stationary individuals (or populations) undergo relatively fine-scale movements, rarely leaving a habitat patch, while mobile individuals actively seek new environmental conditions, often travelling substantial distances. The rationale for these behaviours is not always clear or associated with cues like spawning migrations. Understanding the incidence of these behaviours and how (or if) they are driven by abiotic or biotic factors has implications for understanding how spatial population structure is influenced by environmental conditions.

Investigating the stationary and mobile aspects of Redside Dace populations is necessary for several reasons. Several authors (Poos and Jackson 2012, van der Lee et al. 2020) have shown that extinction risk in Redside Dace is influenced by metapopulation structure and the way in which sub-populations experience mortality. However, it is unclear whether spatial population structure changes seasonally and if so, the potential role of environmental conditions in causing these changes. This has implications for understanding how environmental catastrophes at the reach or stream scale lead to changes in mortality. For example, summer drought conditions might promote a high degree of stationarity due to migration barriers between pools, leaving the sub-population exposed to mortality in isolated patches. Alternatively, extremely high flows, common in urban streams following storm events (Reid and Parna 2017), may flush fishes downstream if swimming thresholds are surpassed (e.g., Neufeld et al. 2018). Flushed individuals may exit the metapopulation if sufficiently poor conditions (unsuitable habitat or increased predation risk) exist at downstream sites, which may be compounded by low-flows and resulting stationarity that prevent upstream recolonization after the storm event. Intermediate, stable stream flows may maximize the opportunity for movement between stream reaches, but hypotheses between the incidence and extent of movement and hydrologic conditions have not been formally tested for Redside Dace.

Here, we analyze seasonal movement of Redside Dace within two tributaries of the Rouge River, a medium-sized drainage in the central Lake Ontario basin in Ontario, Canada. Our objectives are threefold: First, we describe the movement of Redside Dace, focusing on the stationary and mobile components of fish activity across eight sampling intervals and a 14 month tag-recapture period. Second, we derive a directional weighted mean statistic to determine if population-level movement is biased in an upstream or downstream direction, and whether this bias varies seasonally and in relation to hydrologic conditions. Lastly, we explore factors at the scale of the stream reach to determine how habitat features and biotic variables (e.g., co-occurring stream fishes) influence the scale and frequency of movement.

METHODS

The analysis of Redside Dace movement in the Rouge River drainage involved:

1. capturing and tagging adult Redside Dace at 1, 2, 3, and 7 month intervals over a 14-month study period during 2007 and 2008;

2. enumerating habitat attributes at each stream reach where fish sampling and tagging occurred; and,
3. obtaining flow characteristics for the study period to test hypotheses between movement patterns and dominant hydrological conditions.

FIELD SAMPLING

Field collections were conducted at Berczy Creek and Leslie tributary, two tributary streams within the Rouge River drainage, between May 2007 and July 2008. Field collections encompassed eight tagging periods (2007: May, July, August, September, October, 2008: early May, late May, July; k_1 – k_8) and seven movement periods (May – July, July – August, August – September, September – October, October – early May, early May – late May, late May - July; k_{12}-k_{78}; Table 1). Collections followed Poos and Jackson (2012), with sampling locations selected based on *a priori* knowledge of relatively abundant Redside Dace populations in consultation with the Ontario Redside Dace Recovery Team. Thirteen stream reaches at Berczy Creek, and 10 stream reaches at Leslie tributary, were selected for fish and habitat sampling (Figure 1). Each stream reach was defined as a single crossover-to-crossover unit based on the Ontario Stream Assessment Protocol (Stanfield 2010) and reaches were separated by a minimum of 15 m. The physical stream distance between the centroid of all stream reaches (i.e., reach centroid to reach centroid distance) was calculated using the Origin-Destination Cost Matrix function of Network Analyst in ArcGIS, resulting in a stream distance matrix (meters) for each tributary (Table A1.1, A1.2).

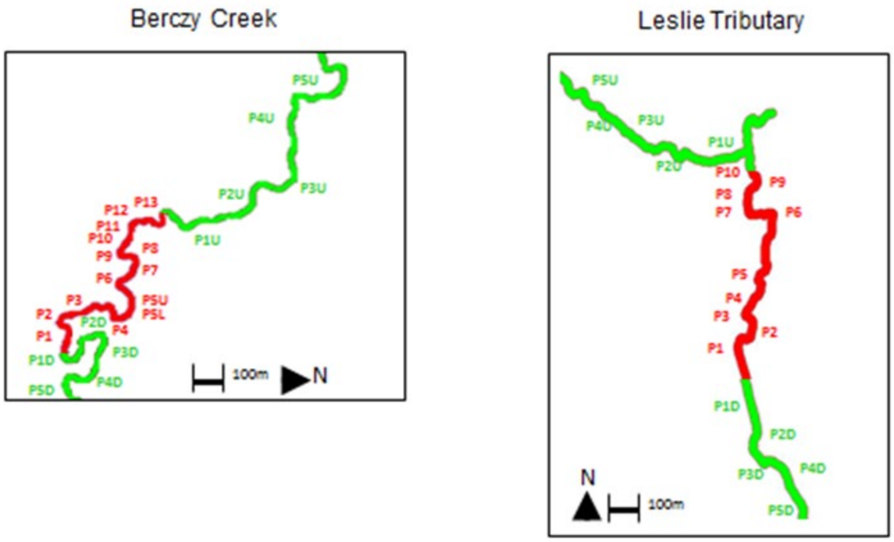
Prior to collecting fishes, block nets (30 foot straight seines with 3/16” mesh) were placed at each crossover and held in place with large rocks. Redside Dace and co-occurring fishes were captured with three successive downstream hauls of a 30 m straight seine (3/16” mesh) across the length of each stream reach. Captured fishes were enumerated by haul, placed in recovery bins, and held until sampling was complete.

Captured Redside Dace were tagged with Visual Implant Elastomer tags (Northwest Marine Technology, Inc.) using reach and season-specific marks, which provided an index of *n* fish tagged within stream reach *i* and time *k*. Tag placement on individual Redside Dace varied depending on season, but included dorsal and ventral surfaces at several reference points (e.g., anterior of the caudal peduncle, anterior of the anal fin; anterior and posterior of the dorsal fin). Only adult Redside Dace were tagged with a minimum size threshold of ~ 50 mm. Following tagging, Redside Dace were placed in recovery bins and monitored for ~ 30 minutes, after which they were released at the capture site along with other co-occurring species. Tagging mortality was low (< 1%) based on observation of tagged fished in recovery bins.

Following fish sampling, rapid habitat assessment procedures outlined in the Ontario Stream Assessment Protocol (Stanfield 2010) were conducted. The protocol involves measuring stream depth, substrate class, and hydraulic head at equidistant locations across perpendicular stream transects, which also measures the stream width throughout the reach (m). Substrate classes included detritus, silt, sand, gravel, cobble, and boulder, with particle size classes following Stanfield (2010). An assessment of the percentage of overhead cover (e.g., overhanging terrestrial vegetation) was made at each transect. The transect-level measurements were used to construct aggregate reach-level variables, including total reach area. The average and standard deviation of stream depth, volume, percent areal coverage of each substrate class, proportion of the reach classified as pool, run, or riffle, and average and standard deviation of substrate particle size within the reach were also calculated. Habitat measurements were made during the July 2007 sample period and were assumed to be reflective of habitat condition during the remaining capture periods.

Table 1. Fish tagging and recapture during the 2007-2008 sampling period. Mean length describes the mean total length (mm) of Redside Dace that were recaptured at the close of the movement period.

				Berczy Creek		**Leslie Tributary**	
Tagging Period	**Recapture Period**	**Movement Period**	**Season**	**Number Recaptured**	**Mean Length**	**Number Recaptured**	**Mean Length**
May 2007 (k_1)	July 2007 (k_2)	k_{12}	Spring	210	73.4	61	73.6
July 2007 (k_2)	August 2007 (k_3)	k_{23}	Summer	74	70.7	21	76.6
August 2007 (k_3)	September 2007 (k_4)	k_{34}	Summer	102	75.6	58	77.1
September 2007 (k_4)	October 2007 (k_5)	k_{45}	Fall	102	77.0	69	77.8
October 2007 (k_5)	Early May 2008 (k_6)	k_{56}	Overwinter	11	78.6	13	72.1
Early May 2008 (k_6)	Late May 2008 (k_7)	k_{67}	Spring	13	75.33	28	76.64
Late May 2008 (k_7)	July 2008 (k_8)	k_{78}	Spring	28	77.03	23	82.73
-	-	All	-	499	74.5	220	76.5



Berczy Creek

Leslie Tributary

Figure 1. Schematic drawing of the study reaches. Pool labels coincide with the distance matrices shown in Table A1.1 and Table A1.2. The red study area signifies the core tagging reaches, while the green study area signifies additional recapture areas.

Table A1.1. Distance matrix for Berczy Creek tagging sites. Origin and destination labels refer to reach identity. Values are in meters.

	1	0												
	2	21	0											
	3	49	28	0										
	4	69	48	20	0									
	5	86	65	37	17	0								
	6	105	84	56	36	19	0							
	7	123	102	74	54	37	18	0						
Destination	**8**	142	121	93	73	56	37	19	0					
	9	174	153	125	105	88	69	51	32	0				
	10	190	169	141	121	104	85	67	48	16	0			
	11	207	186	158	138	121	102	84	65	33	17	0		
	12	226	205	177	157	140	121	103	84	52	36	19	0	
	13	238	217	189	169	152	133	115	96	64	48	31	12	0
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**

Origin

Table A1.2. Distance matrix for Leslie tributary tagging sites. Origin and destination labels refer to reach identity. Values are in meters.

Destination	**1**	0									
	2	28	0								
	3	52	24	0							
	4	66	38	14	0						
	5	86	58	34	20	0					
	6	126	98	74	60	40	0				
	7	154	126	102	88	68	28	0			
	8	174	146	122	108	88	48	20	0		
	9	195	167	143	129	109	69	41	21	0	
	10	215	187	163	149	129	89	61	41	20	0
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
		Origin									

In addition to the 13 (Berczy) and 10 (Leslie) core stream reaches, an additional 10 stream reaches (five upstream, five downstream) were sampled during each sampling interval to detect tagged individuals that moved beyond the core tagging area. Detailed habitat assessments were not made at these locations.

FLOW CHARACTERISTICS

To understand the relationship between seasonal Redside Dace movement and stream flow attributes, flow measurements of the Rouge River at the Markham discharge station (station ID 02HCO22) were downloaded as daily mean flows (m^3/s) from the Water Survey of Canada website. The discharge station is located approximately 10 km downstream of Berczy Creek and Leslie tributary, resulting in a single set of flow values that were assumed to reflect upstream flow conditions. The daily mean values were used to create three seasonal statistics:

1. the seasonal grand daily mean discharge (m^3/s) for a given tag-recapture interval (e.g., mean daily flow for the May to July 2007 period);
2. the seasonal 90th percentile of daily mean flow for the tag-recapture interval; and,
3. the Richards-Baker flashiness index (Baker et al. 2004; see Reid and Parna (2017) for the use of these flow statistics in evaluating population status of Redside Dace).

The R-B index is a unitless statistic that describes the relative variability in daily flow across a defined sampling interval (Baker et al. 2004). High R-B values indicate higher daily mean flow variability across a given number of days or months; whereas, lower values indicate lower variability. Flow attributes were summarized for each sample period (e.g., May – July, July – Aug) and were used as predictor variables in subsequent analysis (Table 2, Figure 2).

Table 2. Flow characteristics in the Rouge River, Markham station, for the duration of the study period. Mean and 90th percentile values are m^3/s.

Movement Period	**Mean**	**90th Percentile**	**RB Index**
May - Jul	0.942	1.259	0.552
Jul - Aug	0.529	1.12	0.543
Aug - Sept	0.422	0.726	0.305
Sept - Oct	0.395	0.5374	0.209
Oct - Early May	2.289	4.518	0.411
Early - Late May	1.56	2.55	0.392
Late May - July	1.785	4.184	0.476

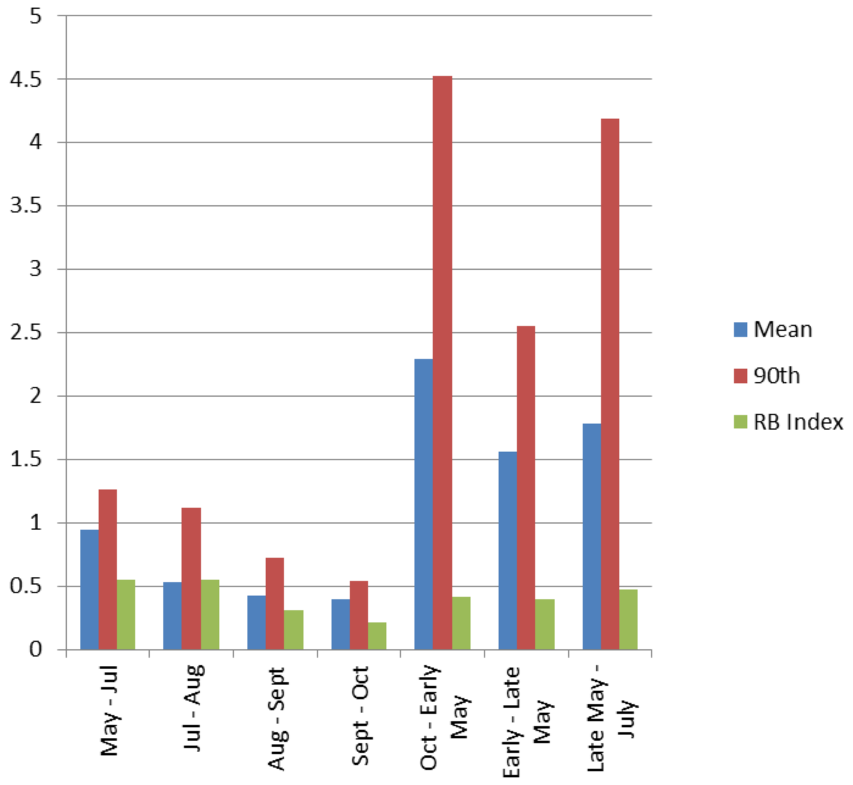


Figure 2. Stream flow characteristics for the Rouge River, Markham discharge station 02HC022, May 2007 – July 2008. The y-axis values describe daily mean discharge (m^3/s), the 90th percentile of daily mean flow, and the R-B flashiness index (higher R-B values indicate greater flow variability over the sample interval).

STATISTICAL ANALYSES

Following tagging and recapture, spatial interaction matrices (**T**) of Redside Dace seasonal movement were developed. The untransformed matrix elements describe the count of *n* tagged Redside Dace moving from stream reach *i* to stream reach *j* across movement period *k*. Movement period k_{12} describes the capture and tagging of fish during tag period *k* (e.g., May 2007) and recapture of those tagged fish during tagging period *k*+1 (e.g., July 2007). Diagonal elements (e.g., T_{11}) describe the count of fish remaining in a reach across the tag-recapture period; therefore, the matrix provides estimates of stationary and mobile observations among *n* stream reaches and *n* movement intervals. The spatial interaction matrices were used in subsequent statistical analysis to evaluate stationary and mobility in relation to the stream distance matrix. As the matrix **T** is directional (e.g., stream reaches are listed in increasing order and indicate position from downstream to upstream), travel direction can be derived with the upper right quadrant of the matrix indicating upstream movement and the lower left quadrant of the matrix indicating downstream movement.

$$\mathrm{T} = \begin{bmatrix} T_{11} & T_{12} & T_{13} & T_{14} & T_{15} \\ T_{21} & T_{22} & 0 & 0 & 0 \\ T_{31} & 0 & T_{33} & 0 & 0 \\ T_{41} & 0 & 0 & T_{44} & 0 \\ T_{51} & 0 & 0 & 0 & T_{55} \end{bmatrix}$$

The statistical analysis of Redside Dace movement has three components. First, summary statistics of the stationary (p_{stat}) and mobile (p_{mobile}) components of fish activity are presented (Radinger and Wolter 2014). Here, p_{stat} is the probability that a fish tagged at stream reach *i* at time *k* will be captured at reach *i* at time *k*+1. Although it is possible that fish tagged at stream reach *i* left the reach at some point during the sampling interval only to return to the initial point of capture during resampling, the discrete tag and recapture interval did not allow for a finer level of temporal resolution to be incorporated. Therefore, p_{stat} describes the outcome of two independent sampling events across the course of the 1 – 7 month movement intervals (Table 1), with stationarity considered as the recapture of tagged fish at the initial point of tagging. The probability of a fish tagged at reach *i* being recaptured at reach *j…n* at time *k*+1 (the probability of being mobile, p_{mob}), was 1-p_{stat}.

We also evaluated the minimum, mean, and maximum absolute travel distance (m) of fish that were mobile (σ_{mob}), as well as directional upstream or downstream movement, where negative values indicate downstream movement and positive values indicate upstream movement. The directional statistic was weighted based on aggregate counts (e.g., a weighted directional mean; σ_{mobdir}) to describe average distance-by-direction of fishes between two sampling periods. The σ_{mobdir} statistic infers mean movement bias, where a negative value indicated that a collection of tagged individuals experienced average downstream movement of -*x* meters relative to their starting position, while a positive value indicated upstream movement. Kernel density functions of σ_{mobdir} were derived to include only mobile fish, as well as density functions that included both the mobile and stationary components. The latter describes the empirical probability that fish will remain stationary, move upstream, or move downstream during a given movement period. The absolute movement values (non-zero components) followed a negative binomial process and parameters of these distributions were derived using maximum likelihood in the R package MASS.

The second component of the analysis was to evaluate the extent to which seasonal variation in p_{stat} and σ_{mobdir} was influenced by flow characteristics (sensu Reid and Parna [2017]). Flow characteristics may prevent fish movement if water availability is poor; alternatively, high flows may force fish downstream. Intermediate flows may promote the widest opportunity for movement. In addition to environmental factors, there is evidence that fish movement is influenced by body size and the duration between tag and recapture intervals (Smithson and Johnston 1999, Radinger and Wolter 2014). To account for these factors, the duration of the sampling interval was included as a predictor variable (mean tagged fish size was relatively constant and was not included as a predictor variable). The relationship between the movement statistics (p_{stat} and σ_{mobdir}) and flow attributes was evaluated using multiple linear regression of the form $y = \beta_0 + \beta_1 x_1 \ldots \beta_n x_n$, where y is the response variable (p_{stat} or σ_{mobdir}), β are coefficients, $x_1 \ldots x_n$ are predictors (intercept, mean daily flow, 90th percentile of mean daily flow, R-B index of daily mean flow, and the tag and recapture interval (months)). Due to low sample sizes (7 movement seasons and flow observations), model variables were selected deterministically. Model significance was evaluated at $\alpha = 0.05$ and adjusted R^2 was used to evaluate model performance.

The final component of the analysis was to understand factors associated with reach-to-reach movements by the mobile fraction of the population. We constructed models to relate tagged fish movements between reach *i* and reach *j* to features at reach *j* that would influence Redside Dace to choose reach *j* relative to all others. We used a modification of the production-constrained gravity model (Fotheringham and Kelly 1989, Drake and Mandrak 2010) to predict fish movement. Here, the model has been derived as a statistical spatial interaction model, which estimates T_{ij} as the count of fish moving between reach *i* and *j* (stationary occurrences were excluded). With this formulation, the model ensures that fish leaving each stream reach will experience redistribution somewhere among the stream reaches.

Due to the autocorrelated nature of spatial interaction models (i.e., movement from *i* to *j* is functionally dependent on starting abundance at *i*) and the potential degree of multicollinearity between the predictor variables (habitat and species co-variates), we used boosted regression trees (Elith et al. 2008). Boosted regression trees are a machine learning technique that use an iterative process to learn the relationship between a response variable, *Y*, and a series of predictor variables, $X_1, X_2 \ldots X_n$. The model works by randomly sampling the data, building individual regression trees (see De'ath and Fabricius 2000 and De'ath 2007) on the resampled data, and continuing the process to learn which variables are important across *n* randomly permuted trees. The boosted tree models incorporated the tagged abundance of Redside Dace at reach *i*, the distance separation between *i* and *j*, Ontario Stream Assessment Protocol (OSAP)-derived aquatic habitat measurements, and the CPUE (the 3-pass sum) of co-occurring fishes at reach *j* as predictors in the model. Flow attributes were also incorporated to determine if certain *ij* routes were more or less likely to be travelled during particular flow regimes. Due to sample size limitations, the model was run across all movement seasons and therefore reflects the aggregate factors responsible for reach-level movement over a 14 month period. All statistical analyses were performed in R v.3.3.1 (R Core Team 2016).

RESULTS

SEASONAL MOVEMENT STATISTICS

A summary of p_{stat}, σ_{mobdir}, and other movement statistics is presented in Table 3. Both sites were characterized by relatively high Redside Dace stationarity during the May – July 2007 sample period (Berczy, 0.74; Leslie, 0.67), low stationarity during the July – August period (Berczy, 0.23; Leslie, 0.19), and moderate stationarity during the August – September period

(Berczy, 0.44; Leslie, 0.51; Table 3). Berczy experienced moderate stationarity during the fall period (October – May, 0.41); whereas, Leslie had almost no stationary fish between September – October. The overwinter period was characterized by no stationarity (Berczy) and extremely low stationarity (Leslie), although both estimates had low sample sizes (Bercy, *n* = 11 individuals; Leslie, *n* = 13 individuals) and a lengthy tag-recapture delay. The probability of stationarity in May – July 2008 was extremely low in contrast to the previous year, indicating that yearly variation exists in both populations.

Empirical kernel density functions including and excluding stationary fish are presented in Figures 3 – 6. The vertical dashed line in Figures 3 – 6 corresponds to the weighted directional mean (σ_{mobdir}) in Table 3, with deviation to the right or left side of zero indicating mean directional bias. The 14-month distribution functions of the zero and non-zero periods resembled Laplace distributions typically used to model directional movement, though seasonal distributions were usually skewed and often not centered around zero. For the mobile fraction of recaptured fish, both tributaries experienced similar directional bias (Table 3), as indicated by σ_{mobdir}. Despite low probability of movement in May – July, when fish moved they exhibited slight net downstream bias (σ_{mobdir} = -10.6 m for both tributaries; 35 downstream vs. 20 upstream movements in Berczy; 9 downstream vs. 11 upstream movements Leslie). Higher probability of movement in July - August at both sites was characterized by net upstream movement (σ_{mobdir} = 25.1 m in Berczy and 67.64 m in Leslie), while September – October exhibited net downstream movement at both sites. October to May was associated with net upstream movement for both sites (average upstream dispersal distance of 129.18 m at Berczy and 221.5 m at Leslie), and maximum movement distances at both sites were observed during the overwinter period (411 m Berczy, 680 m Leslie, both in an upstream direction). Measured over the entire 14 – month sample period, σ_{mobdir} was negative for both populations.

The negative binomial dispersal kernels, representing theoretical movement expectations during a given sample period, reflected the empirical patterns well, with both sites characterized by high peaks (grey lines, Figure 7) to reflect the May – July 2007 period, and the highest mean values of 174.92 m (early – late May, Berczy, yellow line) and 217.42 m (Leslie, pink line). The values in the right three columns of Table 4 indicate the probability of a mobile fish travelling at least *x* meters (50, 100, and 500 m). The highest probability of travelling at least 500 m was found during the October to early May period in Berczy (0.032) and the late May to July period in Leslie (0.078).

Table 3. Summary statistics of Redside Dace movement during the 2007 – 2008 study period.

Tributary	**Movement Period**	p_{stat}	σ_{mob} **(mean)**	σ_{mob} **(sd)**	σ_{mob} **(min)**	σ_{mob} **(max)**	$\sigma_{mob\ us}$ **(mean)**	$\sigma_{mob\ ds}$ **(mean)**	$freq_{up}$	$freq_{down}$	σ_{mobdir} **Weighted directional bias**	**Directional Dominance**
Berczy Creek	May - July	0.74	35.98	19.47	10	125	34.85	36.62	20	35	-10.6	Downstream
	July - Aug	0.23	108.92	72.81	10	290	131.72	85.32	29	28	25.1	Upstream
	Aug - Sep	0.44	117.15	85.16	21	357	103.6	127.75	25	32	-26.28	Downstream
	Sep - Oct	0.41	131.25	104.63	21	315	122.22	135.12	18	42	-57.91	Downstream
	Oct - May	0	129.1	147.8	15	411	129.18	NA	11	0	129.18	Upstream
	Early - late May	0	174.92	104.36	40	411	191.72	82.5	11	2	149.53	Upstream
	Late May - Jul	0.28	114.85	102.41	22	275	90.25	121	4	16	-78.75	Downstream
	All samples	0.47	100.68	89.2	10	411	104.15	98.05	103	137	-11.275	Downstream
Leslie Tributary	May - July	0.67	63.6	31.6	25	175	48.18	82.44	11	9	-10.6	Downstream
	July - Aug	0.19	112.7	55.21	27	227	127.75	76.6	12	5	67.64	Upstream
	Aug - Sep	0.51	147.82	126.18	25	547	153	144.94	10	18	-38.53	Downstream
	Sep - Oct	0.02	143.88	154.01	25	680	186.9	136.33	10	57	-88.08	Downstream
	Oct - May	0.07	188.58	192.27	53	680	221.55	89.6	9	3	143.75	Upstream
	Early – late May	0.142	212.13	179.93	27	649	161.3	262.92	12	12	-50.79	Downstream
	Late May - Jul	0.173	217.42	189.3	52	547	84.75	313.91	8	11	-146.05	Downstream
	All samples	0.28	133.54	135.46	25	680	143.38	127.97	52	92	-29.98	Downstream

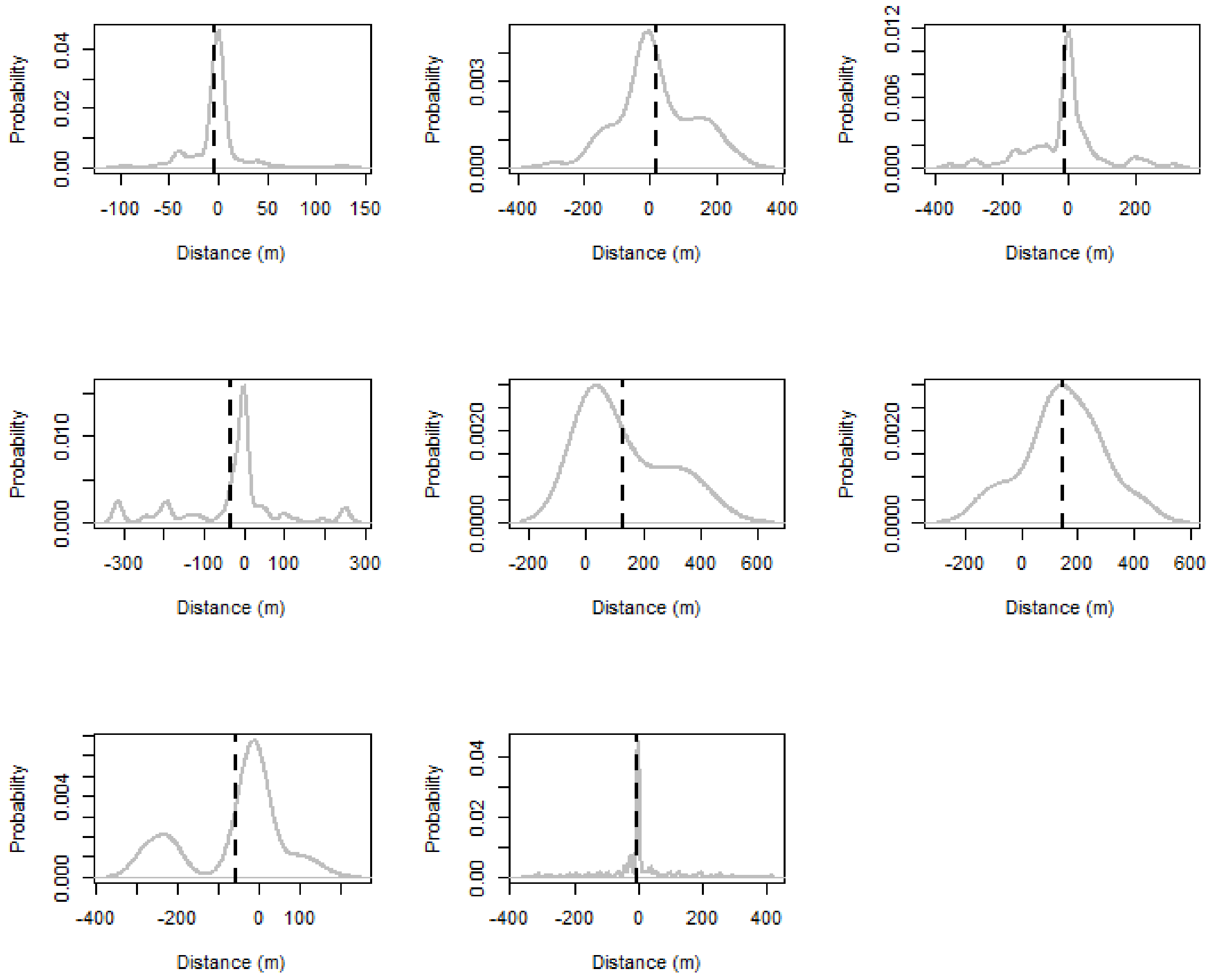


Figure 3. Kernel density functions of directional Redside Dace movement in Berczy Creek. The sample periods, from top left to bottom right, are, May – July, July – Aug, Aug – Sept, Sept – Oct, Oct – early May, early May – late May, late May - July; and, all sample periods combined. Zero-counts, indicating stationarity fish at distance marker 0, are included in the distribution functions. The mean value is indicated by the dashed vertical line.

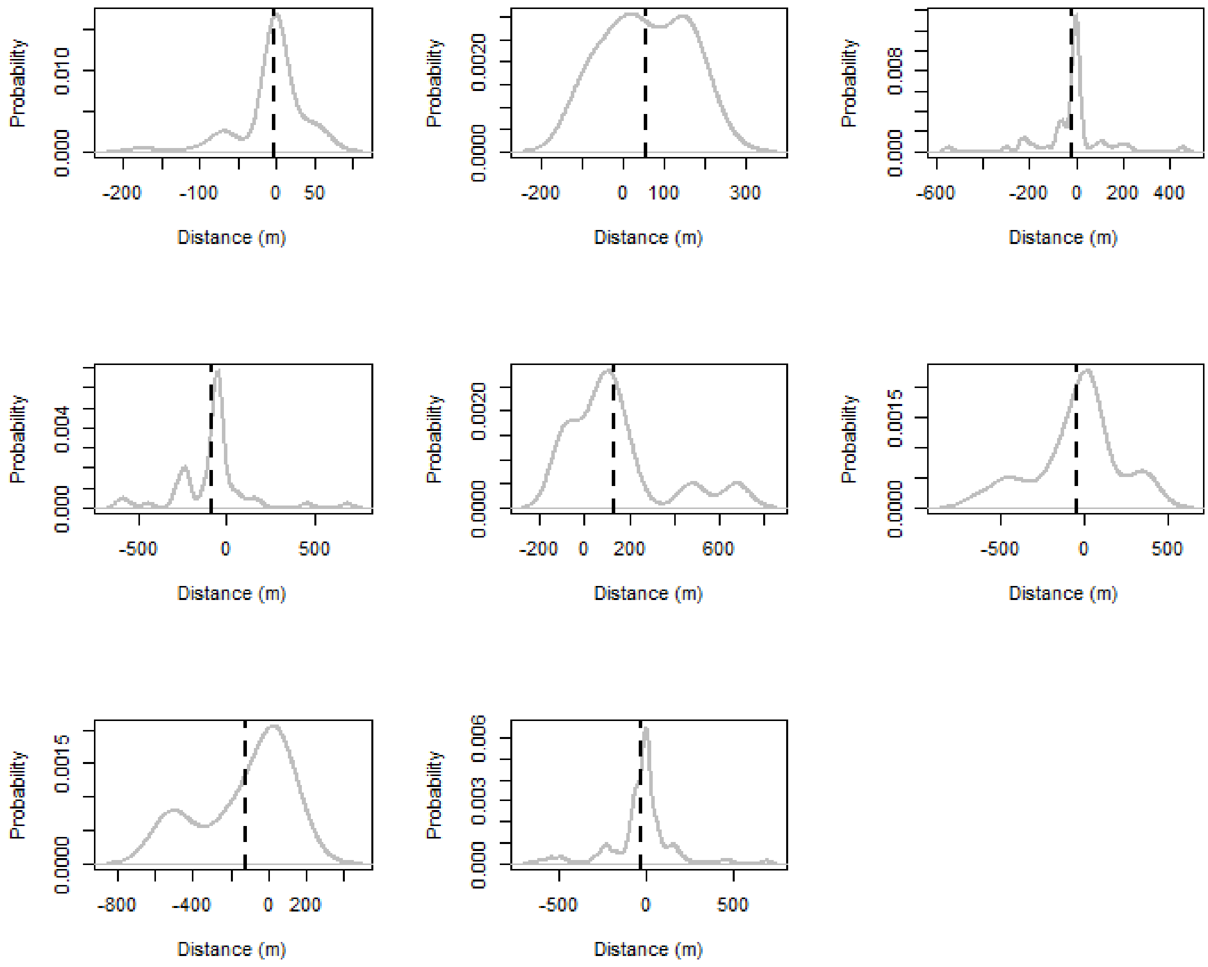


Figure 4. Kernel density functions of directional Redside Dace movement in Leslie tributary. The sample periods, from top left to bottom right, are, May – July, July – Aug, Aug – Sept, Sept – Oct, Oct – early May, early May – late May, late May - July; and, all sample periods combined. Zero-counts, indicating stationarity fish at distance marker 0, are included in the distribution functions. The mean value is indicated by the dashed vertical line.

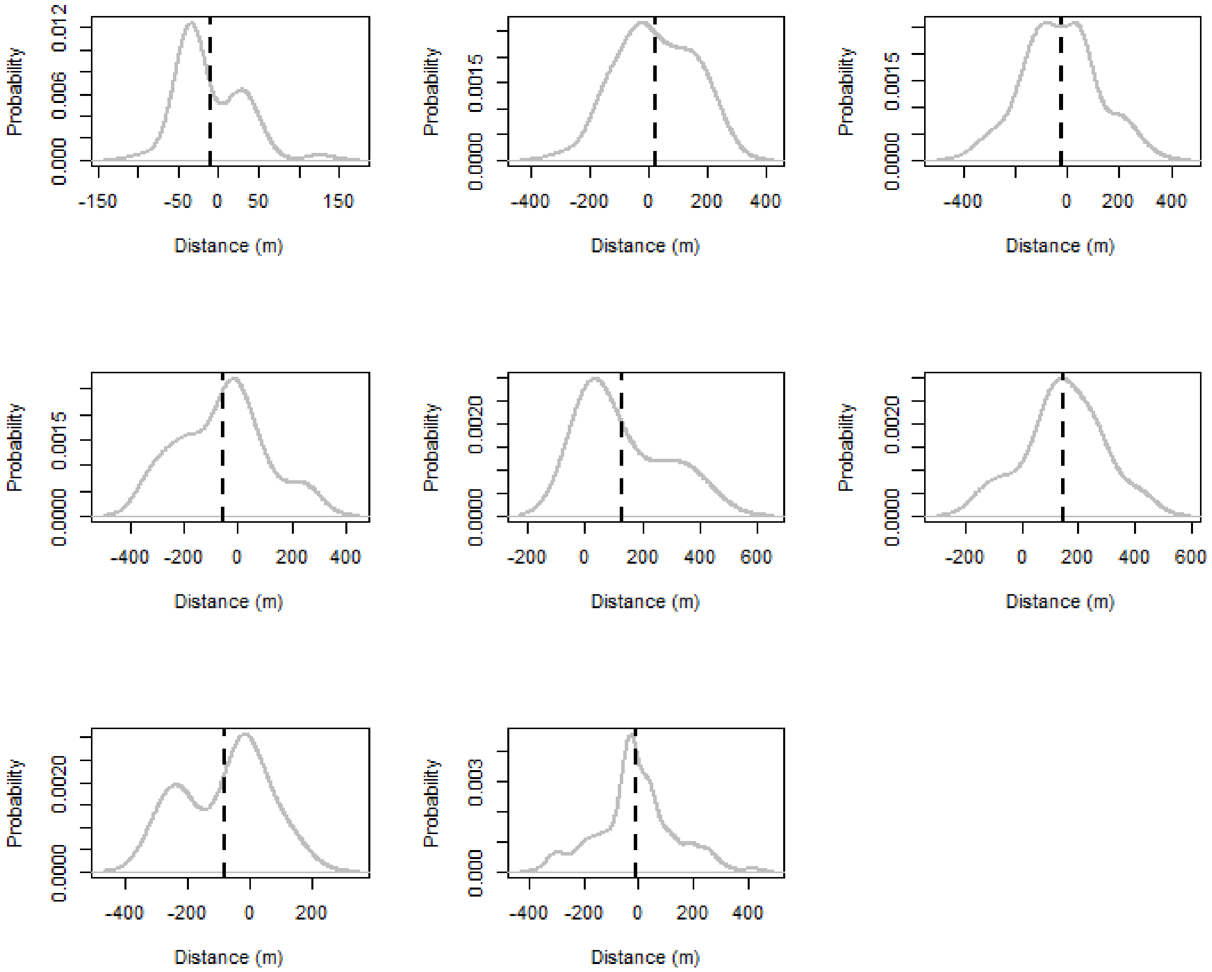


Figure 5. Kernel density functions of Redside Dace movement in Berczy Creek with zero-counts removed. The sample periods, from top left to bottom right, are, May – July, July – Aug, Aug – Sept, Sept – Oct, Oct – early May, early May – late May, late May - July; and, all sample periods combined. The mean value is indicated by the dashed vertical line.

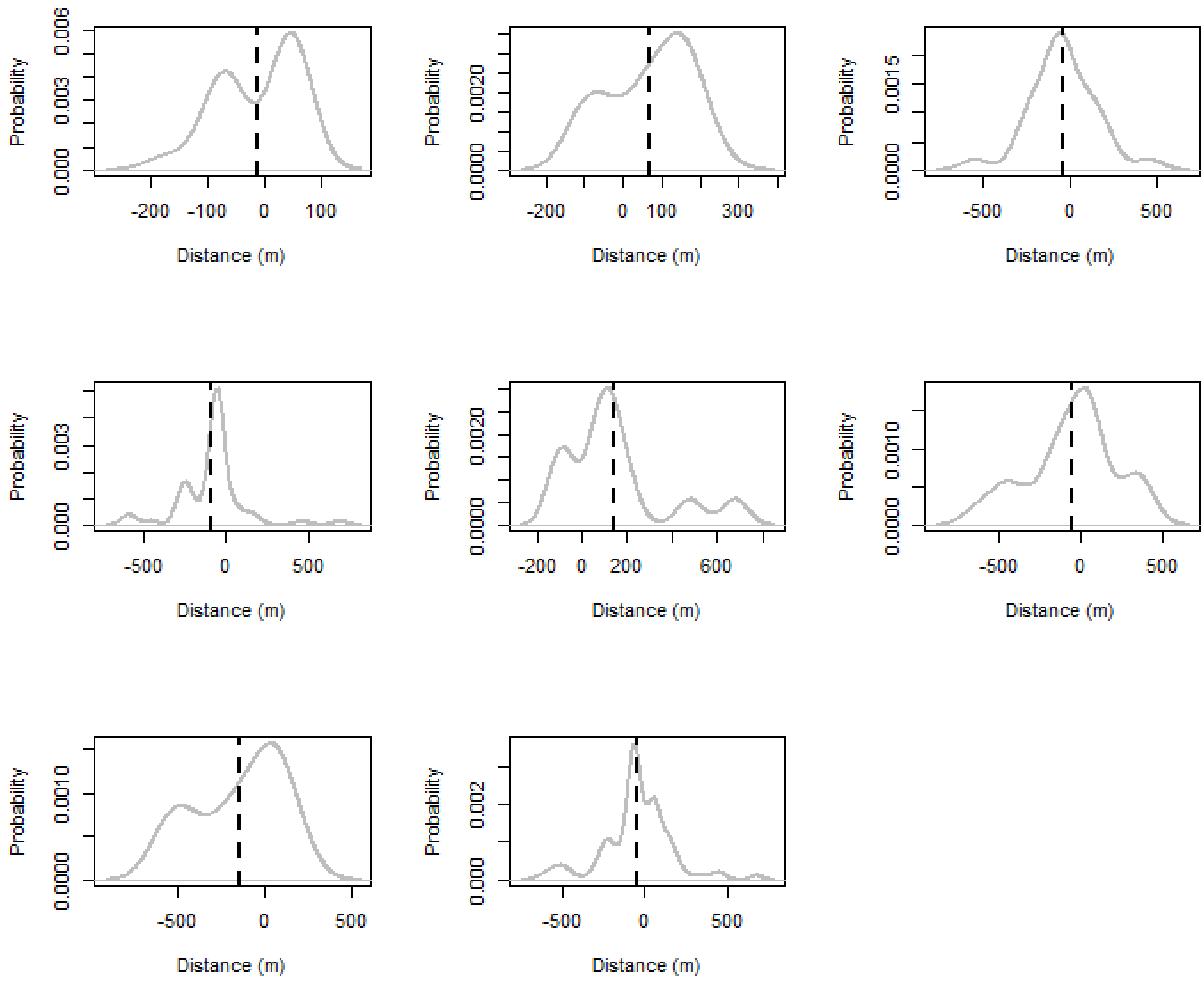


Figure 6. Kernel density functions of Redside Dace movement in Leslie tributary with zero counts removed. The sample periods, from top left to bottom right, are, May – July, July – Aug, Aug – Sept, Sept – Oct, Oct – early May, early May – late May, late May - July; and, all sample periods combined. The mean value is indicated by the dashed vertical line.

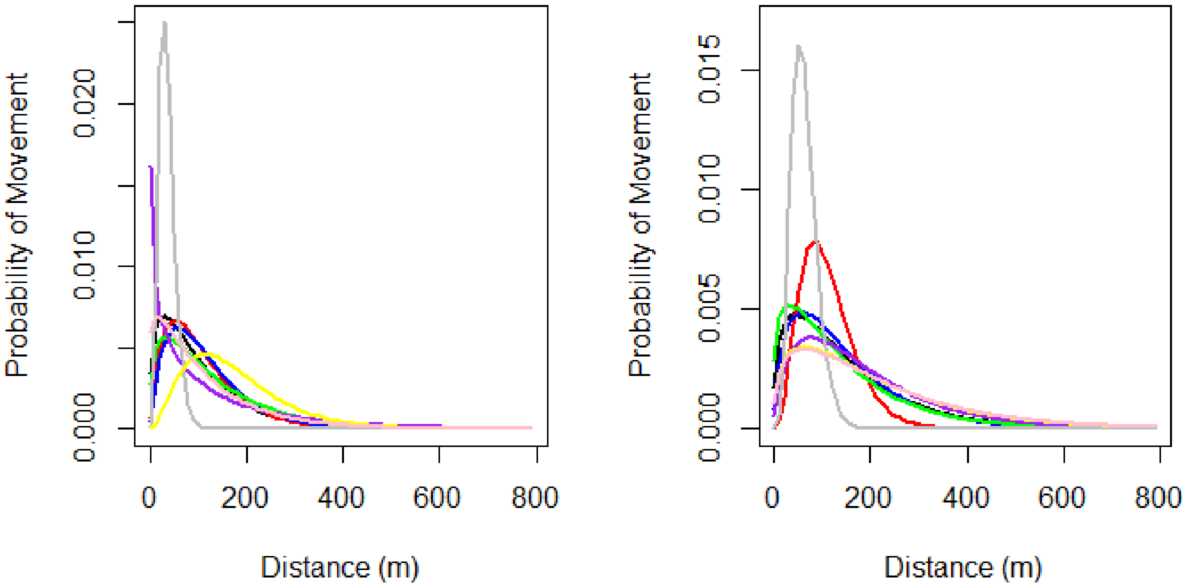


Figure 7. Negative binomial probability distribution functions for Redside Dace movement from Berczy Creek (left panel) and Leslie tributary (right panel) across the sample period. Colours are (2007): May – July (grey), July – Aug (red), Aug – Sep (blue), Sep – Oct (green), Oct – early May (purple), (2008): early May – late May (yellow), late May – July (pink).Parameters for the distribution functions are listed in Table 4.

Table 4. Parameters of the fitted negative binomial probability distribution functions. The column labels Pr>50, Pr>100, and Pr>500 indicate the cumulative probability of moving greater than each distance (m) in any direction (upstream or downstream) within the sample period.

Tributary	**Sample Period**	**Negative Binomial *u***	**Negative Binomial *k***	***Pr* > 50**	***Pr* > 100**	***Pr* > 500**
Berczy	May - July	35.98	4.96	0.184	0.0029	4.38e-23
	July - Aug	108.92	1.95	0.754	0.447	0.0012
	Aug - Sep	117.15	2.01	0.783	0.488	0.0019
	Sept - Oct	131.25	1.34	0.738	0.499	0.0127
	Oct – early May	129.18	0.738	0.611	0.423	0.032
	Early – late May	174.92	2.99	0.939	0.747	0.0090
	Late May - July	114.85	1.13	0.667	0.427	0.0099
	All	105.25	1.37	0.677	0.407	0.003
Leslie	May – July	63.6	6.33	0.65	0.092	3.42e-12
	July – Aug	112.70	4.02	0.88	0.52	2.51e-05
	Aug - Sep	147.82	1.69	0.81	0.58	0.013
	Sep - Oct	143.88	1.29	0.75	0.53	0.020
	Oct – early May	188.58	1.70	0.87	0.68	0.04
	Early – late May	212.13	1.43	0.859	0.690	0.073
	Late May - Jul	217.42	1.43	0.863	0.698	0.078
	All	152.15	1.43	0.79	0.569	0.022

Table 5. Results of among-season regression between p_{stat}*,* σ_{mobdir}*, and flow attributes in the Rouge River.*

Tributary	**Response**	**β₀**	**β₁**	***x*1**	**β₂**	***x*2**	**Overall *P***	**Adjusted R^2**
Berczy	p_{stat}	0.483	-0.105	90th Percentile	0.014	Sampling Interval	0.391	0.061
	p_{stat}	0.526	-0.237	Mean	0.014	Sampling Interval	0.404	0.046
	p_{stat}	0.285	0.260	R-B Index	-0.034	Sampling Interval	0.854	-0.386
Leslie	p_{stat}	0.358	-0.065	90th Percentile	0.012	Sampling Interval	0.705	-0.260
	p_{stat}	0.367	-0.119	Mean	-0.006	Sampling Interval	0.795	-0.337
	p_{stat}	0.003	0.748	R-B Index	-0.022	Sampling Interval	0.693	-0.249
Berczy	σ_{mobdir}	-38.13	12.41	90th Percentile	11.20	Sampling Interval	0.679	-0.236
	σ_{mobdir}	-58.246	54.075	Mean	6.103	Sampling Interval	0.527	-0.088
	σ_{mobdir}	-50.75	60.42	R-B Index	16.36	Sampling Interval	0.73	-0.281
Leslie	σ_{mobdir}	-97.13	-17.29	90th Percentile	44.50	Sampling Interval	0.140	0.440
	σ_{mobdir}	-93.23	-33.73	Mean	42.40	Sampling Interval	0.152	0.414
	σ_{mobdir}	-182.52	176.57	R-B Index	34.58	Sampling Interval	0.147	0.428

RELATIONSHIPS BETWEEN SEASONAL STATISTICS AND FLOW ATTRIBUTES

The relationships between p_{stat}, σ_{mobdir}, and flow conditions (mean daily flow, 90th percentile of daily flow, or R-B index) were not significant for any of the variables tested (see Table 5 for regression results). In general, p_{stat} had a negative, non-significant relationship with mean daily discharge and 90th percentile of daily discharge at Berczy, while σ_{mobdir} had a weak positive or negative, non-significant relationship with mean daily discharge and 90th percentile of daily discharge (Figure 8). Neither p_{stat} nor σ_{mobdir} had relationships with R-B values (all non-significant). Similar trends between seasonal movement and flow conditions were apparent at Leslie (Figure 9), with a weak negative relationship between p_{stat} and mean daily discharge and the 90th percentile of daily discharge, and very weak positive relationship between σ_{mobdir} and those variables. As with Berczy, the R-B index provided little correlation with seasonal movement statistics.

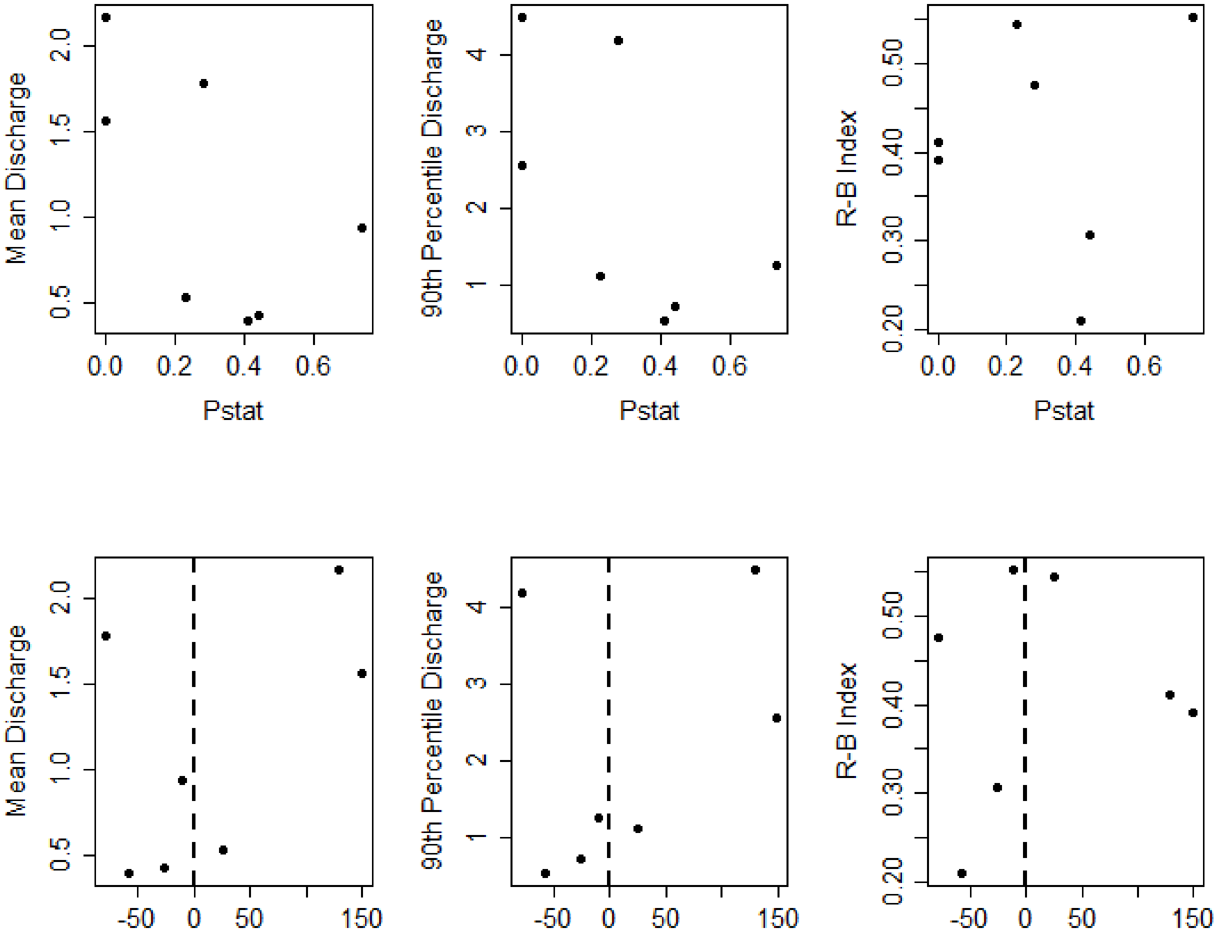


Figure 8. Relationship between p_{stat} (top panel) and directional weighted mean (σ_{mobdir}; bottom panel) for Berczy Creek over the study period. Each point represents a movement statistic and corresponding flow statistic for a given period (May – Jul, Jul – Aug, Aug – Sep, Sep – Oct, Oct – early May, early May – late May, late May – July).

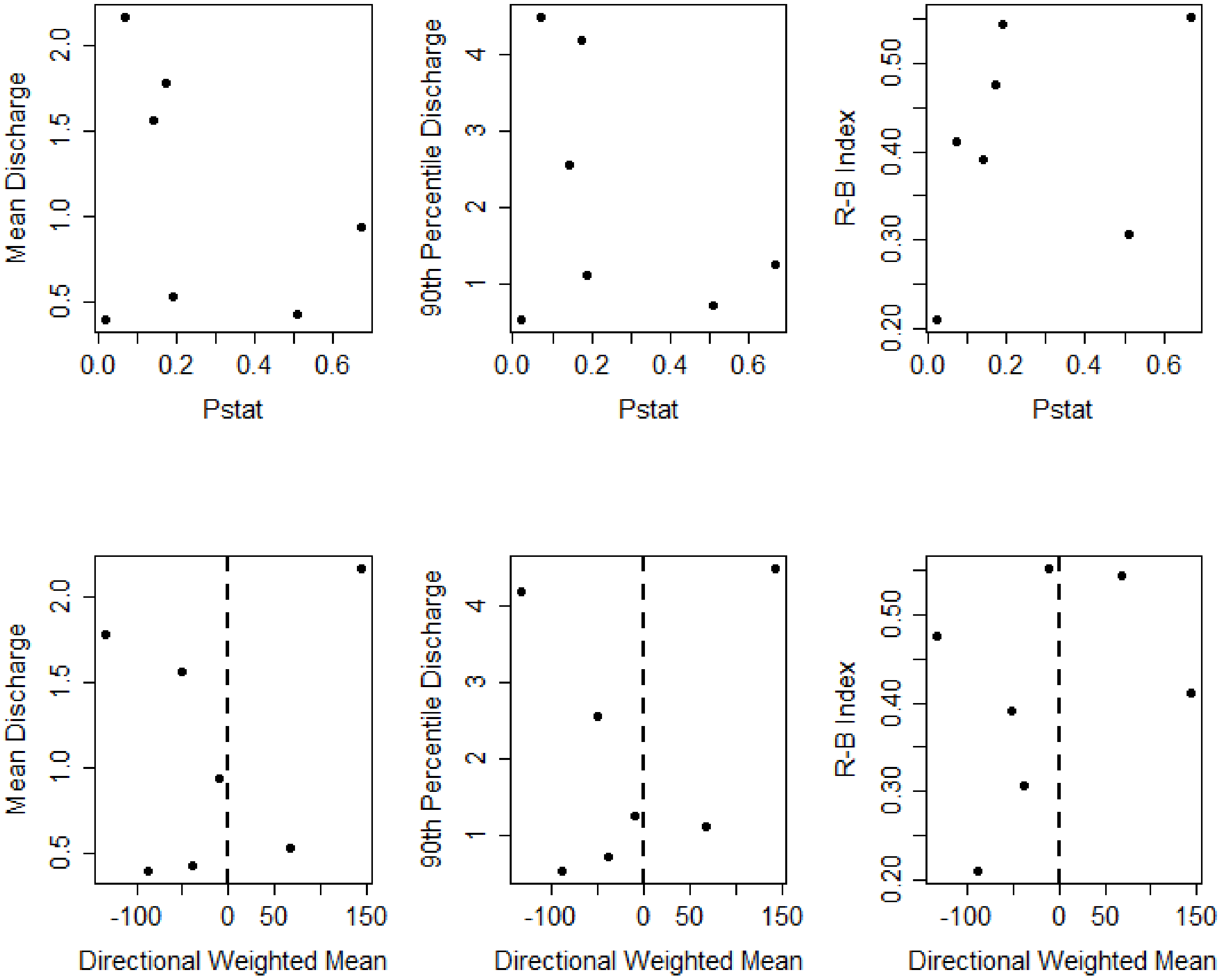


Figure 9. Relationship between p_{stat} (top panel) and directional weighted mean ($\sigma_{mobdir;}$ bottom panel) for Leslie tributary over the study period. Each point represents a movement statistic and corresponding flow statistic for a given period (May – Jul, Jul – Aug, Aug – Sep, Sep – Oct, Oct – early May, early May – late May, late May – July).

PERFORMANCE OF BOOSTED REGRESSION TREES

Boosted regression tree outputs for Berczy had a high correlation with training data (0.939), with cross-validated correlation of 0.549, indicating that the boosted tree structure explained roughly 50% of the deviance in T_{ij} based on an independent hold-out dataset (Table 6). The relative influence of predictor variables selected by boosted trees is displayed in Figure 10 and Table 7. The first five co-variates explained 74.9% of model deviance (variable importance sums to 100%), and included: ORedside (42.8%), a variable describing the tagged abundance of fish available to leave stream reach *i* at time *k*, *ij* distance (m; 12.7%), the standard deviation of reach volume (m^3) in *j (*8.2%), the CPUE of Creek Chub (*Semotilus atromaculatus*) in *j (8%)*, and the CPUE of Common Shiner (*Luxilus cornutus*) in *j* (3.9%). The partial dependency plots in Figure 6 can be interpreted as the effect of an individual variable on T_{ij} (the count of fish movement between reach *i* and *j*) when all other variables are held at their mean. For example, on average, there is a negative relationship between T_{ij} and distance, and a positive relationship between T_{ij} and the CPUE of Creek Chub at reach *j*. Notably, a dummy variable included to indicate the direction of movement (upstream vs. downstream, “UpDown”), the duration of the tag-recapture period (“TagDuration”), seasonal flow variables such as mean daily discharge (“MeanFlow”) or the 90th percentile of daily discharge (“X90Flow”), and other factors hypothesized to be important, such as the CPUE of Brown Trout (*Salmo trutta*) (“DBrownTrout”) or Rainbow Trout (*Oncorhynchus mykiss*) (“DRainbowTrout”), had low importance in the overall model.

Boosted regression tree outputs for Leslie had slightly lower correlation with training data (0.687), but had relatively high correlation through cross-validation (0.537; Table 6). The first five co-variates explained 86% of model deviance and included: ORedside (40.1%), CPUE of White Sucker (*Catostomus commersonii*) in reach *j* (30.3%), *ij* distance (m; 5.9%), CPUE of Bluntnose Minnow (*Pimephales notatus*) (4.1%) in reach *j*, and depth of reach *j* (3.2% Figure 11; Table 7). As with Berczy, variables related to the direction of movement, flow attributes, and predatory species (Brown Trout, Rainbow Trout) had minor or no influence on the model.

Table 6. Performance of the boosted regression tree models for spatial interaction of Redside Dace in Berczy Creek and Leslie tributary, 2007 – 2008.

Model Evaluation	***Berczy Creek***	***Leslie Tributary***
Mean total deviance	*0.901*	*1.246*
Mean residual deviance	*0.159*	*0.646*
Estimated cross-validated	*0.465*	*0.83*
Training data correlation	*0.939*	*0.687*
Cross-validated correlation	*0.549*	*0.537*

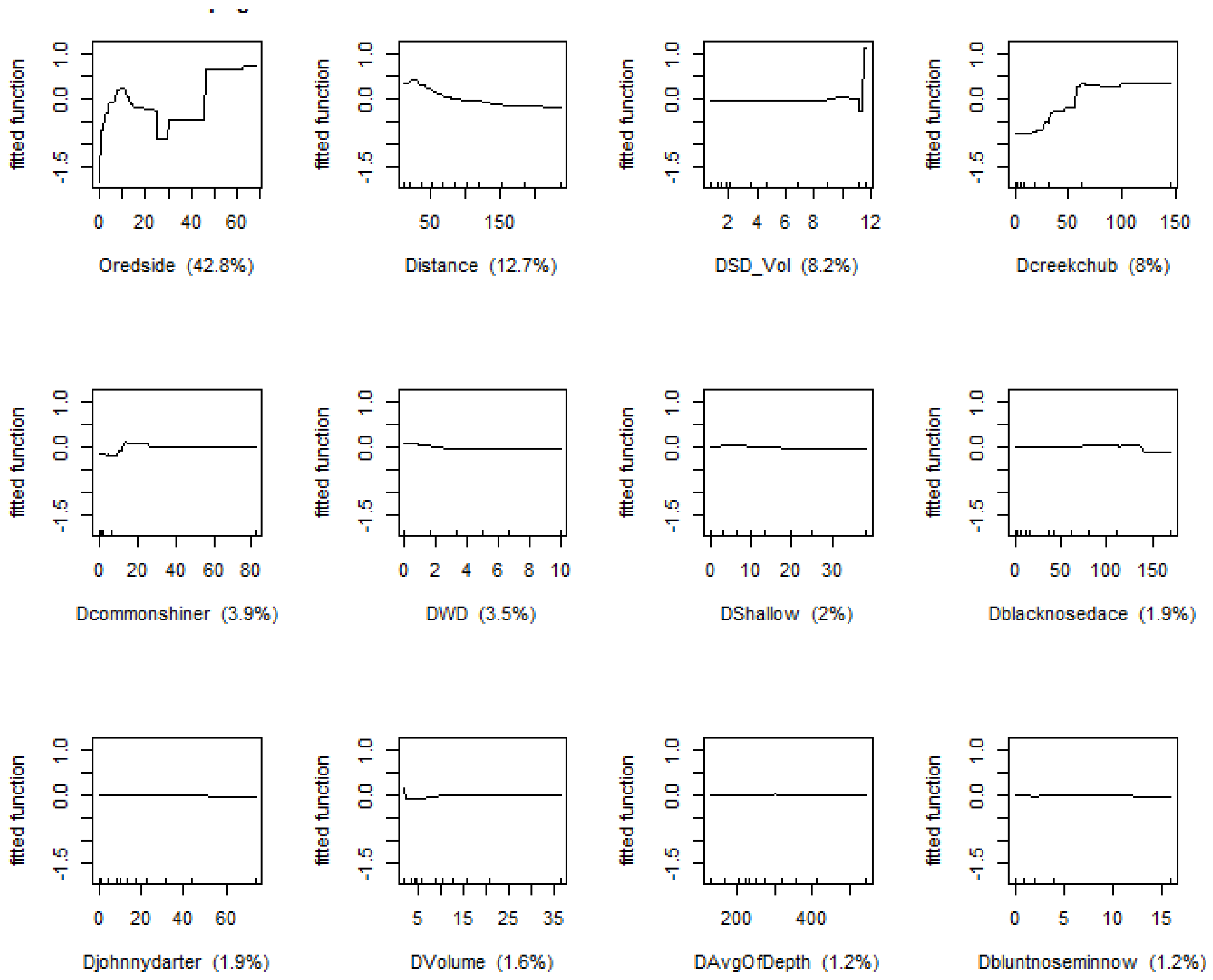


Figure 10. Partial dependency plots of the boosted regression tree model to predict spatial interaction of Redside Dace in Berczy Creek across all movement periods. The first five variables explained 75.6% of modelled variance.

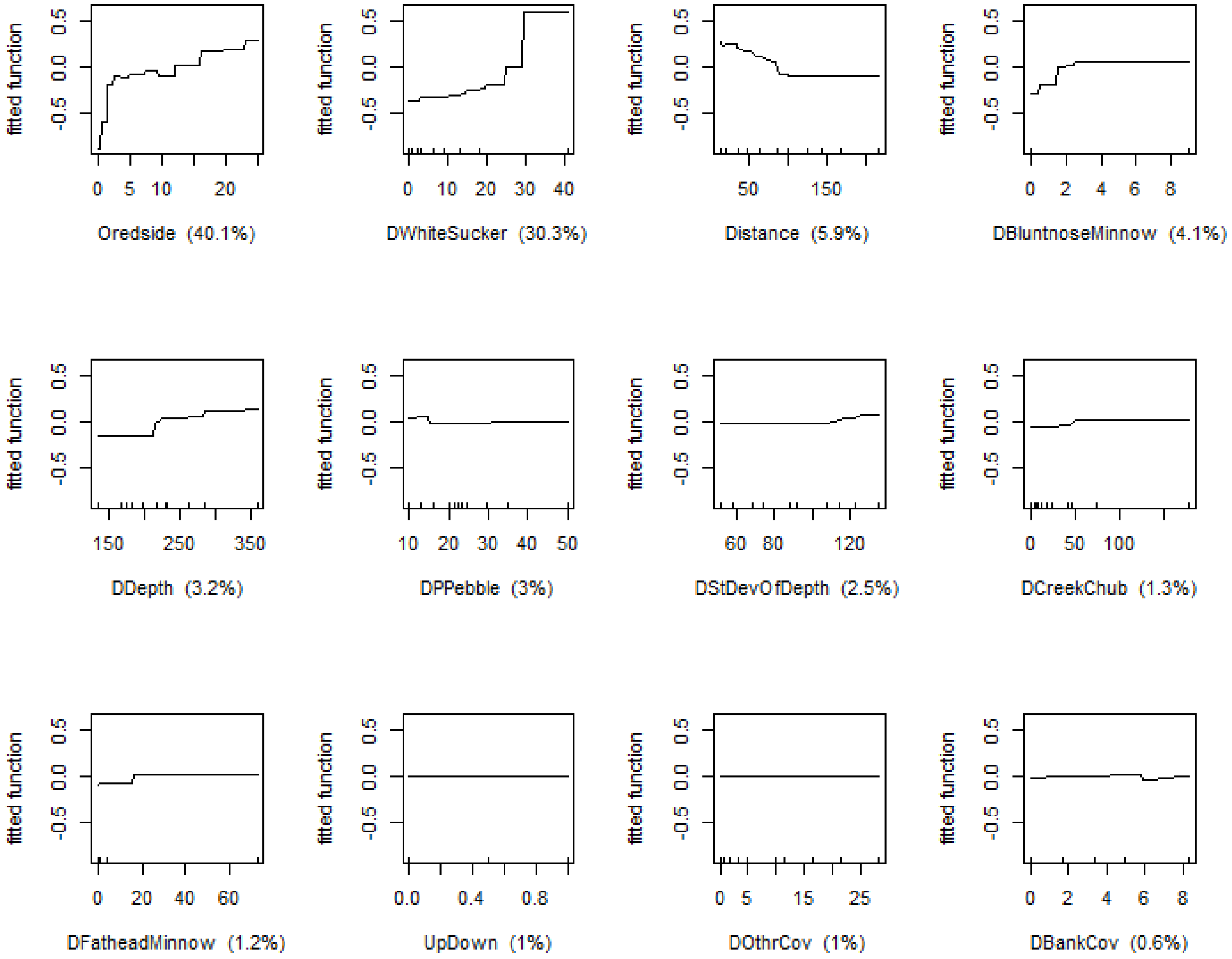


Figure 11. Partial dependency plots of the boosted regression tree model to predict spatial interaction of Redside Dace in Leslie tributary across all movement periods. The first five variables explained 83.6% of modelled variance.

Table 7. Results of boosted regression trees to predict spatial interaction (T_{ij}) of Redside Dace in Berczy Creek and Leslie tributary. Relative influence values sum to 100% and indicate the fraction of total model variance explained. The prefix 'D' indicates that the variables was measured at the destination reach.

Berczy Creek		**Leslie Tributary**	
Variable	**Relative Influence (%)**	**Variable**	**Relative Influence (%)**
Redside Dace at Origin Pool	42.1	Redside Dace at Origin Pool	40.1
Distance	12.7	DWhiteSucker	30.3
DSD_Vol	8.6	Distance	5.9
DCreekChub	7.8	DBluntnoseMinnow	4.1
DCommonShiner	3.7	DDepth	3.2
DWD	3.1	DPPebble	2.9
Dshallow	2.4	DStDevOfDepth	2.4
Dvolume	1.7	DCreekChub	1.3
DBlacknoseDace	1.6	DFatheadMinnow	1.2
DJohnnyDarter	1.5	UpDown	1.0
DBluntnoseMinnow	1.3	DOthrCov	0.9
Darea	1.2	DBankCov	0.6
DWhiteSucker	1.1	DIntermediate	0.6
DAvgOfDepth	1.1	DBrookStickleback	0.5
DRainbowDarter	1.0	DLargemouthBass	0.4
DCreekChubJub	1.0	DPSand	0.4
DBrookStickleback	0.9	DVolume	0.3
DFlatRock	0.8	DRndRock	0.3
DStDevOfDepth	0.6	DJohnnyDarter	0.3
DPGravel	0.6	DAvgOfMaximum.Particle.Size	0.3
DStDevOfMaximumParticleSize	0.5	DBlacknoseDace	0.3
DPCobble	0.5	DSD_Volume	0.2
DStDevOfParticleSize	0.4	DCov	0.2
DModerate	0.3	DShallow	0.2
DBankCov	0.3	DAvgOfParticle.Size	0.2
MeanFlow	0.3	DArea	0.2
UpDown	0.2	DPGravel	0.1
Dredsidedacejuv	0.2	DStDevOfHydraulic.Head	0.1
DPSand	0.2	DRainbowDarter	0.1
DPPebble	0.2	DModerate	0.1
RBIndex	0.2	DCommonShiner	0.09
DIntermediate	0.2	DFlatRock	0.08
DRndRock	0.1	DPClay	0.06
DPClay	0.1	DAvgOfHydraulic.Head	0.05
DAvgOfParticle.Size	0.1	DPCobble	0.04

Berczy Creek		***Leslie Tributary***	
Variable	***Relative Influence (%)***	***Variable***	***Relative Influence (%)***
DMacCov	*0.1*	*DGlide*	*0.04*
Dfatheadminnow	*0.09*	*MeanFlow*	*0.03*
Drainbowtrout	*0.09*	*DLongnoseDace*	*0.03*
Dcommonshinerjuv	*0.05*	*DPool*	*0.03*
DOthrCov	*0.04*	*DStDevOfParticle.Size*	*0.02*
TagDuration	*0.04*	*RBIndex*	*0.02*
DCov	*0.03*	*DNorthernRedbellyDace*	*0.02*
DAvgOfMaximum.Particle.Size	*0.02*	*DAmericanBrookLamprey*	*0.009*
DPBoulder	*0.01*	*DStDevOfMaximum.Particle.Size*	*0.006*
Dpumpkinseed	*0.008*	*TagDuration*	*0.005*
DPool	*0.007*	*DPBoulder*	*0.003*
DAvgOfHydraulic.Head	*0.002*	*DFastRif*	*0.003*
Dnorthernredbellydace	*0.0008*	*DMacCov*	*0.003*
X90Flow	*0*	*DBrookTrout*	*0.0008*
DStDevOfHydraulic.Head	*0*	*X90_Flow*	*0*
DGlide	*0*	*DSlowRif*	*0*
DSlowRif	*0*	*DWD*	*0*
Dbrownbullhead	*0*	*DBrownTrout*	*0*
Dbrowntrout	*0*	*DPumpkinseed*	*0*
Dlongnosedace	*0*	*DRainbowTrout*	*0*

DISCUSSION

This study contributes information relevant for the conservation and recovery of Redside Dace in Canada. Results provide estimates of movement in two relatively stable populations of Redside Dace. The extent to which these results are applicable to other populations is unknown, but several conclusions can be drawn. First, there appeared to be synchrony of seasonal movement between populations. Both populations experienced high stationarity and downstream bias in May – July 2007, moderate stationarity in July – August and August – September, with upstream – then downstream bias – in both populations. The overwinter period was characterized by low stationarity and high upstream bias in both populations, with variable movement the following spring. Synchrony among populations can often be explained by higher-level environmental factors (e.g., temperature, flow, spawning migrations), yet flow attributes were only weakly negatively correlated with stationary and weakly positively or negatively correlated with directional bias. It is possible that the weak relationships are the result of flow attributes measured well downstream of the study sties, which may have provided a poor proxy for the flow conditions experienced by both populations.

The weak relationships provide some support that the decision to remain in a stream reach is influenced by flow attributes (higher probability of remaining at lower mean flow; Figures 8 and 9), but even in the highest mean daily flows (> 1.5 m^3/s), a portion of fish remained in reaches over extended periods (1 – 3 months). These results indicate that individual movement behaviours may be confounding the movement-flow relationship, in that some fraction of the population may always remain stationary despite flow conditions. During the lowest flows (Aug – September and September – October 2007), stationarity was moderate in both reaches, except in Leslie, where the probability of moving was high. Downstream bias during these periods was high, though both populations experienced upstream movements (Berczy, 43% and 30% of movements were upstream, with mean upstream travel distances of 103 m and 135 m; Leslie, 35% and 14% of movements were upstream, with mean upstream travel distances of 153 m and 186 m). During the highest flows of the study period (October – early May 2008; late May – July 2008), stationarity was low, with high upstream bias overwinter and downstream bias during the late May – July sample. These results indicate that the low-flow periods during summer and early fall 2007 were not sufficiently severe as to preclude fish movement. Additional tag-recapture sampling across a wider gradient of flow conditions, combined with a finer tag-recapture interval, would help to resolve the strength and ubiquity of the movement-flow relationships. Few authors have explored asymmetry in movement of stream fishes (but see Neufeld et al. 2018), which is expected to be important for Redside Dace as flow variability becomes extreme.

The aggregate 14-month directional weighted mean indicates a possible long-term downstream bias (Figures 5 and 6; similar findings exist when the study period is contracted to 12-months, May 2007 – May 2008), yet these results should be treated with caution. The tag-recapture intervals in this study represent a static view of a continuous process, and it is possible that any potential downstream bias is overcome within a relatively short period of time and not captured in the tagging dataset. The potential for widespread upstream movement over a short period of time was seen in Berczy in the May 2008 period, where all individuals moved upstream on average 190 m, up to a total of 411 m. Results suggest that fish are responding dynamically to environmental cues, of which only a portion can be attributed to flow attributes.

Results of the spatial interaction model to predict T_{ij} provide some resolution about the drivers of movement among stream reaches between tag-recapture intervals. Reach-level models indicated that 1) both populations are constrained by distance (Berczy; 12.7% of model variance; Leslie; 5.9% of model variance, where T_{ij} declines as distance increases), 2) both populations have associations between T_{ij} and the CPUE of cyprinids and catostomids in destination reaches (Berczy, Creek Chub and Common Shiner; Leslie, White Sucker); and, 3) aquatic habitat variables had different relative influence (positive relationship between the standard deviation of reach volume in Berczy, 8.2%; positive relationship between the depth of Leslie reaches, 3.2%, negative relationship between the width of Berczy reaches; 3.5%). Flow attributes, the direction of movement, and predator CPUE were not important variables in the reach-level models. The strong effect of distance is supported by movement observations across the tag-recapture intervals (Figures 5 and 6). Biotic associations are also not surprising: Redside Dace have known nest associations with other cyprinids (COSEWIC 2017), yet the relationships observed in the reach-level model were apparent at multiple points throughout the sample season. The underlying relationship between T_{ij} and co-occurring species may be causative, in that Redside Dace is responding directly to schooling effects provided by Creek Chub, Common Shiner, and White Sucker; or correlative, in that Redside Dace and co-occurring species are responding to aquatic habitat attributes not readily measured with the relatively coarse assessment tools of the Ontario Stream Assessment Protocol. Taken together, these results indicate that Redside Dace may overcome potentially large travel distances when the CPUE of certain co-occurring species in the destination reach is high.

Movement summaries and models provide context to the scale of movement and possible influence of stream-level (stream flow) and reach-level (co-occurring species) drivers on the movement of Redside Dace. Results provide strong support for seasonal spatial population structure, and moderate support for the relative influence of abiotic and biotic variables. However, what remains unknown is the significance of seasonal and reach-level movement as it relates to vital rates or environmental catastrophes, both of which have implications for Redside Dace population viability (van der Lee et al. 2020).

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