ORIGINAL RESEARCH

Integrated analysis of marked and count data to characterize fine-scale stream fish movement

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Abstract

Immigration and emigration are key demographic processes of animal population dynamics. However, we have limited knowledge on how fine-scale movement varies over space and time. We developed a Bayesian integrated population model using individual mark-recapture and count data to characterize fine-scale movement of stream fish at 20-m resolution in a 740-m study area every two months for 28 months. Our study targeted small-bodied fish, for which imperfect capture was accounted for (bluehead chub *Nocomis leptocephalus*, creek chub *Semotilus atromaculatus* and mottled sculpin *Cottus bairdii*). Based on data from 2021 individuals across all species, we found that proportions of immigrants in 20-m sections averaged 30–42% among the study species, but they varied over space and time. Creek chub immigrants increased during warmer intervals when individuals grew more and transitioned between body size classes, suggesting that immigration was due to ontogenetic habitat shifts. There was a weak pattern across the species that individuals were more likely to leave 20-m sections when flow was higher. Water-column species (bluehead chub and creek chub) were more likely to immigrate into and stay in deeper sections with more pool area. Across all species and occasions, number of immigrants to stream sections did not decrease with number of individuals that survived and stayed in the same sections. Thus, the habitat did not appear saturated, and our data provided no evidence that intra-specific interactions affected fine-scale movement at our fish densities. In conclusion, high turnover rates characterized fish movement among stream sections and their variation was associated with temporal and spatial shifts in abiotic conditions.

Keywords Animal behavior · Cormack–Jolly–Seber models · Dispersal · Freshwater fish · Integrated population models · State-space models

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Introduction

Animal movement occurs at multiple spatial scales from home range, natal dispersal, ontogenetic habitat shift to migration, which consequently affects ecological patterns and processes such as behavioral interactions, population dynamics, and ecosystem functions (Hansson and Akesson 2014). Regardless of spatial scales of investigation, immigration refers to a flux of individuals to a defined area and emigration is movement of individuals away from the defined area. Conceptually, the current population of a species in a defined area over a time interval is composed of local survivors and immigrants (Abadi et al. 2010a, b; Zipkin et al. 2014). Although individuals in the study area could be tracked for emigration and survival analysis has advanced (Lebreton et al. 1992), immigrants are harder to track because they originate from outside the study area (Abadi

et al. 2010a). In addition, many animals are cryptic and their capture probability of individuals is imperfect, meaning that animal abundance estimation per se is not a trivial issue (Royle 2004). Immigration and emigration are most often estimated over a broader spatial scale to characterize meta-population dynamics (Hanski 1994; Weegman et al. 2016; Paquet et al. 2020). Rarely have immigration and emigration been rigorously quantified at fine spatial scales despite their importance in habitat selection, predatory-prey encounter, competitive interactions, and disease transmission (Schlägel et al. 2019; Wilber et al. 2022; Beumer et al. 2023).

Integrated population models (IPMs) have emerged as a flexible modeling framework to synthesize multiple data types for robust demographic inferences (Schaub and Abadi 2011). Advantages of IPMs include increased precision of parameter estimates due to more input data, more explicit linkages between demographic processes and population trajectories, and estimation of parameters that would not be possible via analysis of individual data types (Zipkin and Saunders 2018). Immigration has been successfully estimated by a joint analysis of mark-recapture data, which inform apparent survival, and count data, which include information on survivors and immigrants (Abadi et al. 2010a; Paquet et al. 2021). IPMs have been applied to quantify demographic rates other than immigration and their linkage to population dynamics, and their development has been facilitated by data-rich terrestrial species (i.e., mammals and birds) (Arnold et al. 2018; Millon et al. 2019). Although marine fisheries stock assessment contributed to the initial conception of IPMs (Maunder and Punt 2013), freshwater applications have been limited (Doll et al. 2021; Scheuerell et al. 2021) due partly to challenges of collecting demographic data on cryptic, small-bodied aquatic species. Yet, such applications are needed to advance this rapidly-developing technique and extend its application to other data types, such as depletion-based count data collected commonly in stream fish surveys in our case.

Stream fish movement is characterized by high individual variation (Skalski and Gilliam 2000; Rodríguez 2002). Many individuals are sedentary (i.e., high fidelity) and are recaptured in the same location (< 20 m) over time, resulting in an early claim that restricted movement is the norm (i.e., low immigration rates even at fine spatial scales) (Gerking 1959). More recently, intensive mark-recapture surveys and modern techniques (e.g., PIT antennas and genetics) have shown that stream fish move more frequently than initially considered and a portion of stream fish populations move long distances (Gowan et al. 1994; Skalski and Gilliam 2000; Albanese et al. 2004; Comte and Olden 2018; Steffensmeier et al. 2022), highlighting the importance of movement in fulfilling their ecological requirements in spatially and temporally heterogeneous riverscapes (Fausch et al. 2002). This paradigm shift in stream fish movement ecology occurred due

to increased power to detect broad-scale fish movement, but quantitative estimates of fine-scale immigration and fidelity remain scant in stream fishes, referred to as local turnover rates (Rodríguez 2002). Little knowledge is available on how fine-scale fish movement varies spatially and temporally despite our ample understanding of stream habitat heterogeneity (Frissell et al. 1986) and fish habitat requirements that shift through ontogeny (Rosenfeld 2003). This knowledge gap in fine-scale fish movement hinders our understanding of not only fundamental spatial ecology of stream fishes but also evaluations of local-scale conservation measures such as habitat and connectivity restoration (Roni 2019).

Here, we characterized fine-scale movement of three small-bodied stream fishes by developing an integrated population model based on mark-recapture and count data collected every two months over 28 months. Our study objectives were three-fold. First, we characterized proportions of immigrants per 20-m section by time, species, and body size class. Our second objective was to test whether variation in section-scale immigration and fidelity was explained by spatial (i.e., stream depth and substrate) and temporal (i.e., stream temperature and flow) covariates. Finally, we assessed correlation between aspects of demography, another strength of estimating an array of vital rates in IPMs (Zipkin and Saunders 2018). Specifically, we evaluated for each species whether number of immigrants depended on number of survivors at the local 20-m section scale to test for habitat saturation and thus evidence for intra-specific competitive interactions. We posited that numbers of immigrants and local survivors would be negatively correlated if habitat or other resources were limited and individuals competed for them. In addition, we examined signs of fine-scale movement triggered by ontogenetic habitat shifts by comparing proportions of immigrants and probability of body size transitions.

Materials and methods

Study area and species

This study took place in a 740-m stream segment of Indian Creek in the Clemson University Experimental Forest located in the upper Piedmont region of South Carolina, USA (34°44′32″ N, 82°51′05″ W). Indian Creek is a wadeable perennial stream (second-order stream with a mean wetted width of 2.6 m) surrounded by a well-shaded riparian zone. Stream habitat alternated between riffles and pools, and substrate was characterized by a mix of sand, gravel, pebble, and cobble. The downstream boundary of our study segment was located approximately 500 m upstream of Lake Hartwell, which isolated study populations of our lotic species.

We targeted bluehead chub *Nocomis leptocephalus*, creek chub *Semotilus atromaculatus* and mottled sculpin *Cottus bairdii* for our intensive demographic study. These three fish species predominated fish assemblages in Indian Creek, which also included yellowfin shiner *Notropis lutipinnis*, striped jumprock *Moxostoma rupiscartes*, northern hog sucker *Hypentelium nigricans*, and redbreast sunfish *Lepomis auritus*. Bluehead chub and creek chub belong to Family Leuciscidae and are more morphologically and ecologically similar to each other than to mottled sculpin (Family Cottidae) (Fig. 1). Bluehead chub and creek chub are water-column species and occur primarily in deeper and slower habitats (i.e., pools), whereas the horizontally flattened body shape of mottled sculpin allow them to exploit shallower and faster benthic habitats (i.e., riffles). Mottled sculpin require cooler temperatures (i.e., stenothermal species) than bluehead chub and creek chub (McCormick et al. 2001), and their growth is maximized at cooler temperatures (approximately 12–16 °C) than the other two species which are eurythermal (Kanno et al. 2023). Creek chub are the most tolerant of environmental degradation among the three study species (McCormick et al. 2001). Habitat requirements change via ontogeny, with larger individuals occupying deeper microhabitats with more physical cover in bluehead chub and creek chub (Magnan and FitzGerald 1984; Schlosser 1988) and coarser, more stable substrates in mottled sculpin (Petty and Grossman 2007). Mottled sculpin

defend the substrates for territory (Resetarits 1995; Petty and Grossman 2007), but the strength of intra-specific competition is not well known in bluehead chub and creek chub. In Indian Creek, mottled sculpin spawn in March and April, and bluehead chub and creek chub spawn between April and June (Kim and Kanno 2020). Survival probability of the study species decreases with warmer temperatures in the study area (Kanno et al. 2023; Pregler et al. 2023). Movement distance of bluehead chub and creek chub varies by fish body size and time of the year (Terui et al. 2021).

Field sampling

We conducted demographic surveys every two months (mean interval = 61 days; range = 48–70) between November 2015 and March 2018. We marked all individuals encountered in a 620-m main segment and recorded count of individuals in 20-m sections nested contiguously in the main segment (Fig. 1). We sampled additional 60 m upstream and downstream of the main segment (i.e., buffer zones) to quantify fish emigration from the main segment, while recognizing that low recaptures in the buffer sections alone cannot indicate low emigration out of the study segment when movement distances follow leptokurtic distributions (Skalski and Gilliam 2000). Our study segment totaled 740 m in length, and count data were available for the 31 sections in the main segment. We targeted bluehead chub and creek

Fig. 1 Schematic view of the study segment in Indian Creek, South Carolina, USA (left), and photos of the study species: bluehead chub (*Nocomis leptocephalus*), creek chub (*Semotilus atromaculatus*), and mottled sculpin (*Cottus baridii*) (right). Mark-recapture sampling was conducted in the 620- m main segment and count data were collected for each 20-m section by conducting two-pass electrofishing surveys. Additional three sections upstream and downstream of the main segment were designated as buffer zones (60 m each), where fish captured were checked for PIT tags (i.e., recaptures) but fish were not newly marked. Count data for demographic analysis were collected in the 31 sections between the buffer zones
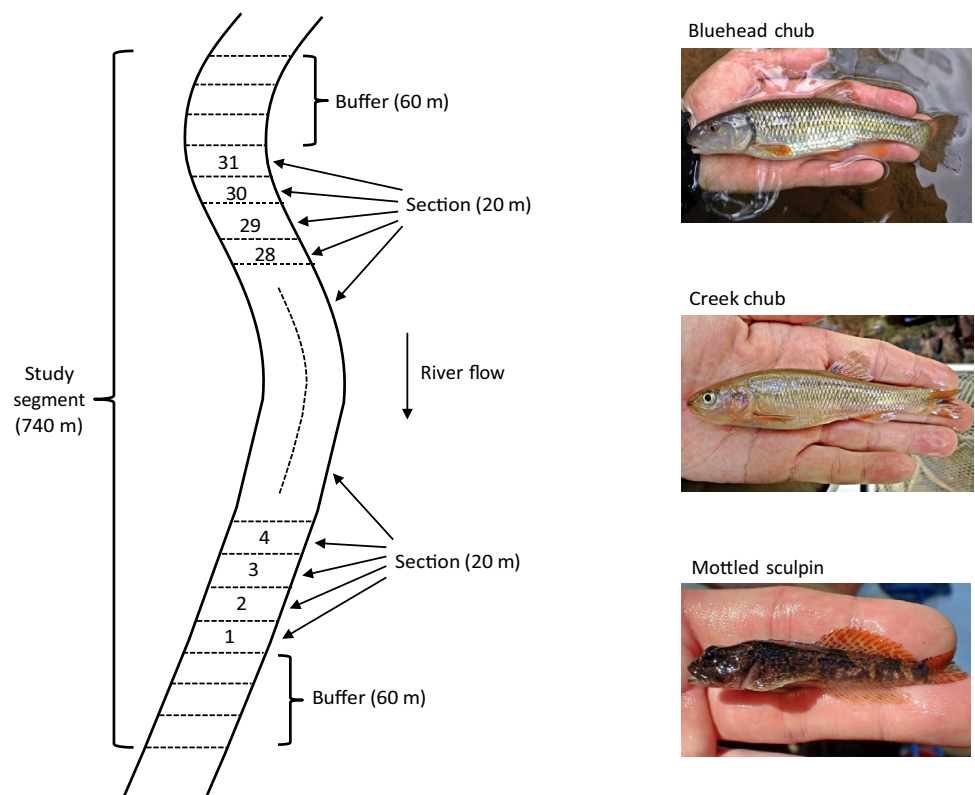
chub ≥ 60 mm in total length (TL) and mottled sculpin ≥ 50 mm in TL due to capture efficiency and feasibility of individual marking. Fish were collected by backpack electrofishing units (Smith Root Model LR-24; and Halltech Aquatic Research Inc. Model HT-2000) using a two-pass depletion approach, meaning that each 20-m section was surveyed twice consecutively while holding fish captured in the first pass outside the section. Multi-pass electrofishing methods are commonly used in stream surveys to estimate capture probability and thus abundance (Zippin 1956).

Upon capture, fish were measured for TL (mm) and weight (g) and marked with 8-mm passive integrated transponder (PIT) tags (Oregon RFID; Biomark). Across 15 sampling occasions over the 28-month study period, we uniquely tagged a total of 429 individuals of bluehead chub (mean = 92 mm; range = 60-185), 664 individuals of creek chub (mean = 93 mm; range = 60-190) and 928 individuals of mottled sculpin (mean = 64 mm; range = 50-90). Handling mortality was minimal, recorded on 13 out of 2021 total individuals (0.6%). We confirmed that tag loss was negligible in a cage experiment (Cary et al. 2017).

Water temperature was recorded hourly and water level was recorded daily using a remote logger (HOBO Onset Model U20L-004) to characterize their temporal variation (Fig. S1). Hereafter, water level is referred to as flow to distinguish it from water depth measured in 20-m sections, and we used mean temperature and maximum flow during each interval (Pearson's $r = -0.35$) as temporal covariates of demography and movement in the subsequent analysis. Maximum and mean temperature were highly correlated with each other (Pearson's $r = 0.96$), and maximum and mean flows were moderately correlated with each other ($r = 0.58$). To characterize spatial habitat heterogeneity, physical habitat data were collected in 20-m sections during base-flow conditions on October 18–27, 2017. Mean depth was based on measurements taken at three evenly-spaced points on a transect for three transects spread evenly per section. Maximum depth was recorded at the single deepest point in each section. Pool, riffle and run habitat was visually identified, and a total longitudinal length of each habitat type was measured to quantify proportion of pool habitat in each section. We measured area associated beneath undercut bank, which provided habitat for the water-column species. At each transect, substrate was classified as silt/sand (< 2 mm), gravel (2–16 mm), pebble (17–64 mm), cobble (65–256 mm), boulder (257-512 mm), and bedrock (> 513 mm) (Wolman 1954) to quantify proportion of pebble and cobble substrates (hereafter referred to as coarser substrates) in each section. Mean depth, maximum depth, pool proportion, and undercut area were highly or moderately correlated with each other (Pearson's $r > 0.40$). Thus, we used mean depth and proportion of coarser substrates (Pearson's $r = -0.30$) as spatial covariates of demography and movement

throughout our analyses, and ecological justification is provided below. The temporal and spatial covariates were standardized by mean and standard deviation prior to analysis, and their summary statistics are presented in Table S1.

Data analysis

Overview

To infer demographic processes leading to spatiotemporal changes in fish abundance across stream sections, we developed a size-structured IPM for our study species combining their section-scale count data in the N-mixture modeling framework and segment-scale capture-recapture data in the multi-scale Cormack–Jolly–Seber (CJS) model. Two size classes were designated and their threshold approximated the mean TL of each species (92 mm for bluehead chub, 93 mm for creek chub, and 64 mm for mottled sculpin). The small size group was 60-89 mm and the large size group was ≥ 90 mm for bluehead chub and creek chub, and the small size group was 50–64 mm and the large size group was ≥ 65 mm for mottled sculpin. Over the 2-month sampling intervals, section-scale abundance of the large size group changed as a function of local survival, local recruitment from the small size group via growth, and immigration (Fig. 2a). The same set of demographic processes were responsible for section-scale abundance dynamics of the small size group, but individuals gained via immigration and local recruitment to the small size group were not distinguishable because individuals smaller than the minimum size could not be effectively sampled by electrofishing for count and could not be physically marked for capture-recapture data (Fig. 2a). Therefore, we focus our reporting on immigration of the large size group, and this aligned with previous mark-recapture work on stream fish movement based on larger and older individuals (Gerking 1959; Gowan et al. 1994). Our definition of the two size classes ensured that individuals smaller than the minimum size did not recruit directly to the large size group by skipping the small size group based on the body growth rates over two months in Indian Creek (Kanno et al. 2023). Depletion-based count data and capture-recapture data provided shared information on segment-scale survival, fidelity to sections, local recruitment from the small to large size group, and capture probability, but immigration was uniquely informed by the count data (Fig. 2b).

Survival and body size transitions

Capture-recapture data were analyzed using a multi-state CJS model (Lebreton et al. 1992) to infer state-specific survival (ϕ) and state transition (ψ), while accounting for imperfect capture of individuals (p). Because states were represented by size classes, the state transition characterized
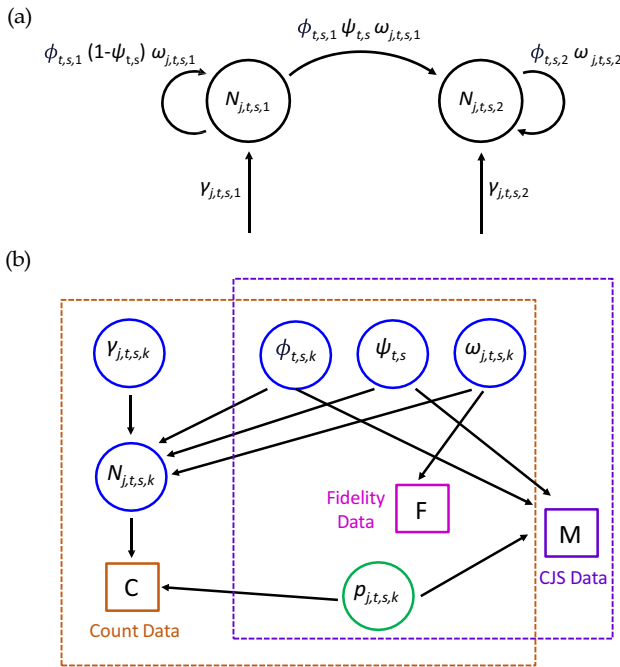
(a)

(b)

Fig. 2 Graphic representation of **a** changes in size-structured abundance in a 20-m stream section and **b** integrated population model, for analysis of demographic data in Indian Creek. Panel **a**: Abundance of small-sized individuals ($N_{j,t,s,1}$) and large-sized individuals ($N_{j,t,s,2}$) of species s in section j on occasion t changed over time due to survival in the study segment ($\phi_{t,s,k}$), transition from small to large size classes ($\psi_{t,s}$), site fidelity ($\omega_{j,t,s,k}$), and immigration ($\gamma_{j,t,s,k}$). Panel **b**: Count and Cormack-Jolly-Seber (CJS) data shared information on the demography and capture probability ($p_{j,t,s,k}$), except immigration ($\gamma_{j,t,s,k}$), which was informed solely by count data. Fidelity data were count of marked individuals captured over two consecutive occasions, based on location of recapture (i.e., inside or outside section of original release). Blue circles refer to latent parameters, a green circle is a nuisance parameter, large dotted squares are the individual models, small solid squares are the data, and arrows show the dependency of information

recruitment from the small to large classes. A two-dimensional input data matrix for the multi-state CJS model were a state history of individuals (rows) across sampling occasions (columns), with their entries being 1 (observed as small), 2 (observed as large), or 3 (not observed). The model was developed using a state-space approach, composed of ecological and observation processes (Kéry and Schaub 2012). The ecological process characterized latent state transitions (Table 1) from occasion t to t +1 from the first capture occasion of each individual until the last sampling occasion, or until the occasion of handling mortality, if known. State dynamics over time were modelled using a categorical distribution:

$$z_{i,t+1}|z_{i,t} \sim Categorical(\Omega_{z[i,t],1\ldots3,i,t}), \tag{1}$$

Table 1 State transition matrix used in the multi-state Cormack-Jolly-Seber model

		True state on occasion $t+1$		
		Small	Large	Dead
True state on occasion t	Small	$\phi_{t,s,1}(1-\psi_{t,s})$	$\phi_{t,s,1}\psi_{t,s}$	$1-\phi_{t,s,1}$
	Large	0	$\phi_{t,s,2}$	$1-\phi_{t,s,2}$
	Dead	0	0	1

Survival probability on occasion t for species s and size class k is denoted by $\phi_{t,s,k}$ and the transition probability from the small to large size classes is denoted by $\psi_{t,s}$. Survival refers to the probability that individuals survive and stay in the 740-m study segment

where $z_{i,t}$ refers to true state of individual i on occasion t and the first two dimensions of Ω are states on occasion t and t +1 (Table 1). State-specific survival and state transition were modelled as a function of temperature because survival and growth depended on temperature in Indian Creek (Kanno et al. 2023);

$$logit(\phi_{t,s[i],k}) \sim Normal\left(\alpha_{\phi,s,k} + \beta_{\phi,s,k} \times temperature_t, \sigma^2_{\phi,s}\right)$$

$$logit(\psi_{t,s[i]}) \sim Normal\left(\alpha_{\psi,s} + \beta_{\psi,s} \times temperature_t, \sigma^2_{\psi,s}\right), \tag{2}$$

where $\phi_{t,s[i],k}$ is survival probability of individual i belonging to species s and size class k on occasion t as a function of intercept ($\alpha_{\phi,s,k}$), effect of mean temperature between occasion t and t +1 ($\beta_{\phi,s,k}$), and variance ($\sigma^2_{\phi,s}$); $\psi_{t,s[i]}$ is probability of individual i belonging to species s transitioning from small to large size classes on occasion t as a function of intercept ($\alpha_{\psi,s}$), effect of mean temperature ($\beta_{\psi,s}$), and variance ($\sigma^2_{\psi,s}$). To account for sampling intervals that differed, we standardized survival and transition probabilities, as well as immigration and fidelity, at 60 days (see JAGS code).

The observation process accounted for imperfect capture of individuals, following a categorical distribution:

$$M_{i,t}|z_{i,t} \sim Categorical(\Theta_{z[i,t],1\cdots3,i,t}), \tag{3}$$

Table 2 Observation matrix used in the multi-state Cormack-Jolly-Seber model

		Observed state on occasion t		
		Small	Large	Dead
True state on occasion t	Small	$q_{t,s,1}$	0	$1-q_{t,s,1}$
	Large	0	$q_{t,s,2}$	$1-q_{t,s,2}$
	Dead	0	0	1

Two-pass electrofishing capture probability of individuals belonging to species s and size class k on occasion t is denoted by $q_{t,s,k}$

where $M_{i,t}$ is the observed state (i.e., data) of individual i on occasion t and the first two dimensions of Θ are true and observed states of individual i on occasion t (Table 2). Capture probability was assumed to differ by occasion, species, and size class, with an exception that capture probability of bluehead chub and creek chub was set to be equal based on a previous study (Kanno et al. 2023). Capture probability was informed by both capture-recapture data and count data (Fig. 2b), but they quantified capture probability differently. Let $q_{t,s,k}$ be capture probability of individuals after two-pass depletion sampling estimated for the stream segment in the multi-state CJS model for species s and size class k on occasion t. Depletion-based count data quantified capture probability of individuals "per pass" for each section; let $\hat{p}_{t,s,k}$ be per-pass capture probability of individuals for species s and size class k on occasion t, averaged across sections. Then, $q_{t,s,k}$ is equal to sum of 1st- and 2nd-pass capture probabilities:

$$q_{t,s,k} = \hat{p}_{t,s,k} + (1 - \hat{p}_{t,s,k})\hat{p}_{t,s,k} \tag{4}$$

We will complete the observation process in describing analysis of count data later.

Section fidelity

We characterized spatiotemporal variation in fish staying in the same 20-m section over 2-month sampling intervals, hereafter called fidelity. Thus, probability of section fidelity was one minus probability of emigration. Probability of section fidelity was assumed to follow a binomial distribution;

$$F_{j,t,s,k,2} \sim Binomial(F_{j,t,s,k,1}, \omega_{j,t,s,k}) \tag{5}$$

For section j, species s and size class k, we counted number of marked individuals that survived and were recaptured anywhere in the study segment from occasion t to $t+1$ ($F_{j,t,s,k,1}$) and number of individuals that survived and were captured again in section j ($F_{j,t,s,k,2}$). Fidelity probability ($\omega_{j,t,s,k}$) was modelled using mean depth and proportion of cobble and boulder substrates in section j and mean temperature and maximum flow from occasion t to $t+1$ as covariates;

$$logit(\omega_{j,t,s,k}) = \alpha_{\omega,t,s,k} + \theta_{1,\omega,t,s,k} \times depth_j + \theta_{2,\omega,t,s,k} \times substrate_j$$
$$\alpha_{\omega,t,s,k} \sim Normal(\mu_{\alpha,\omega,s,k} + \beta_{1,\omega,s,k} \times temperature_t + \beta_{2,\omega,s,k} \times flow_t, \sigma^2_{\alpha,\omega,s,k})$$
$$\theta_{1,\omega,t,s,k} \sim Normal\left(\mu_{\theta,1,\omega,s,k}, \sigma^2_{\theta,1,\omega,s,k}\right)$$
$$\theta_{2,\omega,t,s,k} \sim Normal\left(\mu_{\theta,2,\omega,s,k}, \sigma^2_{\theta,2,\omega,s,k}\right), \tag{6}$$

where the overall intercept ($\alpha_{\omega,t,s,k}$) is a function of a fidelity probability when the temperature and flow were at their mean values across sampling occasions due to mean standardization ($\mu_{\alpha,\omega,s,k}$), temperature effect ($\beta_{1,\omega,s,k}$), flow effect ($\beta_{2,\omega,s,k}$), and variance ($\sigma^2_{\alpha,\omega,s,k}$). We let the depth ($\theta_{1,\omega,t,s,k}$) and substrate ($\theta_{2,\omega,t,s,k}$) effects to vary by occasion for each species and size class, drawn from normal distributions, and we evaluated their mean, $\mu_{\theta,1,\omega,s,k}$ and $\mu_{\theta,2,\omega,s,k}$, as overall effects of depth and substrate effects. We posited that the water-column species, particularly for large individuals, would more likely stay in deeper sections and the benthic mottled sculpin would more likely stay in sections with higher proportions of cobble and boulder substrates as their primary microhabitat types (Petty and Grossman 2007). We further tested whether individuals are less likely to stay in the same sections when temperature and flow increased (Albanese et al. 2004; Petty and Grossman 2004). Body growth and size transitions of aquatic ectotherms increase with temperature up to some thresholds (Railsback and Rose 1999; Kanno et al. 2023), and flow conditions affect food availability and habitat quality for stream-dwelling fishes (Rosenfeld 2003; Dewson et al. 2007). Flows of high magnitude have been associated with increased stream fish movement (Taylor and Cooke 2012).

Population process and count observation

Temporal changes in section-scale abundance were characterized in the dynamic N-mixture modeling framework (Dail and Madsen 2011; Zipkin et al. 2014). Number of individuals in section j on the first sampling occasion, $N_{j,1,s,k}$, was assumed to follow $N_{j,1,s,k} \sim Poisson(\lambda_{s,k})$, where $\lambda_{s,k}$ was the mean abundance of species s and size class k across sections. For subsequent occasions, abundance in section j on occasion t belonging to species s and size class k, $N_{j,t,s,k}$, was determined by local demography and immigration from occasion t-1 (Fig. 2a);

$$N_{j,t,s,1} = S_{j,t-1,s,1} + G_{j,t-1,s,1}$$
$$N_{j,t,s,2} = S_{j,t-1,s,2} + R_{j,t-1,s} + G_{j,t-1,s,2}. \tag{7}$$

Here, $S_{j,t-1,s,1}$ denotes number of individuals of species s belonging to the small size class on occasion t-1 that survived, stayed in section j and did not transition to the large size class on occasion t, $R_{j,t-1,s}$ is number of individuals that survived, stayed in section j and transitioned to the large size class, and $S_{j,t-1,s,2}$ is number of

large-sized individuals that survived and stayed in section j; $G_{j,t-1,s,k}$ refers to number of immigrants to section j for species s and size class k on occasion t-1 (Fig.2a). Once again, $G_{j,t-1,s,1}$ included immigrants and local recruits of individuals that had not been tagged previously, and they were not distinguishable. Local demography was characterized by capture-recapture data, such that;

$$
\begin{aligned}
&S_{j,t,s,1} \sim Binomial\big(N_{j,t-1,s,1}, \phi_{t-1,s,1} \times (1 - \psi_{t-1,s}) \times \omega_{j,t-1,s,1}\big) \\
&R_{j,t,s} \sim Binomial(N_{j,t-1,s,1}, \phi_{t-1,s,1} \times \psi_{t-1,s} \times \omega_{j,t-1,s,1}) \\
&S_{j,t,s,2} \sim Binomial(N_{j,t-1,s,2}, \phi_{t-1,s,2} \times \omega_{j,t-1,s,2}).
\end{aligned}
\tag{8}
$$

As described earlier, segment-scale survival (ϕ) and section-scale fidelity (ω) were independently estimated, and interpretation of the fidelity term was the probability of individuals staying in the 20-m sections, given that they have survived. Because survival varied over time (see Results), we considered that accounting for survival was important to infer the site fidelity accurately.

Number of immigrants, $G_{j,t,s,k}$, was modelled as a Poisson process using mean temperature and maximum flow as temporal covariates and mean depth and proportion of cobble and boulder substrates as spatial covariates;

$$
\begin{aligned}
&G_{j,t,s,k} \sim Poisson(\gamma_{j,t,s,k}) \\
&log(\gamma_{j,t,s,k}) = \alpha_{\gamma,t,s,k} + \theta_{1,\gamma,t,s,k} \times depth_j + \theta_{2,\gamma,t,s,k} \times substrate_j \\
&\alpha_{\gamma,t,s,k} \sim Normal(\mu_{\alpha,\gamma,s,k} + \beta_{1,\gamma,s,k} \times temperature_t + \beta_{2,\gamma,s,k} \times flow_t, \sigma^2_{2,\gamma,s,k}) \\
&\theta_{1,\gamma,t,s,k} \sim Normal(\mu_{\theta,1,\gamma,s,k}, \sigma^2_{\theta,1,\gamma,s,k}) \\
&\theta_{2,\gamma,t,s,k} \sim Normal(\mu_{\theta,2,\gamma,s,k}, \sigma^2_{\theta,2,\gamma,s,k}).
\end{aligned}
\tag{9}
$$

This structure for modelling immigration followed that for fidelity (Equation 6). That is, $\gamma_{j,t,s,k}$ was the expected number of immigrants for section j, occasion t, species s and size class k, and $\alpha_{\gamma,t,s,k}$ was the intercept on the log scale. We similarly used $\mu_{\theta,1,\gamma,s,k}$ and $\mu_{\theta,2,\gamma,s,k}$ to evaluate overall effects of depth and substrate effects on immigration across sampling occasions. In addition, we predicted that immigration would increase with temperature ($\beta_{1,\gamma,s,k}$) and flow ($\beta_{2,\gamma,s,k}$) and the effects of mean depth ($\theta_{1,\gamma,t,s,k}$) and proportion of coarser substrates ($\theta_{2,\gamma,t,s,k}$) would depend on species, with more immigrants moving into deeper sections for the water-column species and sections with more coarser substrates for the benthic mottled sculpin.

Due to imperfect capture of individuals, observed section-scale count is less than or equal to true abundance;

$$
\begin{aligned}
&C_{j,t,s,k,1} \sim Binomial(N_{j,t,s,k}, p_{j,t,s,k}) \\
&C_{j,t,s,k,2} \sim Binomial(N_{j,t,s,k} - C_{j,t,s,k,1}, p_{j,t,s,k})
\end{aligned}
\tag{10}
$$

where $C_{j,t,s,k,1}$ is observed count of individuals in the first pass of electrofishing and $C_{j,t,s,k,2}$ is that from the second pass of electrofishing for section j, occasion t, species s, and size class k. Because this was a depletion method, individuals captured in the first pass were not available for capture in the second pass. This model characterized per-pass capture probability of individuals, $p_{j,t,s,k}$, which was modeled as a function of mean depth and proportion of pebble and cobble substrates in section j.

$$
\begin{aligned}
&logit(p_{j,t,s,k}) = \mu_{p,t,s,k} + \theta_{1,p,s,k} \times depth_j + \theta_{2,p,s,k} \\
&\times substrate_j \mu_{p,t,s,k} \sim Normal(\mu_{p,s,k}, \sigma^2_{p,s,k}),
\end{aligned}
\tag{11}
$$

where $\theta_{1,p,s,k}$ is the effect of mean depth, $\theta_{2,p,s,k}$ is the effect of coarser substrates, and the random effect, $\mu_{p,t,s,k}$, accounted for temporal variation in capture probability, with a mean of $\mu_{p,s,k}$ and variance of $\sigma^2_{p,s,k}$ for species s and size class k.

Earlier, we stated that mark-recapture and count data quantified capture probabilities differently but they were linked (Equation 4). In addition, capture probabilities were estimated at the 20-m section scale for the count data and at the 740-m study segment for the mark-recapture data. The random effect term, $\mu_{p,t,s,k}$, characterized the mean capture probability of individuals across stream sections on occasion t, so that;

$$
\hat{p}_{t,s,k} = logit^{-1}(\mu_{p,t,s,k}).
\tag{12}
$$

Model fitting

We fit the integrated population model using a Markov Chain Monte Carlo (MCMC) method using Program JAGS (Plummer 2007) through Program R (R Core Team 2023), and JAGS code is available in Appendix. Diffuse priors were used for all parameters in the Bayesian approach. Posterior

distributions of model parameters were characterized from 100,000 iterations of four chains after a burn-in period of 20,000 iterations with a thinning rate of 10. Model convergence was checked by visually assessing the MCMC chains for good mixture as well as confirming R-hat statistic < 1.1 for all parameters (Gelman and Rubin 1992). Covariate effects on demographic rates were considered statistically significant when their 95% credible intervals (CI) did not overlap 0, and we also used 50% CI for effect visualization and evidence of weak effects.

Derived quantities and post-hoc analysis

We estimated the proportion of immigrants for section j, occasion t, and species s as $G_{j,t,s,2}/N_{j,t,s,2}$ (Equation 7), again focusing this analysis on the large size class ($k = 2$), and reported posterior distributions of immigrant proportions averaged across sections to characterize temporal variation in immigration. To evaluate whether number of immigrants depended on number of survivors at the 20-m section, we ran simple linear regression using their posterior mean values for each unique combination of occasion and species (14 occasions and 3 species for a total of 42 tests). We used a sum of $S_{j,t-1,s,2}$ (large individuals that survived) and $R_{j,t-1,s}$ (small individuals that survived and transitioned to the large size class) (Equation 7) to represent survivors, and $G_{j,t-1,s,2}$ as number of immigrants. Finally, to test whether immigration was triggered by ontogenetic habitat shift due to body size transitions, we regressed posterior mean proportion of immigrants on each sampling occasion against posterior mean probability of size transition (ψ) for each species. We used $\alpha = 0.05$ for these post-hoc analyses.

Results

During the 28-month study period, we captured and uniquely marked 429 individuals of bluehead chub, 664 individuals of creek chub, and 928 individuals of mottled sculpin. Of those, we recaptured at least once 254 individuals (59%) in bluehead chub, 365 individuals (55%) in creek chub, and 444 individuals in mottled sculpin (48%). Individuals were recaptured up to 10 times in bluehead chub, 9 times in creek chub, and 8 times in mottled sculpin out of 14 possible recapture occasions. Ninety-three of 2,376 total recapture events (3.9%) were recorded in the buffer zones (uppermost and lowermost 60m each in the 740-m study segment) (Fig. 1). Observed count of individuals per 20-m section, when body size classes and electrofishing passes were combined, averaged 2 individuals (range: 0–10) in bluehead chub, 2 individuals (range: 0–23) in creek chub, and 3 individuals (0–18) in mottled sculpin across sampling occasions and sections. Based on count data that included

recaptures of the same individuals, 526 fish belonged to the small size class and 436 fish to the large size class in bluehead chub, 716 small fish and 655 large fish in creek chub, and 892 small fish and 843 large fish in mottled sculpin.

Proportions of immigrants to 20-m sections varied by species and time (Fig. 3). When posterior mean values were averaged across sampling occasions, 42% of individuals were immigrants in bluehead chub (range: 24–54%) and creek chub (range: 25–59%). Immigration of creek chub followed a seasonal cycle, with their highest proportions between March and September and the lowest between November and March. Proportions of immigrants were the lowest in mottled sculpin, with a mean of 30% across occasions (range: 20–41%), and the proportions were most consistent over time. These proportions of immigrants showed that local turnover rates were high, with immigrants accounting for a majority of individuals on some occasions in bluehead chub and creek chub. In addition, the probability of site fidelity depended on body size class. When averaged across sections and occasions ($\mu_{\alpha,\omega,s,k}$ in Equation 6), small individuals (mean = 0.67; 95% CI = 0.58, 0.76) were more likely to stay in the same section than large individuals (mean = 0.42; 95% CI = 0.22, 0.62) in bluehead chub, but large individuals (mean = 0.72; 95% CI = 0.62, 0.80) were more likely to stay than small individuals (mean = 0.49; 95% CI = 0.33, 0.62) in mottled sculpin. Probability of site fidelity was most similar between the size classes in creek chub, with a mean of 0.42 (95% CI = 0.30, 0.53) for small individuals and a mean of 0.52 (95% CI = 0.42, 0.62) for large individuals.

As predicted, stream temperature explained temporal variation in movement and demography (Fig. 4, Table S2).
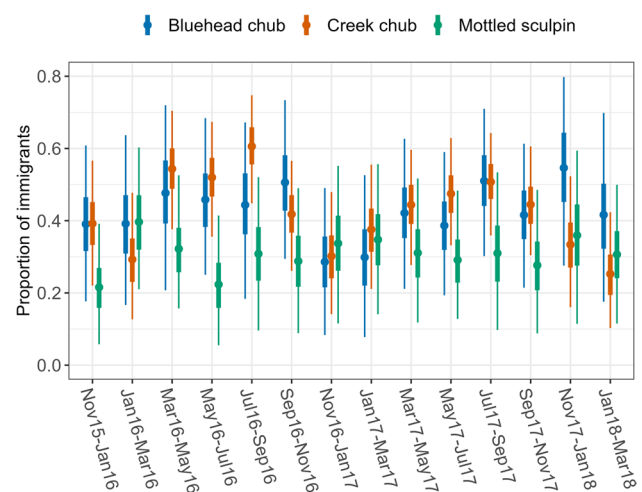

Fig. 3 Posterior distributions of proportion of immigrants averaged across 20-m sections in sampling period for each species. Posterior mean values are shown by points with 50% (thick lines) and 95% (thin lines) credible intervals
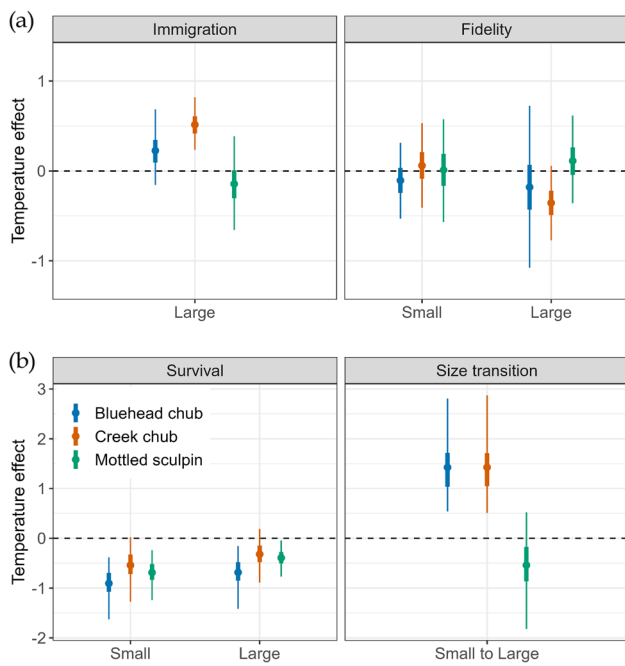
Fig. 5 Posterior distributions of flow effects on immigration and fidelity of small and large size classes of each species. Values are regression coefficient estimated in the integrated population model, shown on the log scale for immigration and on the logit scale for fidelity. Posterior mean values are shown by points with 50% (thick lines) and 95% (thin lines) credible intervals

Fig. 4 Posterior distributions of temperature effects on **a** section-scale immigration and fidelity and **b** segment-scale survival and transition from small to large body size classes. Values are regression coefficient estimated in the integrated population model, shown on the log scale for immigration and on the logit scale for site fidelity, survival, and size transition. Posterior mean values are shown by points with 50% (thick lines) and 95% (thin lines) credible intervals

Number of immigrants increased significantly on warmer occasions in creek chub ($\beta_{1,\gamma}$: 95% CI = 0.23, 0.82), but number of immigrants did not depend on temperature in bluehead chub ($\beta_{1,\gamma}$: 95% CI = −0.16, 0.69) or mottled sculpin ($\beta_{1,\gamma}$: 95% CI = −0.66, 0.39) (Fig. 4a). Probability of section fidelity did not depend on temperature in any species, with 95% CI of $\beta_{1,\omega}$ overlapping 0 (Fig. 4a). Probability of survival was lower when temperature increased in bluehead chub (β_{ϕ}: 95% CI = −1.63, −0.38 in small size class; −1.42, −0.16 in large size class) and mottled sculpin (β_{ϕ}: 95% CI = −1.24, −0.24 in small size class; −0.77, −0.05 in large size class) (Fig. 4b). In addition, higher temperature nearly significantly decreased survival of small creek chub (β_{ϕ}: 95% CI = −1.28, 0.02). The probability of transitioning from small to large size classes increased with temperature in the two eurythermal species (β_{ψ}: 95% CI = 0.54, 2.81 in bluehead chub; 0.51, 2.87 in creek chub), but not in the stenothermal mottled sculpin (β_{ψ}: 95% CI = −1.82, 0.52) (Fig. 4b). Temporal variability in flow had weak but consistent effects on immigration and fidelity across species and size classes (Fig. 5, Table S2). Flow had a nearly significant positive effect on number of immigrants in creek chub ($\beta_{2,\gamma}$: 95% CI = −0.05, 0.44), and 50% CI was positive in all species, lending a weak support for our prediction. Small creek chub were less likely to stay in the same sections when flow
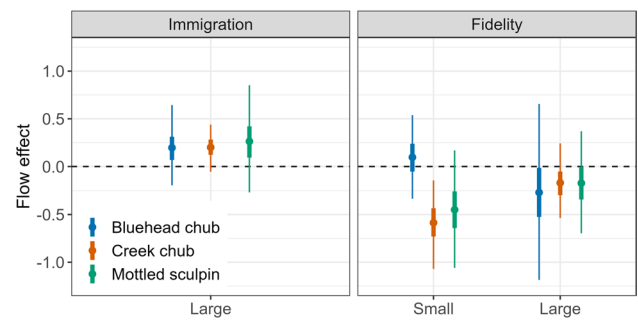
increased, and 50% CI of flow effect on site fidelity was negative in all cases except small bluehead chub (Fig. 5). We report in Appendix temporal patterns of survival (Fig. S2) and body size transition (Fig. S3) probabilities.

Immigration and fidelity at the section scale also varied spatially and some of its variation was explained by stream depth and substrate size, as predicted (Fig. 6, Table S3). When averaged across occasions, creek chub immigrants increased in deeper sections ($\mu_{\theta,1,\gamma}$: 95% CI = 0.03, 0.45) and those with higher proportions of coarser substrates (i.e., cobble and boulder) ($\mu_{\theta,2,\gamma}$: 95% CI = 0.45, 0.98). Individual bluehead chub were more likely to stay in the same sections when they were deeper ($\mu_{\theta,1,\omega}$: 95% CI = 0.09, 1.45 in small size class; 0.10, 1.03 in large size class), and small creek chub individuals were were less likely to stay in sections with predominantly coarser substrates ($\mu_{\theta,2,\omega}$: 95% CI = −1.48, −0.20). Contrary to our prediction, immigration and fidelity of mottled sculpin did not depend on substrates, although 50% CI of substrate effects on fidelity were positive in small and large size classes. In addition, capture probability of individuals also depended on stream depth and substrate size in a complex manner. Creek chub were more readily captured in deeper sections ($\theta_{1,p}$: 95% CI = 0.32, 1.01 in small size class; 0.56, 1.02 in large size class), but mottled sculpin were more readily captured in shallower sections ($\theta_{1,p}$: 95% CI = −0.94, −0.38 in small size class; −0.68, −0.13 in large size class). In bluehead chub, large individuals were more readily captured in deeper sections ($\theta_{1,p}$: 95% CI = 0.29, 1.10), but small individuals were more readily captured in shallower sections ($\theta_{1,p}$: 95% CI = −0.77, −0.06). Finally, substrate size had opposite effects on capture probability of creek chub versus mottled sculpin (Fig. 6, Table S3). Specifically, creek chub were harder to catch in sections predominated by coarser substrates ($\theta_{2,p}$: 95% CI = −0.75, −0.12 in small size class; −1.19, −0.66 in large size class), but mottled sculpin were easier to catch in those

Fig. 6 Posterior distributions of **a** stream depth and **b** cobble and boulder substrate effects on immigration, fidelity, and capture probabilities of small and large size classes of each species. Values are regression coefficient on the logit scale estimated in the integrated population model. Posterior mean values are shown by points with 50% (thick lines) and 95% (thin lines) credible intervals
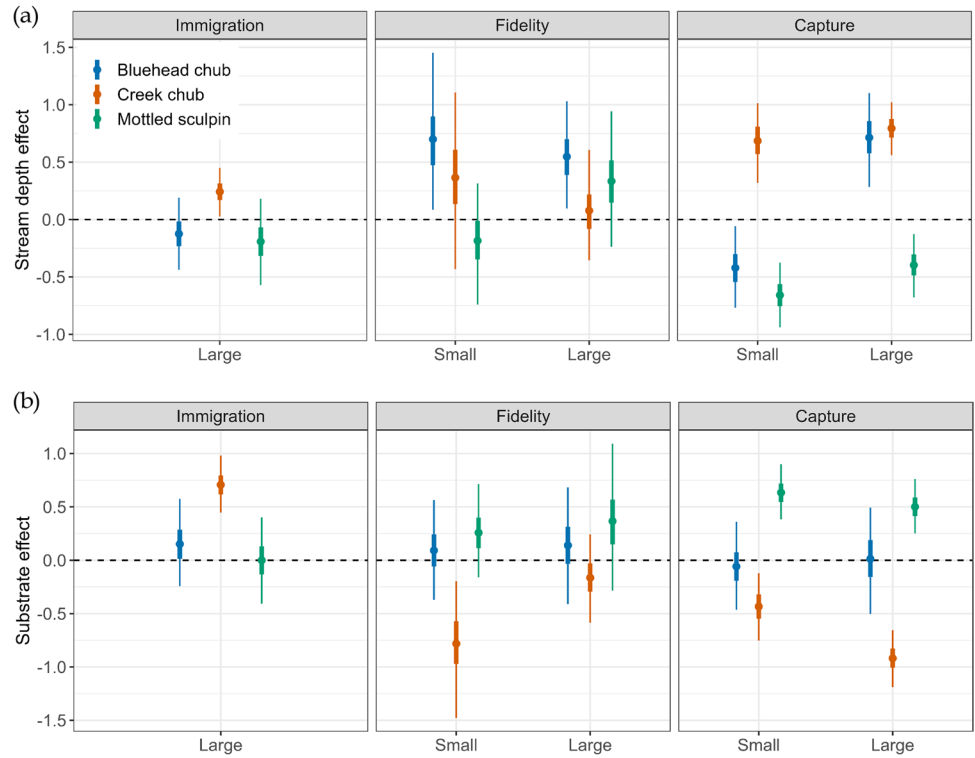
sections ($\theta_{2,p}$: 95% CI = 0.38, 0.90 in small size class; 0.25, 0.76 in large size class).

There was no negative correlation between number of survivors and immigrants at the section scale, indicating no evidence of habitat saturation and intra-specific competition for limited resources (Fig. 7). Among unique combinations of sampling intervals and species ($n = 42$), there were significantly positive relationships between

number of survivors and immigrants in 30 of them and there were no significant relationships in the remaining 12. Notably, there was no significantly negative relationship on any sampling occasion in any species. Finally, there was a positive relationship between proportion of immigrants and probability of transitioning from small to large size classes in creek chub ($P = 0.002$), suggesting that immigration was triggered by ontogenetic habitat shifts in
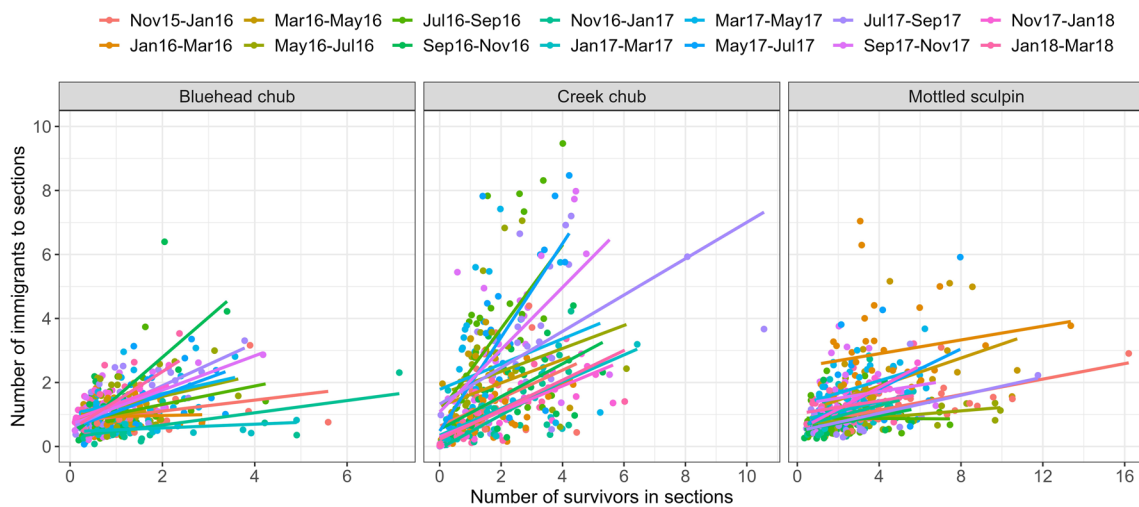

Fig. 7 Relationships between posterior mean number of survivors and immigrants belonging to the large size class of each species among 20-m sections in each 2-month sampling interval. Number of survi-

vors was a sum of large-sized individuals that survived ($S_{j,t,s,2}$) and small-sized individuals that survived and transitioned to the large size class ($R_{j,t,s}$) in section j for occasion t and species s
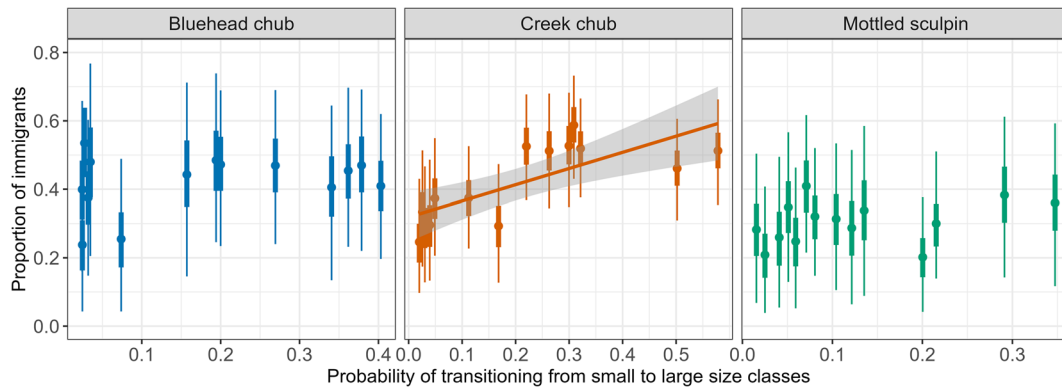
Fig. 8 Relationship between proportion of immigrants belonging to the large size class and probability of transitioning from small to large size groups during 2-month sampling intervals. The transition probability refers to the posterior mean value on sampling occasion t for species s ($\psi_{t,s}$). Proportion of immigrants shows posterior dis- tributions averaged across 20-m sections in sampling period for each species. Posterior mean values are shown by points with 50% (thick lines) and 95% (thin lines) credible intervals. Statistically significant relationships are shown by regression lines with 95% confidence intervals

this species (Fig. 8). Such patterns were not observed in bluehead chub ($P = 0.32$) or mottled sculpin ($P = 0.24$). We report in Appendix temporal patterns of capture probabilities (Fig. S4).

Discussion

Our integrated analysis of marked and count data showed high local turnover rates, with immigrants accounting for an average of 30-42% of individuals among the three small-bodied stream fishes at the 20-m section scale over 2-month intervals. Proportions of immigrants differed among the study species, and mottled sculpin had the lowest immigration rates. This result was not surprising given their smallest body size, benthic habitat requirement, and lack of air bladder, which suggest that mottled sculpin were the most movement-limited among the three species (Petty and Grossman 2004). Despite the high immigration rates to local sections, our previous work showed that movement distances were limited for most individuals and their distributions were leptokurtic in Indian Creek (Terui et al. 2021). These data combine to show high local turnover rates but mostly short movement distances, similar to patterns reported in stream salmonids (Rodríguez 2002). In other words, it was common for individuals to leave their local habitat (e.g., 20 m scale) and the habitat vacated was most typically colonized by individuals who moved from nearby locations with some long-distance movements, possibly including those originating from outside of our 740-m study segment. Literature on stream fish movement has been predominated by stream salmonids, but our work suggests that other stream fishes share key properties of movement, which contributes to

synthetic understanding of stream fish movement (Radinger and Wolter 2014).

The integrated population model was required for estimating immigration in this study. In our exploratory analysis, we fit a dynamic N-mixture model (Dail and Madsen 2011) to the depletion-based count data, but we found that section-scale immigration and fidelity were not identifiable based on count data alone. Spatially and temporally replicated count data can reveal these demographic rates in some cases (Kanno et al. 2014; Zipkin et al. 2014), but it becomes harder when population heterogeneity increases in a model (e.g., size structure). One caveat of our study design was to use the same individuals both in the mark-recapture and count data, which violated an assumption of independence among data sets (Zipkin and Saunders 2018). However, complete independence among the data sets and thus likelihoods rarely occurs in studies of animal populations, and a simulation study showed that violating the independence assumption had negligible impacts on parameter estimates in their IPMs (Abadi et al. 2010b). In fact, we think that using mark-capture and count data from the same stream was important in this study for two reasons. First, Pregler et al. (2023) found that the temporal dynamics of survival in Indian Creek were not synchronous with those of the same species in a nearby creek of the same stream size, located just 3 km away. Combining data sets from different locations in such a situation would be appropriate only if the study goal were to generate a regional-scale inference on demography. Second, we collected count data at the local section scale (20 m) and mark-recapture data at the segment scale (740 m). This approach resulted in spatial pseudo-independence, providing an opportunity to compare demographic rates quantified at different spatial scales (i.e., immigration at the section scale and body size transition at the segment scale).

Our prediction that immigration and emigration (one minus fidelity) increase with temperature and flow was partially supported. Although temperature had no significant effects in many cases and a significant positive effect was observed only on immigration of creek chub, we also did not find any instance where immigration or emigration decreased significantly due to warmer temperatures, as expected for ectotherms in the temperate region. For creek chub, we interpret that temperature may have influenced their immigration indirectly via body growth. Specifically, creek chub were more likely to transition from small to large size classes during warmer intervals, and increased body size should have prompted fine-scale movement to accommodate shifting habitat requirements through ontogeny (Magnan and FitzGerald 1984). Although the effects were not significant at the 95% level, there was a tendency that increased flow triggered more fine-scale movement in this study, a pattern reported for bluehead chub (Albanese et al. 2004) and another sculpin species (Wells et al. 2017) elsewhere. The study period coincided with a dry condition experienced by this region (Williams et al. 2017). Several punctuated precipitation events and associated flow increases were recorded, but overall the flow was relatively stable over the study period in this well-forested, small creek. Stronger flow effects on fine-scale fish movement could be more readily detected in streams characterized with higher temporal flow variability and magnitude, whether caused naturally (e.g., rain or snow) or by humans (e.g., dams).

Immigration and fidelity differed spatially and this pattern varied by species. We predicted that more immigrants would move into deeper sections, and more would stay there, which was partially supported by three significant positive effects (immigration in creek chub, and fidelity of both sizes of bluehead chub). Recall that depth was correlated with pool proportions and undercut bank area, thus it remains unclear whether fine-scale movement was influenced by depth per se or other habitat characteristics associated with depth (e.g., physical cover and water velocity). Additional investigations are warranted to understand how fish movement is influenced by certain aspects of stream habitat and such knowledge is critical to implementing and evaluating stream habitat restoration projects such as wood addition, channel reconfiguration, and riparian reforestation (Roni 2019). In contrast, our prediction that coarser substrates would increase immigration and fidelity of the benthic mottled sculpin was not supported. But immigration of creek chub increased in sections with more coarser substrates and small creek chub were less likely to stay in those sections. Given that immigration was based on large individuals, this result suggests that substrate preferences of creek chub changed via ontogeny. Although stream depth and substrate effects on fine-scale movement were admittedly complex, such heterogeneous responses among species and size classes in

combination with their different habitat preferences might facilitate coexistence of these species in this riverscape and elsewhere (Schlägel et al. 2020).

We did not find evidence for intra-specific competition for limited habitat resources. If such a carrying capacity effect had existed, we would have detected negative relationships between numbers of survivors and immigrants to sections. Instead, we found positive relationships in a majority of species and sampling interval combinations, showing that the sections in which more individuals survived and stayed also received more immigrants. We attribute our results to two reasons. First, fish density was relatively low in Indian Creek. Densities of bluehead chub and creek chub combined were more than three times higher in a nearby creek (Pregler et al. 2023), and the estimated density of mottled sculpin after accounting for capture probability (an average of 14 individuals per 20m section) was comparable to or lower than those reported elsewhere (McCleave 1964; Petty and Grossman 2004). Second, agonistic behavior or intra-specific competition has been mostly limited in our study species (Petty and Grossman 2007; Colby et al. 2022). Using fine-scale movement data to infer intra-specific competition for limited habitat resources could prove more useful for territorial animals occurring at high densities. In Indian Creek, we conclude that section-scale distributions of the study species were structured primarily by habitat sorting and fine-scale movement, instead of intra-specific biotic interactions (Brown et al. 2011).

Movement decisions by stream fish have fitness consequences; they need to decide whether to leave or stay in their local habitat, and where to settle once they have left their habitat (i.e., departure and destination rules) (Railsback et al. 1999). The positive correlation between numbers of apparent survivors (an index of departure) and immigrants (an index of destination) at the 20-m section scale across sampling occasions and species suggests that fish cue in on the same criteria to make these different decisions, although the spatial covariates (i.e., mean depth and coarser substrates) did not consistently influence fidelity and immigration in our study. More research is warranted to evaluate how stream fish make decisions at different phases of movement behavior. Such investigations can be pursued by examining departure and destination habitats of the same individuals, which we did not address in our IPM because count data were used at the section scale. In addition, fish location and stream habitat may need to be characterized at a finer spatial resolution than 20-m intervals or by meso-habitat type (e.g., riffles, pools). Our 20-m sections typically contained more than a single meso-habitat type, but standardizing sampling areas by a fixed section length assisted analysis of count data. Finally, we measured spatial habitat variability once during the study period, but more frequent sampling might help elucidate factors affecting movement decisions of individuals in

streams subjected to temporally shifting habitat conditions due to factors such as disturbances (e.g., floods that reconfigure stream habitat) and less stable substrates.

Section-scale stream habitat characteristics affected capture probability of individuals differently by species, and also by body size class in one species (bluehead chub). A water-column species (creek chub) was more readily captured in stream sections that were deeper or characterized with fewer cobbles and boulders, and the benthic mottled sculpin showed the opposite patterns. Sections of high capture probabilities coincided with their preferred habitat characteristics observed in this study and others (McCormick et al. 2001; Bramblett et al. 2005). The body-size-dependent effects of stream depth on capture probability was unique to bluehead chub, and it was interesting that depth affected capture of large individuals of bluehead chub and creek chub similarly, but small individuals of these species differently. Based on our field observations, small individuals of the two species were more spatially segregated in their distributions within and among stream sections, but their distributions were less predictable than those of large individuals of both species which were most commonly found in pools with physical cover. Our data suggest that habitat overlap between the two species could depend on their body size; this ecological insight was a byproduct of our IPMs and capture probability is typically considered a nuisance parameter in state-space ecological models (Kéry and Schaub 2012). Most importantly, we think that accounting for spatial variation in capture probability resulted in accurate inferences of movement and demography, the parameters of interest which motivated the development of our integrated population model.

In conclusion, this study demonstrated high immigration rates into local stream sections, although immigration was heterogeneous due to abiotic factors over space and time, species, and body size. We did not find evidence for habitat saturation and density-dependent immigration in any species, and immigration triggered by ontogenetic habitat shift was found only in one species. Applications of IPMs to freshwater species have been limited, but opportunities exist for innovative development to quantify immigration and other vital rates. These extensions may include, but are not limited to, spatial mark-recapture data, multi-species analysis for community interactions, other data types such as snorkeling count and angler catch data, and integrated integral project models for demographic mechanisms (Plard et al. 2019). They would advance our knowledge on meta-population and meta-community dynamics, density-dependent processes, and species coexistence in the riverscape. Approaches developed for freshwater species would, in turn, be applicable to terrestrial species for which multiple data types are available.

Data and code availability The data are available from the corresponding author on reasonable request. Code can be found in the online appendix.

Declarations

Conflict of interest There is no conflict of interest to declare.

Ethical approval The fieldwork was conducted in accordance with protocols approved by the Clemson University Institutional Animal Care and Use Committee (IACUC Protocol Number 2014-047 and 2017-039).

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