



# Ontogenetic habitat shifts and vulnerability: lake-outlet-spawning sockeye salmon (*Oncorhynchus nerka*) sensitivity to habitat connectivity and hydrologic change

Elissa K. Sweeney-Bergen · Donna Macintyre · Jonathan W. Moore

Received: 1 March 2020 / Accepted: 14 February 2021  
© The Author(s), under exclusive licence to Springer Nature B.V. 2021

**Abstract** Sockeye salmon that spawn downstream of rearing lakes are an important example of the challenges faced by organisms with complex life histories requiring connectivity in aquatic habitat complexes. Specifically, newly emerged juvenile sockeye salmon must migrate upstream, against the flow of water, if they are to reach lake rearing habitat. Here, we examine the spatial and temporal dynamics of the water velocity landscape and juvenile sockeye salmon movement and condition at increasing distances downstream from the lake outlet of an important sockeye salmon system, the Babine Lake of British Columbia, one of Canada's largest and most important sockeye salmon rearing lakes. The results of this study indicate that (i) there were seasonal and spatial patterns of water velocities that exceed the ability of juveniles to swim upstream to lake rearing habitat, (ii) higher water discharge was associated with more velocity barriers and potentially with less upstream movement of juveniles, and (iii) juveniles rearing in the lake obtained larger sizes (30% longer and 150% heavier) than those in downstream river habitats. Multiple processes that may be influencing these patterns could include more abundant food resources, lower metabolic

demands, or size-selective immigration, emigration, or mortality among habitats. Years and seasons with high discharge may temporarily create one-way, downstream transport routes at lake outlets. Long-term changes in hydrology, perhaps driven by climate variability or land-use change, may control the degree to which lake outlets function as bidirectional travel corridors or one-way travel routes for young sockeye salmon.

**Keywords** Salmon · Life history · Habitat · Migration · Ontogeny

## Introduction

The spatial arrangement of habitats and their connectivity is of critical importance to species with complex life cycles (Dunning et al. 1992; Schlosser 1995; Wiens 2002). Many aquatic species use different habitat types throughout their life history, ranging from freshwater ontogenetic shifts of suckers (e.g., *Deltistes luxatus*, *Chasmistes brevirostris*) and trout (e.g., *Oncorhynchus mykiss*, *Salvelinus namaycush*) to large-scale migrations of anadromous Pacific salmon (*O. spp.*). For aquatic organisms in freshwater ecosystems, habitat connectivity is constrained by the presence of water (Hermoso et al. 2012) and is determined by both habitat patch quality (e.g., cover, prey) and the properties of habitat connections (e.g., distance, flow characteristics; Wiens 2002). Thus, the spatial arrangement of aquatic habitats, such as the dendritic structure of river networks, can determine the productivity of freshwater habitat

---

E. K. Sweeney-Bergen · J. W. Moore  
Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia, Canada

E. K. Sweeney-Bergen (✉) · D. Macintyre  
Fisheries Department, Lake Babine Nation, Burns Lake, British Columbia, Canada  
e-mail: elissas@sfu.ca

complexes (Wiens 2002; Fausch et al. 2002; Fagan 2002). Further, connectivity may be asymmetric; aquatic habitat connectivity can be influenced by habitat features such as waterfalls or high velocity reaches that can block upstream movement for some species or life-stages. However, barriers between habitats are not always fixed. Hydrologic variation can transform bidirectional movement corridors to one-way travel routes; for example, in high flows, organisms may be able to travel downstream, but not upstream. Thus, the spatial arrangement of aquatic habitats and potential dynamic barriers may challenge species with complex life-histories.

Sockeye salmon (*O. nerka*) that spawn downstream of rearing lakes are an important example of the challenges faced by organisms with complex life-histories requiring connectivity in aquatic habitat complexes. There is often productive spawning habitat in river sections immediately downstream of lakes, which we refer to as the lake outlet reach, due to moderated water flow and temperature (McCart 1967). Yet, sockeye salmon generally rear in lakes as juveniles for 1 to 2 years. Thus, unless there is a downstream lake, juveniles that emerge downstream of lake outlets have the challenge of swimming upstream to reach lake rearing habitats. In many outlet spawning populations, some proportion of the brood cohort is carried downstream upon emergence, where habitat conditions can be drastically different than those in upstream rearing lakes and potentially unsuitable (Hartman et al. 1962; Brannon 1967; Raleigh 1971; Clarke and Smith 1972). In some cases, outlet juveniles that move downstream, rear in off-channel habitat or estuaries for 6 to 24 months before migrating further downstream to the ocean (Gilbert 1913; Semko 1954). Yet, the vast majority of sockeye salmon rear in lakes as juveniles. Upon emergence, outlet juveniles have been observed to navigate to their upstream lake by first orienting themselves towards the nearest river bank and swimming at an angle to the main current, then schooling into large groups once they reach the river's edge, and finally moving upstream to their rearing lake using the river margins (Andrew and Geen 1960; Clarke 1967; McCart 1967; Clarke and Smith 1972). A time lag has been observed prior to the initiation of upstream migration (Clarke 1967; McCart 1967) likely due to poor initial swimming ability and challenging water velocities (Killick 1949; Hoar 1958; Byrne 1971). While sockeye salmon migrate thousands of kilometers over their migratory life-cycle, lake outlets

represent specific habitats where configuration and conditions (e.g., water velocities) could determine the fate of individuals and the productivity of populations. Thus, while there is general appreciation for the potential importance of the early life history of lake-outlet-rearing sockeye salmon, there is a need for studies of large spatial scales that examine the potential area that juveniles may inhabit temporarily while trying to reach upstream rearing lakes.

The early life-history stages of salmon can have both direct and indirect influences on population dynamics. Juvenile salmon have high mortality while transitioning from endogenous to exogenous energy acquisition, when juveniles begin to obtain their own food in the first few weeks after emergence (Elliot 1989; Armstrong 1997; Einum and Fleming 2000). This high mortality could be due to low prey accessibility, subsequent intense intraspecific competition for food, high predation, or downstream losses (McCart 1967). Survival depends heavily on whether environmental conditions meet juvenile requirements (Underwood and Fairweather 1989; Cushing 1990). Growth in early life allows individuals to survive size-selective threats (e.g., predation) and maximize later growth potential (e.g., large gape, superior fitness; Sogard 1997). For example, in Babine Lake, size-selective mortality is present in juvenile sockeye salmon, and faster growth rates in larger individuals maintain a hierarchy of lengths within a cohort (West and Larkin 1987). Large size upon migration to the ocean subsequently increases marine survival (Percy 1992; Beamish and Mahnken 2001; Beamish et al. 2004; Zabel and Achord 2004; Moss et al. 2005; Claiborne et al. 2011; Thompson and Beauchamp 2014). Thus, body size during early life and the factors that impact it, may influence individual survival and potentially population performance.

Here we examine the spatial and temporal dynamics of water velocity and juvenile sockeye salmon movement and condition across the lake-outlet reach of an important sockeye salmon system. We focus on the lake outlet of Babine Lake, British Columbia, the longest natural lake in B.C. and most productive sockeye lake in the Skeena River watershed (Wood et al. 1998). We ask the following questions with corresponding predictions. First, what are the water velocity landscapes of the lake outlet reach in relation to the ability of juvenile sockeye to swim upstream? We predict that the lake outlet reach contains locations with high velocities that could challenge upstream juvenile migration, and these

challenges will be greater during higher river discharge. Second, how does river discharge relate to directional movement by juvenile sockeye salmon? We predict that higher water discharge decreases the probability of upstream movement by juvenile sockeye salmon. Third, what are the seasonal patterns of juvenile size, abundance, and condition across the lake, lake outlet, and downstream rearing habitats? We predict that juvenile sockeye salmon size (i.e., length and weight) and condition will be greater in lake sites compared to sites downstream of the lake outlet. Further, we examine long-term variation in hydrology and discuss how this variation may influence the degree to which lake outlets function as bidirectional corridors or one-way travel routes for young sockeye salmon.

## Methods

### Overview of approach

Our study consists of the following components. First, we mapped nearshore water velocities across a 1.5 km reach on five occasions that varied in river discharge. Second, we used underwater video to examine the relationship between river discharge and juvenile movement. Third, we performed an extensive field study of juvenile abundance and condition across the lake and lake outlet reaches during the emergence and migration period. Specifically, we measured relative abundance, size, and energetics of juvenile sockeye salmon in the lake, outlet, and downstream rearing habitats as well as those that were being transported downstream. Sampling was done between mid-May and mid-August to fully capture juvenile emergence and migration, which generally begins in early June and is complete by late July. We describe these methodologies in more detail below.

### Study system

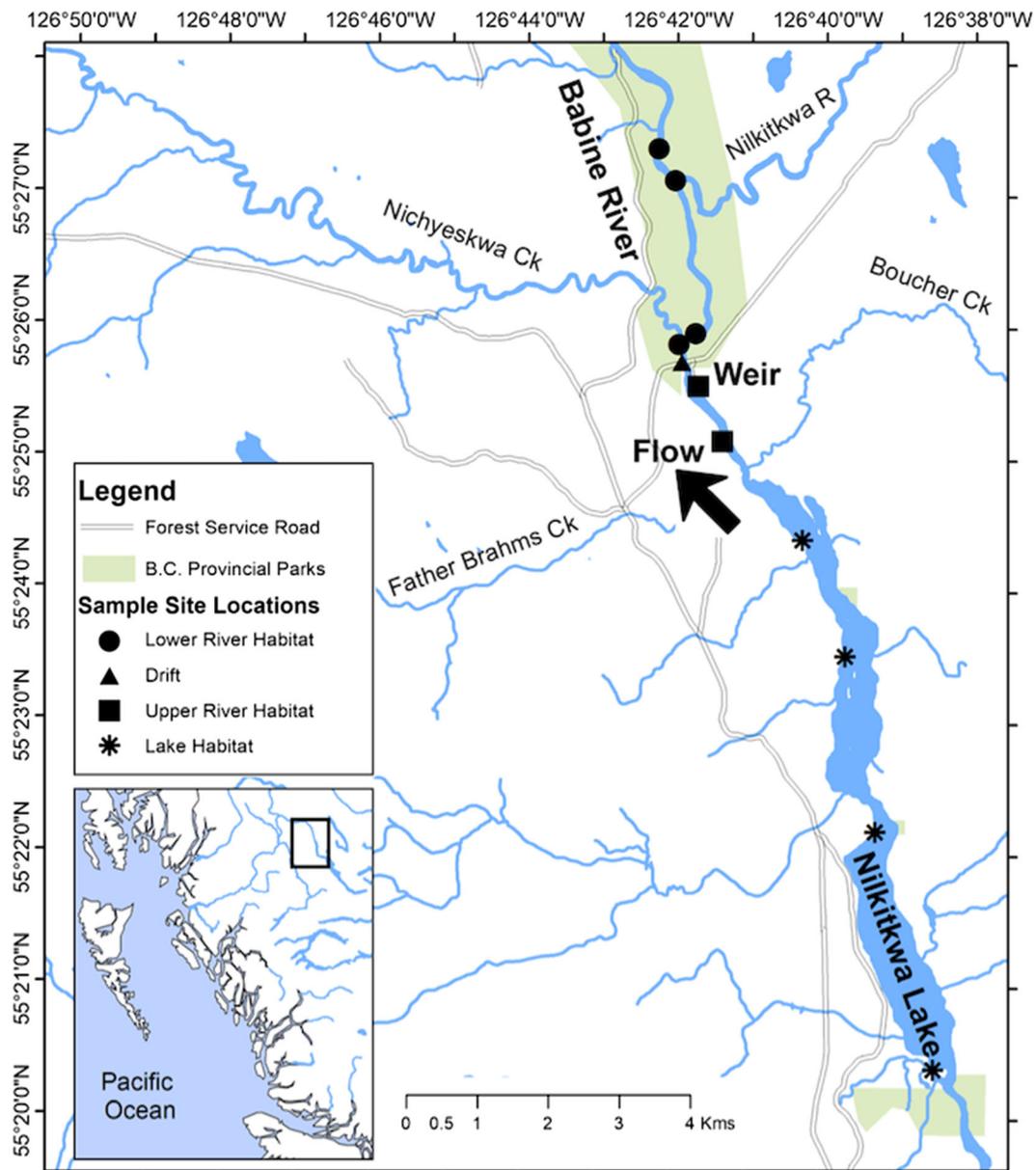
The Babine watershed is the largest tributary basin of the Skeena River, the second largest Pacific salmon producing river system in Canada (Fig. 1). The Babine Lake watershed produces, on average, over 90% of Skeena River sockeye salmon, with at least 24 distinct sockeye populations within the larger lake stock complex (Cox-Rogers and Spilsted 2012). Babine River sockeye were formerly the largest contributing population to the Babine watershed (Cox-Rogers and Spilsted 2012). Babine

River sockeye spawn below the outlets of Nilkitkwa and Babine lakes in the fall, eggs incubate over the winter, and juvenile emergence generally begins in May, with individuals and groups being observed in backwater areas of both upper and lower river habitat. Throughout June, aggregations of juveniles increase in abundance throughout river habitat, and later, juveniles begin to appear and accumulate in lakeshore areas. By the end of July, the migration period is usually complete, and juveniles can no longer be found in river backwater or shallow lakeshore habitats. This phenology likely varies across years due to biological and climatic influences. Throughout the emergence and migration period, juveniles have been observed swimming upstream to reach rearing areas in the lakes (McDonald and Hume 1984; Wood et al. 1998). However, many juvenile sockeye have also been observed being swept some distance downstream, where their fate is unknown (Clarke 1967; Lake Babine Nation Fisheries (LBNF), unpublished data; Table 1). Research in the estuary of the Skeena River found that Babine Lake sockeye spend very little time in the estuary (mostly less than 2 days; Moore et al. 2016), suggesting that estuary rearing does not appear to be a common life-history strategy.

The lake-outlet spawning Babine River sockeye salmon population has declined dramatically over the last several decades, contributing to conservation concerns for the wild Babine Conservation Unit (Cox-Rogers and Spilsted 2012). Returns of Lower Babine River sockeye, the focal population in this study, have fallen by approximately 85%, from over 80,000 during the 1950s and 1960s, to around 12,000 in the last four decades, with two counts of less than 2000 spawners in the last decade (Department of Fisheries and Oceans Canada 2018). All study activities were carried out in the Lower Babine River, downstream of Nilkitkwa Lake. The Lower Babine sockeye population is the only adjacent population that would contribute juveniles to the study area. This is known from almost a century of spawning enumeration counts for this population. This section of the Babine River will be, henceforth, segregated into upper river habitat (above the adult enumeration weir; Fig. 1) and lower river habitat (below the adult enumeration weir; Fig. 1).

### Velocity conditions

Babine River water level and discharge have been recorded near-continuously at the hydrometric station,



**Fig. 1** Locations of sampling sites in Nilkitkwa Lake and Babine River, British Columbia, Canada. Babine Lake is immediately upstream of Nilkitkwa Lake

maintained by the Water Survey of Canada since 1972, about 50 m below the Babine River enumeration weir. To create a large-scale map of the velocity environment in the Lower Babine River, measurements were collected from the downstream extent of known sockeye spawning grounds in the Lower Babine River, for a longitudinal river distance of 1.5 km. This was done between May and August in 2017 and 2018, to capture

the full extent of velocity conditions that emerging and migrating juveniles may encounter. Spring and summer water levels in 2017 and 2018 were low to average, and thus may represent conditions slightly more amenable to juvenile upstream migration than in average or high discharge years. Point velocity measurements were recorded at 25 m intervals, at 0.5 m, 1 m and 2 m from the wetted edge. To obtain the average speed in the water

**Table 1** Hydrologic conditions and estimated number of age 0+ juvenile sockeye (*Oncorhynchus nerka*) transported downstream in springs of 1966 and 2016

Brood year	Peak discharge date	Total spawners	Potential juvenile production (thousands)	Peak downstream displacement date	Total juveniles displaced downstream	Proportion of brood displaced downstream
1965	Jun-17	176,000	40 656 <sup>a</sup>	Jun-07	7,500,000	0.18
2015	May-17	15,644	3 614 <sup>a</sup> –3 989 <sup>b</sup>	May-25	2,456,142	0.62 <sup>b</sup> –0.68 <sup>a</sup>

<sup>a</sup> Assuming 55% female, 2800 egg, 15% egg-to-fry survival (Clarke and Smith 1972)

<sup>b</sup> Assuming 57% female, 2800 egg (LBNF,2016), 16% egg-to-fry survival (West and Mason 1987)

column, velocity was measured at 60% depth from the water's surface when total water depth was less than 1 m or was averaged between 80% and 20% depth from surface when water depth was greater than 1 m (BCMOE 2009). This standardized method approximates average water velocity from river substrate to water surface. We used this method to approximate broad-scale velocity conditions over a large habitat area but acknowledge that velocity refugia within the three-dimensional riverscape may exist (e.g., eddies, interstitial space). To determine thresholds, published estimates of juvenile sockeye salmon sustained ( $0.47 \text{ m}\cdot\text{s}^{-1}$ ) and burst swimming speed ( $0.60 \text{ m}\cdot\text{s}^{-1}$ ; Clarke 1967) were used to categorize areas with velocity near or beyond juvenile sockeye swimming capabilities. From underwater video observations, juveniles were found to be using all parts of the water column (e.g., near-substrate, mid-column, and near-surface). Thus, collecting information that represented average velocity from the substrate to the surface was considered to be the best representation of average velocity conditions experienced by individuals.

### Juvenile movement

Data on juvenile movement in the Babine River were collected across a range of water discharges. These data were collected with LBNF between 2015 and 2017 using underwater cameras at points of interest (e.g., the adult enumeration weir). Juvenile movement along the west and east banks was captured using a GoPro4 camera, positioned immediately upstream of the adult salmon enumeration weir. The camera was fastened to a wooden frame on the west bank, facing the bank, perpendicular to flow, and positioned 1.5 m from the bank. The camera location was fixed and did not change across changes in discharge, and bank armouring (vertical steel sheet piling) provided a constant focal

distance from the camera to the wetted edge, across all discharge levels. Footage from the east bank camera revealed very little juvenile sockeye usage, and thus these data were not analyzed. Extensive anecdotal observations during the juvenile migration period in 2016, 2017, and 2018, confirmed that the west bank camera location was an obligate upstream migration route and key movement bottleneck (due to extremely high velocity and turbulence in the surrounding area). Thus, the data collected on movement from this camera represents a reasonable estimate of upstream movement from lower river habitat.

A viewing grid (a 1 m by 2 m aluminum panel with a 5 cm by 5 cm grid) affixed to the bank was used to observe and track approximate speed and size of fish observed. Video footage was captured in 1-h segments throughout daylight hours and for the duration of the upstream migration (approximately May 20th – June 30th, 2016). These samples allowed for observation of juvenile behaviour along the banks, where juveniles must travel when trying to return upstream. Successful upstream travelling individuals were classified as those facing upstream and travelling upstream. Unsuccessful individuals included (1) juveniles oriented downstream and travelling downstream, (2) juveniles oriented upstream but moving downstream, and (3) juveniles oriented upstream, moving upstream but unsuccessful in travelling to the upstream side of the video frame (i.e., swept backwards, downstream and out of frame).

### Relative abundance

Abundance of juvenile sockeye at lake and river habitat sites was assessed using beach seines. Seining was conducted at four sites in Nilkitkwa Lake and six sites in the Lower Babine River in the spring of 2017 to

observe juvenile condition and size. The seine net dimensions were 1.2 m in height and 2.4 m in length with a mesh size of 0.32 cm. Seine passes were done parallel to shore, with one end following the water's edge. We used catch per seine, averaged over the total area seined, as an index of abundance. Total catch, divided by total distance seined, divided by the length of the seine net, was used to calculate catch per unit effort (CPUE) in units of juveniles $\cdot$ m<sup>-2</sup>. Seining was consistently effective across all river discharge levels, as sampling sites were all located in backwater or natural eddy locations, where the current was manageable or absent, and water depth did not exceed the height of the seine net. To collect information on drifting individuals, downstream trapping was used to collect abundance, size, and condition data on individuals displaced downstream during the spring of 2016 and 2017. Drifting individuals were captured using 30.5 cm diameter square-shaped nets suspended from the adult enumeration weir, fishing the top foot of the water column, following Clarke (1967). CPUE of drift individuals was calculated from total individuals caught, divided by number of 15 min sets fished, multiplied by 10.76 (conversion to m<sup>2</sup>), to give units of juveniles $\cdot$ m<sup>-2</sup> $\cdot$ 15 min set<sup>-1</sup>. Across the monitoring period, 7115 sockeye juveniles were sampled to estimate abundance.

#### Size and condition

Fork length ( $\pm$ 1 mm) and weight ( $\pm$ 0.01 g) data for juveniles from the Lower Babine River and Nilkitkwa Lake was gathered during the seine and drift sampling described above. We calculated Fulton's Condition Factor (CF) with the following:

$$CF = 10^N \times \frac{\text{weight}}{\text{length}^3}$$

where N is generally accepted to be 4 for juvenile salmonids when weight is measured in grams and length is measured in millimeters, giving CF values near to 1. Over the sampling period, up to 25 individuals were measured per sampling site, when possible ( $n = 1876$ ).

Energy density, or the energy (i.e., calories) per gram of body tissue, was assessed using a bomb calorimeter. Some juvenile sockeye samples did not have enough body tissue mass for the calorimeter to operate within manufacturer guidelines, so energy density was

measured of a dried and homogenized pellet made up of all body tissues from two complete juveniles for all samples. Six individuals were drawn at random from a body size sample set and were then grouped into three pairs (two smallest, two medium, two largest) based on wet body mass. Energy density was assessed for six individuals from every sampling site within each habitat type, for sampling weeks four, six and eight. A total of 218 juveniles were analysed, in pairs ( $n = 109$ ).

#### Statistical analysis

All statistical analyses were conducted using the statistical software R, version 3.4.4. (R Development Core Team 2016). We used a generalized linear model to determine the logistic regression curve for upstream travel success at the Babine River enumeration weir as a factor of river discharge. We used a linear mixed model approach to examine how location (lake or river habitat) affected body size and condition of juvenile sockeye salmon recently emerged from incubation gravels. We used the *nlme* package to implement linear and nonlinear mixed-effect models (Pinheiro et al. 2009).

Abundance, size, and condition metrics were modelled as response variables, including relative abundance (CPUE), fork length (FL), weight, CF, and energy density. When necessary, we log-transformed variables to satisfy the assumptions of normality and homogeneity of residual errors. Habitat type (i.e., lake, drift, upper river, and lower river), river discharge, and sampling week (i.e., time) were modelled as fixed covariates. Week and river discharge were highly correlated ( $r = 0.8$ ), so we competed these two covariates instead of including them together in any model. Interaction terms between habitat type and week and habitat type and discharge were tested in all model sets. Size and energy density responses (FL, weight, CF, and energy density) were modeled at the individual fish level, while relative abundance was modeled at the site level. Site was set as a random effect to account for variation among capture sites within habitat types.

Model selection was carried out using Akaike's Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002) using the *model.sel()* function in the *nlme* package (Pinheiro et al. 2009). For each response variable, we reported the top model and all candidate models within a threshold of  $\Delta$ AICc = 2 (Burnham and Anderson 1998; Zuur 2009).

## Results

### Discharge

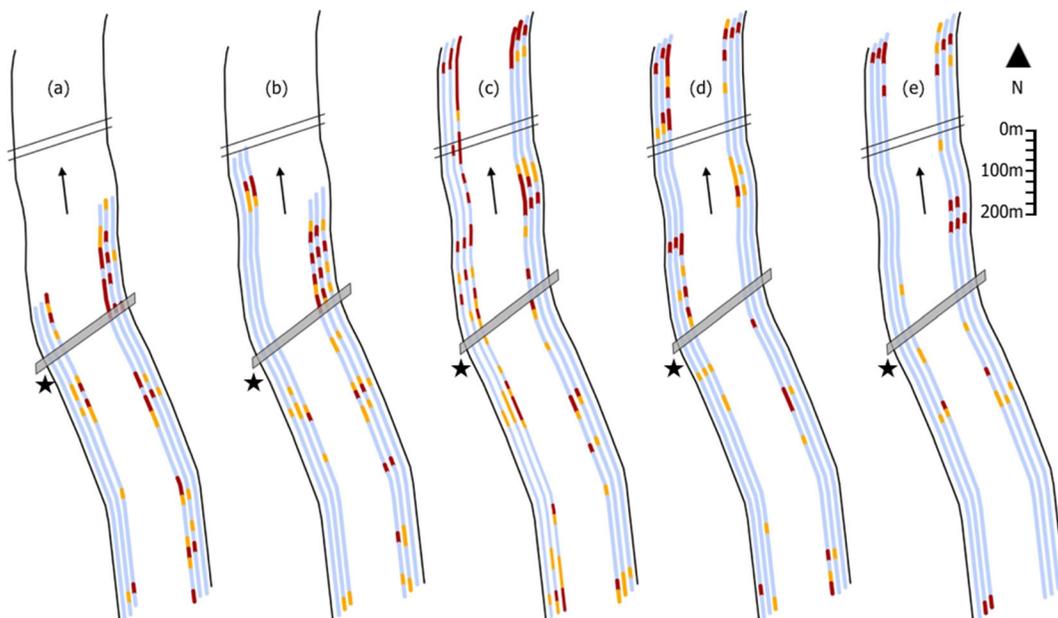
Throughout the lake outlet reach, for 1.5 km below spawning grounds, numerous locations were observed to have water velocities beyond the swimming ability of juvenile sockeye (Fig. 2). Previous observations of this population suggested that juvenile sockeye have sustained and burst swimming abilities of approximately  $0.47 \text{ m}\cdot\text{s}^{-1}$  and  $0.6 \text{ m}\cdot\text{s}^{-1}$ , respectively (Clarke 1967). In general, the number of potential velocity challenges increased with increasing river discharge (Table 2). For example, in areas where complete sampling was possible (over all discharge levels observed), proportional area beyond sustained swimming speed of juvenile sockeye more than doubled from 8% to 21% when discharge increased from  $62 \text{ m}^3\cdot\text{s}^{-1}$  to  $188 \text{ m}^3\cdot\text{s}^{-1}$ . It should also be noted that the estimated proportion of sampled area beyond sustained swim speed at the largest two discharge levels is likely conservative, as the data could not be gathered in river sections where the water

velocity was fastest, due to safety concerns. Thus, when river discharge is higher, it would be more challenging for juveniles to swim upstream.

Locations of velocity challenges were relatively consistent, and grew in extent with increasing discharge, with some anomalies likely due to heterogeneous bed structure and dynamic bank location with changing river discharge (e.g., inundation of riparian vegetation). Areas with particularly high velocities that would impede upstream juvenile movement existed below both the adult enumeration weir and the road bridge, where the shoreline has been armoured. Upstream of the weir, water velocities were generally low enough that juvenile sockeye salmon would be predicted to be able to swim upstream, especially within 1 m of the bank.

### Juvenile movement

Only 33% of the 134 juvenile sockeye observed in underwater video were successfully traveling upstream along the bank during the spring of 2016. Juvenile sockeye tended to be less likely to successfully travel



**Fig. 2** Temporal change in local velocities in the Babine River for 1.5 km below known sockeye salmon (*Oncorhynchus nerka*) spawning grounds (scale bar only representative of longitudinal river distances; river width not to scale, as variation in wetted edge across discharge levels is not depicted). Local velocities are recorded as single point estimates each 25 m in longitudinal river distance at 0.5 m, 1 m, and 2 m from the wetted edge, on each bank. River discharges are (a) 188, (b) 148, (c) 127, (d) 89 and (e)  $62 \text{ m}^3\cdot\text{s}^{-1}$ . Light blue represents velocity below sustained

swimming capability ( $0.47 \text{ m}\cdot\text{s}^{-1}$ ), orange represents velocity greater than sustained swimming speed but below burst swimming capability ( $0.60 \text{ m}\cdot\text{s}^{-1}$ ) and red represents velocity beyond burst swimming capability. Data was collected between May and August of 2017 and 2018. Arrows indicate the direction of flow. Solid grey bars indicate the location of the adult enumeration weir, and parallel black lines indicate the road bridge. Stars indicate the location of the underwater camera

upstream at higher river discharge, but the effect was not found to be statistically significant ( $z$ -value = -1.56,  $p$  value = 0.12; Fig. 3).

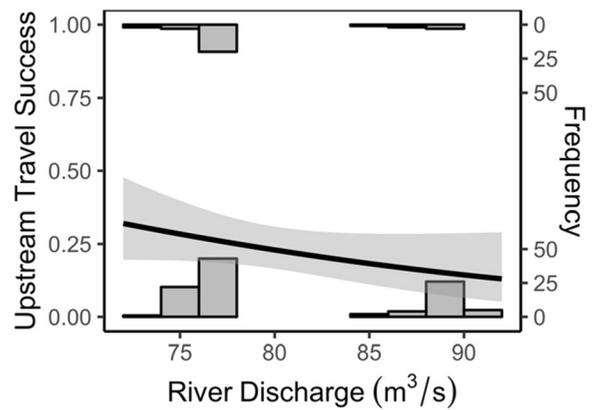
Relative abundance

Spatial and temporal variation in juvenile sockeye abundance were influenced by habitat conditions and river discharge (Table 3). The relative abundance of juvenile sockeye across all habitat types generally increased through the month of May, and then declined for the remainder of the study (Fig. 4). The earliest peak in abundance was observed in upper river habitats (nearest to spawning grounds) around May 22nd (week 2 of the study). Drift, lake, and lower river abundance was greatest three weeks later, around June 12th (week 5). A second, much smaller increase in abundance was observed in lake abundance around July 10th (week 9). The highest abundance of drift individuals, at almost  $850 \text{ fish}\cdot\text{m}^{-2}\cdot\text{hr}^{-1}$  (June 12th, week 5), likely indicated maximum juvenile emergence, which decreased to zero by the end of the study period, when emergence was likely complete. Relative abundance varied within and between samplings, at some sites decreasing from over  $300 \text{ fish}\cdot\text{m}^{-2}$  at peak migration to zero by the end of the study. Upper river habitat sites had the greatest variability in average abundance, ranging from 5 to  $300 \text{ fish}\cdot\text{m}^{-2}$ , while lake and lower river sites generally averaged between 2 and  $100 \text{ fish}\cdot\text{m}^{-2}$ .

The top model common slope term for all habitat types showed a positive relationship between discharge and relative abundance (coefficient =  $0.03 \ln(\text{CPUE}) \cdot \text{m}^{-3}\cdot\text{s}^{-1}$ ; 95% C.I. 0.02–0.04; Table 4). In general, this aligns with the gradual decrease in abundance observed throughout the middle and latter half of the sampling period, during which time discharge values were

**Table 2** Counts (No.) and proportions (Prop.) of river sections with measured velocity below ( $v < 0.47 \text{ m}\cdot\text{s}^{-1}$ ), at ( $0.47 \text{ m}\cdot\text{s}^{-1} < v < 0.60 \text{ m}\cdot\text{s}^{-1}$ ) or above ( $v > 0.60 \text{ m}\cdot\text{s}^{-1}$ ) swimming capability of age 0+ juvenile sockeye (*Oncorhynchus nerka*) at varying levels

Discharge	$188 \text{ m}^3\cdot\text{s}^{-1}$		$148 \text{ m}^3\cdot\text{s}^{-1}$		$127 \text{ m}^3\cdot\text{s}^{-1}$		$89 \text{ m}^3\cdot\text{s}^{-1}$		$62 \text{ m}^3\cdot\text{s}^{-1}$	
	No.	Prop.	No.	Prop.	No.	Prop.	No.	Prop.	No.	Prop.
Total	234		276		360		360		360	
$v < 0.47$	185	0.79	190	0.81	182	0.78	213	0.91	216	0.92
$0.47 < v < 0.60$	23	0.10	28	0.12	32	0.14	11	0.05	9	0.04
$v > 0.60$	26	0.11	16	0.07	20	0.09	10	0.04	9	0.04



**Fig. 3** Logistic regression for upstream travel success of Lower Babine River age 0+ juvenile sockeye salmon (*Oncorhynchus nerka*). Travel behaviour was observed adjacent to Babine River west bank at the Babine River enumeration weir

decreasing, as spring freshet declined. By the end of the sampling season, relative abundance of juveniles had decreased to very low levels.

Fork length (FL)

The body size of juvenile sockeye varied temporally and spatially between habitats throughout the lake-outlet reach (Fig. 5). FL was greatest in the lake habitat at all sampling periods, except during Week 5 when upper river juveniles were approximately 2 mm longer than lake juveniles. During the last sampling period, on average, lake juveniles were 10.55, 6.77, and 10.60 mm longer than drift, upper river, and lower river juveniles respectively. Thus, lake juveniles were, on average, 30% longer than lower river juveniles. AICc model selection indicated that habitat, week, and an interaction between them were the best predictors of juvenile FL (Table 3). In all habitat types, FL increased over time

of discharge in the Babine River, British Columbia. Summary data is only included for those sites that were monitored at all discharge levels

(week), but the fastest FL increase occurred in lake habitat, with a top model slope term of  $2.45 \text{ mm}\cdot\text{week}^{-1}$  (95% C.I. 1.54–3.35). This was almost double the rate of length increase observed in the lower river habitat ( $1.24 \text{ mm}\cdot\text{week}^{-1}$ ; 95% C.I. 0.32–2.16).

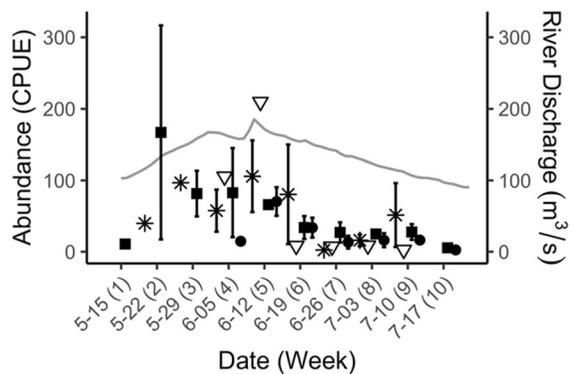
Weight

Juvenile sockeye total wet body weight was influenced by both habitat type and week and the interaction between them (Table 3). Weight was greatest in lake habitat throughout the entire sampling period (Fig. 5). This difference was greatest during the last three weeks of sampling. During the final sampling period, lake juveniles weighed 510.5 mg and 644.3 mg more than upper river and lower river juveniles, respectively, or more than 90% and 150% heavier than upper river and lower river juveniles.

Weight increased over time (week) in all habitat types, but the most rapid increase in weight occurred in lake habitat, with a slope coefficient of  $118 \text{ mg}\cdot\text{week}^{-1}$  (95% C.I. 77–161). This was more than double the rate of weight increase observed in both upper and lower river habitat, which were only  $57$  and  $42 \text{ mg}\cdot\text{week}^{-1}$ , respectively (95% C.I. 15–99 and 0–85, respectively).

Fulton’s condition factor (CF)

Spatial and temporal variation in CF was explained by both habitat type and week and the interaction between these terms (Table 3). CF of juveniles across different habitat types was more variable than the other size



Habitat \* Lake ▽ Drift ■ Upper River ● Lower River

**Fig. 4** Temporal changes in abundance of age 0+ juvenile sockeye (*Oncorhynchus nerka*), expressed as catch per unit effort (CPUE), in fish per square meter sampled between May and July 2017 in the Babine River and Nilkitkwa Lake, British Columbia, Canada. Lake, Upper River, and Lower River habitats were sampled using beach seine nets and represent fish per square meter of lake or river surface area sampled. Drifting individuals were sampled using drift nets and data represent fish  $\cdot \text{m}^{-2} \cdot 15 \text{ min set}^{-1}$ . Study weeks are presented in parentheses following the date (x-axis). Error bars denote  $\pm 1$  standard error. Grey line denotes river discharge ( $\text{m}^3 \cdot \text{s}^{-1}$ ) during the sampling period

metrics over the sampling period (Fig. 5). During the latter half of the study, drift individuals often had the highest CF, followed by lake habitat juveniles.

CF also increased with time (week) in all habitat types except in lower river habitat (Table 3). Drift juveniles had the highest rate of increase at  $0.043 \text{ g}\cdot\text{mm}^{-3}\cdot\text{week}^{-1}$  (95% C.I. 0.025–0.061). Lake and upper river individuals increased in CF by  $0.028 \text{ g}\cdot\text{mm}^{-3}\cdot\text{week}^{-1}$  (95% C.I. - 0.009 - 0.064) and  $0.015 \text{ g}\cdot\text{mm}^{-3}\cdot\text{week}^{-1}$  (95% C.I. - 0.021 - 0.052). CF of lower river juveniles increased the

**Table 3** Akaike’s Information Criterion ranking of top models (delta AICc <2) describing the effects of habitat type, discharge (Q) and time (Week) on abundance (natural logarithm), FL (Length), total body mass (Weight), Fulton’s Condition Factor (CF), and energy density (Energy) of 0+ juvenile sockeye

Model	Response	Covariates	k	Δ AICc	ω
3	ln(Abundance)	Habitat + Q	3	0.00	0.417
7	ln(Abundance)	Q	2	0.25	0.368
2	Length	Habitat + Week + Habitat * Week	4	0.00	1.000
2	ln(Weight)	Habitat + Week + Habitat * Week	4	0.00	1.000
2	CF	Habitat + Week + Habitat * Week	4	0.00	1.000
1	Energy	Habitat + Q+Habitat * Q	4	0.00	0.399
2	Energy	Habitat + Week + Habitat * Week	4	1.21	0.218
4	Energy	Habitat + Week	3	1.63	0.176

(*Oncorhynchus nerka*) in the lake and lake outlet reach. Included are number of parameters (k), difference in Akaike’s Information Criterion (Δ AICc) between top models in the set and the Akaike weights (ω) of each model in the top model set

**Table 4** Model parameter estimates from AICc-selected top models (referenced with model number). Standard errors (SE) and statistical significance (*P* value) for fixed effects of habitat type (Habitat), week, and discharge (Q) on FL (Length), total wet body weight (Weight), CF, and energy density (Energy) of 0+

juvenile sockeye (*Oncorhynchus nerka*) in the lake and lake outlet reach. Intercept values are given in the units of the response variable. Slope value units are given in units of the response variable per week, except as otherwise specified in footnotes

Response variable	Parameter	Intercept			Slope		
		Value	SE	p value	Value	SE	p value
ln(Abundance) [CPUE] (Model 3) <sup>a</sup>	Lake	-1.514	0.954	0.117	0.03	0.007	<0.001
	Lower River	-1.717	1.330	0.607			
	Upper River	-0.704	1.373	0.095			
ln(Abundance) [CPUE] (Model 7) <sup>a</sup>		-1.462	0.919	0.116	0.03	0.007	<0.001
Length [mm]	Drift	23.113	1.713	<0.001	1.34	0.225	<0.001
	Lake	22.342	1.844	0.688	2.45	0.236	<0.001
	Lower River	25.885	1.868	0.181	1.24	0.243	0.674
	Upper River	25.845	1.896	0.193	1.59	0.237	0.302
ln(Weight) [g]	Drift	-2.394	0.149	<0.001	0.16	0.020	<0.001
	Lake	-2.275	0.159	0.480	0.23	0.022	0.005
	Lower River	-1.905	0.162	0.019	0.12	0.022	0.043
	Upper River	-2.071	0.163	0.087	0.16	0.022	0.742
CF [g•mm <sup>-3</sup> ]	Drift	0.587	0.064	<0.001	0.04	0.009	<0.001
	Lake	0.664	0.068	0.292	0.03	0.009	0.110
	Lower River	0.834	0.069	0.009	0.01	0.010	<0.001
	Upper River	0.685	0.069	0.198	0.02	0.009	0.003
Energy [cal] (Model 1) <sup>b</sup>	Drift	6915.88	426.092	<0.001	-8.01	2.914	0.007
	Lake	5487.68	510.348	0.028	0.31	3.486	0.019
	Lower River	4838.11	535.545	0.006	3.96	3.652	0.002
	Upper River	5054.69	598.574	0.017	3.36	4.102	0.003
Energy [cal] (Model 2)	Drift	5543.04	192.061	<0.001	36.63	29.412	0.216
	Lake	5595.86	233.391	0.827	-10.60	36.021	0.193
	Lower River	5725.32	234.328	0.462	-52.25	36.300	0.016
	Upper River	5846.92	268.431	0.295	-51.45	41.594	0.037
Energy [cal] (Model 4)	Drift	5900.90	104.87	<0.001	-23.01	12.393	0.066
	Lake	5670.34	191.13	0.032			
	Lower River	5551.51	191.34	0.004			
	Upper River	5676.28	201.90	0.054			

<sup>a</sup> Slope coefficient units CPUE•m<sup>-3</sup>•s<sup>-1</sup>

<sup>b</sup> Slope coefficient units calories•m<sup>-3</sup>•s<sup>-1</sup>

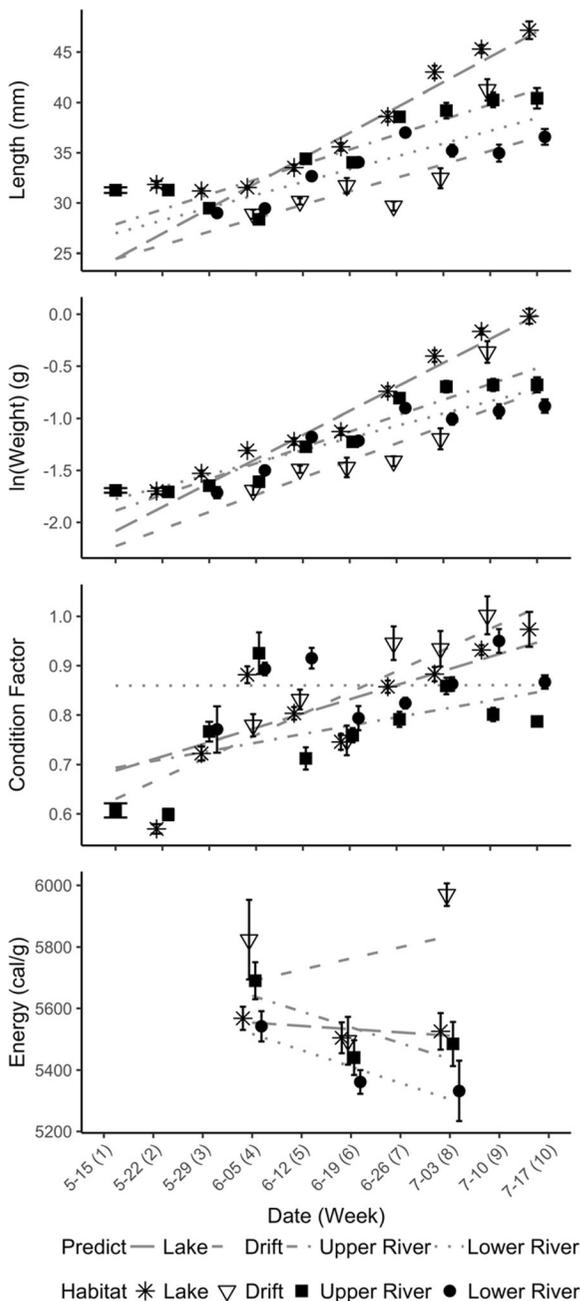
slowest, with an almost stagnant rate, at only 0.005 g•mm<sup>-3</sup>•week<sup>-1</sup> (95% C.I. -0.032 - 0.042).

Energy

At the final sampling, drift individuals had the highest energy density at 5907 cal•g<sup>-1</sup> body weight (Fig. 5).

This is, on average, 9% and 12% greater than upper and lower river individuals, respectively.

We found that habitat, week, discharge, and the interaction between habitat and week, and habitat and discharge were all closely related to energy density of juvenile sockeye (Table 3). In all top models, over time (week), as discharge generally decreased, the energy density of upper and lower river individuals decreased.



**Fig. 5** Temporal changes in fork length, total body weight, condition factor, and energy density of age 0+ juvenile sockeye (*Oncorhynchus nerka*), sampled between May and July 2017 in the Babine River and Nilkitkwa Lake, British Columbia, Canada. Study weeks are presented in parentheses following the date (x-axis). The top AICc-selected models are presented and error bars denote  $\pm 1$  standard error

This relationship was strongest (steeper slope values) in lower river habitat. Interestingly, these were the only declining trends found in all metrics sampled, but we

acknowledge that this is based on only three sampling time points. In the lake, energy density of juvenile sockeye was maintained throughout the sampling period (weak, slightly negative slope over time). For drift individuals, as time increased and discharge decreased, energy density increased. Thus, juvenile sockeye in river habitat were found to be losing body energy, per unit weight, most quickly in comparison to lake and drift sockeye individuals.

### Discussion

Here we described the habitat variability of a lake outlet reach across space and time, and the linked patterns in body size and condition of juvenile sockeye salmon. There were both seasonal and spatial patterns in water velocity across the lake-outlet reach that exceeded the ability of juveniles to swim upstream to lake rearing habitat. At high river discharge, more velocity barriers were measured which may have been associated with less upstream movement of juveniles. Juvenile sockeye in different locations also had different sizes and conditions; lake rearing habitat was associated with larger sized juvenile sockeye, specifically 30% longer and 150% heavier, compared to juveniles displaced to downstream river habitats. Overall, our results suggest that juveniles in lake habitat experience superior growth conditions, but movement of individuals to downriver habitats and elevated river discharge may prevent some juvenile sockeye from accessing these superior growth conditions.

The hydrological landscape of the lake outlet reach was spatially and temporally dynamic and may exert control on movement. This study took place during the spring, when juvenile sockeye emerge from the gravel and when snowmelt leads to high water discharge. As freshet progressed and river discharge increased, the number and size of areas of high velocity that exceed swimming capabilities of juvenile sockeye, also increased. In addition to velocity challenges, colder water temperature associated with snowmelt likely impeded the swimming performance, and thus upstream migration abilities, of juveniles during freshet (Brett et al. 1958; Brett 1971; Griffiths and Alderdice 1972). Thus, at the broad scale, higher river discharge is likely associated with more downstream transport, rather than successful upstream migration, than lower river discharge. During our study, migration occurred at high river

levels, during and immediately following spring freshet, but we acknowledge that this phenology may shift between years, altering the discharge and velocity conditions experienced by recently emerged sockeye juveniles. We also acknowledge that juvenile salmon may be able to exploit fine-scale velocity refugia, but also may be subject to additional areas of high velocity, that were not captured with our methodology. To provide a focused observational counterpart to the larger-scale velocity survey, we used underwater video analyses at a single site with an armoured river bank. This video analysis suggested that higher water flows tended to be associated with more downstream movement of juveniles. We acknowledge that this single location of video analysis does not capture all spatial variation in the outlet reach but does provide observational data from one known point in the migratory path to the lake. Although not analyzed in this study, temperatures associated with the snowmelt-driven freshet likely influences the ability of juvenile salmon to swim upstream, as water temperature affects the aerobic scope, and swimming capabilities of salmonids (Fry 1947; Gibson and Fry 1954; Brett 1971). Collectively, these data suggest that temporary velocity barriers exist downstream of the lake outlet, dependent on discharge. The outlet may be bidirectionally connected at lower discharge but may function as a one-way travel route at high freshet flows.

Juvenile fish in the lake outlet reach may be extremely sensitive to land-use alterations that change patterns of flows across space. For example, in our study and others, juveniles have been observed using flooded riparian vegetation to hold or begin moving upstream towards lake rearing habitat (McCart 1967; LBNF unpublished data). Anthropogenic channelization or straightening, and bank armoring (e.g., addition of riprap boulders or cement blocks) decreases energy dissipation capacity of the shoreline and likely increases nearshore flows, and blocks access to flooded riparian refugia (Strayer and Findlay 2010), which could further challenge juvenile upstream migration to lake rearing habitat. For example, the infrastructure associated with the adult enumeration weir and the Forest Service Road bridge across Babine River, namely the removal of riparian vegetation and extensive bank armoring, may serve as one such barrier. Thus, altered and armoured shoreline habitat in the Babine River would be valuable to target for habitat restoration to facilitate upstream juvenile migration. Similarly, in Upper Klamath Lake,

Oregon, intact marsh and irregular, diverse shoreline habitat have been shown to improve juvenile retention of Lost River suckers (*Deltistes luxatus*) and shortnose suckers (*Chasmistes brevirostris*) in nursery lake habitat (Markle et al. 2009). Both of these species are listed as endangered under the United States Federal Endangered Species Act, and survival and recruitment in a given year is closely linked to the ability of juveniles to reach nursery habitat in the lake (Cooperman et al. 2009). Here, researchers suggested that retention of these freshwater fish depended largely on shoreline topography and habitat, which were noted as highly at-risk to channelization and alteration (Markle et al. 2009). Thus, anthropogenic habitat simplification may exacerbate challenges in aquatic connectivity, a potentially underappreciated stressor for aquatic species with complex life-histories that rely on multiple habitats.

Relative abundance and condition of juvenile sockeye salmon revealed differences among habitat types over the season. The earliest peak in relative abundance was observed in upper river habitats (nearest to spawning grounds) near the end of May with drift, lake, and lower river abundances observed at maximum about three weeks later. This suggests that, following emergence, it may take a couple of weeks for juveniles to move upstream to lake rearing habitat, and in the process some individuals may be swept downstream. Additionally, the presence of large, heavy individuals in drift samples near the end of the study (week 8), suggest that older, more developed juveniles may move downstream, intentionally or otherwise, late in the migratory period. Importantly, juvenile abundances did not persist into the summer in the downstream river habitats—thus, juveniles are not rearing long term in these habitats. The fate of these individuals is unknown, as they may perish by predation, move further downstream to rear (although as discussed later, options seem limited), or migrate upstream to rearing habitat in the lake. Further research is needed to investigate the ultimate fate of individuals in downstream habitat following emergence.

The conditions determining which individuals are transported downstream after emergence remain unclear. Anecdotal observations suggest that early-returning adults in this population choose redd sites nearest the lake and along the river margins, nearest the bank, where spawning gravels are less embedded

(lower proportion of fine sediment), and water is shallower and slower flowing. Similar preference has been found in other systems, where early arriving females choose nest sites in shallower locations, and later arriving individuals make redds in deeper pools (Adkison et al. 2014). This might mean that those returning later to the Babine River, who build redds in the middle of the channel and further downstream, subject their offspring to higher velocity environments upon emergence, and potentially a higher probability of downstream transport. Thus, the proportion of juveniles that are at risk of downstream transport may be a function of the density of spawning adult salmon. It is also possible the smaller-sized juveniles are more vulnerable to downstream transport. Indeed, we found that drift individuals were among the smallest juvenile sockeye observed. This suggests that those transported downstream may be the slower-growing or more recently-emerged individuals.

The lake-outlet reach exhibited spatially and temporally varying patterns of juvenile sockeye size. In general, we observed consistent increases in size over the sampling period, but individuals in lake habitats were 30% longer and 150% heavier than those in lower river habitats, at the end of the sampling period. Individuals sampled in the lake also increased in both length and weight at around twice the rate of individuals in the river. These data suggest that juveniles increase in size more rapidly in lake habitat, compared to those in river rearing habitat. It is also possible that larger or faster growing individuals emigrate from river habitats. Thus, more abundant lake food resources, lower metabolic demands in lake habitat, size-selective immigration or emigration, differential size-selective mortality among habitats, as well as other processes, could be influencing these patterns. River habitat may, however, provide beneficial growth opportunities in other sockeye systems. In the Karluk River, Alaska, later river migrants were found to be about 70% longer than earlier migrants to the upstream lake, although no comparison was made to juveniles that had been rearing in the lake environment during the migration period (McCart 1967). This suggests that juvenile salmon may wait for reduced flows to migrate upstream, or that, in some cases, increased size later in the season may be a function of time, rather than habitat. In contrast, in the Chilko River, British Columbia, upstream migrating juveniles were nearly

the same size as recently emerged juveniles, suggesting that even if juveniles had held in the river for some time, little growth had occurred (Brannon 1972). Together with our findings, it is evident that juvenile sockeye face different ecological pressures along spatially and temporally varying lake-outlet reaches. Key drivers of these selective pressures across reaches likely include habitat quality in the lake and downstream river, hydrologic patterns, and the strength of competitive interactions and density dependence throughout the migration and early rearing life stages. These forces may play a role in the evolution of population-specific migration patterns.

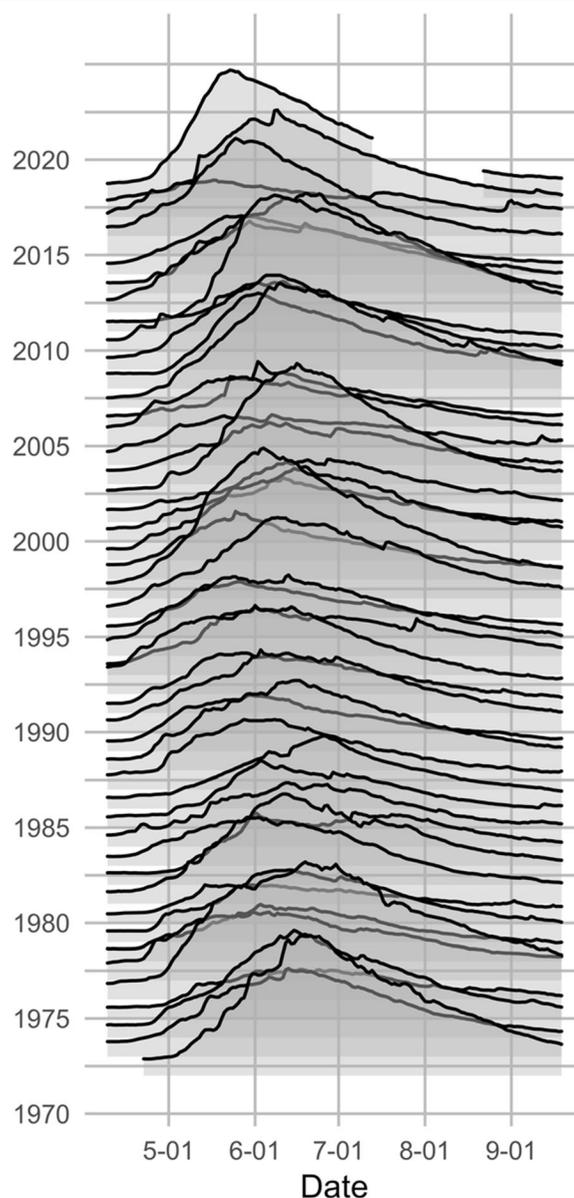
We acknowledge that juvenile attributes were measured at the population-level as individuals were not tracked through time, and thus changes in distributions will be driven by both individual processes (e.g., growth) as well as by non-random patterns of mortality, immigration, and emigration. While it is possible that juveniles displaced downstream could rear in downstream habitats, we sampled all the major off-channel habitat prior to a 17 km canyon section of the Babine River, where no suitable rearing habitat exists. Sampling in river habitats was carried out until few (e.g., 1–5) to zero juveniles were found at any site within the upper and lower river sections. Previous work downstream in the Skeena River estuary also found that Babine Lake sockeye salmon pass through the estuary quickly, suggesting minimal estuary rearing (Moore et al. 2016). Collectively, these lines of evidence suggest that downstream habitats do not sustain juvenile sockeye populations into the summer nor are comparable growth habitats. Thus, displaced juveniles likely have poor growth and survival.

One interesting result was that drifting juvenile sockeye salmon tended to have higher energy density than juveniles in lake or river habitats. Post hoc analyses revealed no significant relationship between juvenile size, wet mass nor dry mass and energy density of individuals ( $R^2$  values from simple linear regression equal to 0.009, <0.001, and 0.018). Although our methods cannot determine the cause of high energy density observed in drifting individuals late in the sampling period (week 8), nor that of low energy density observed in downstream habitats throughout the study, these patterns may be driven by a number of factors, including energy balance (insufficient food resources to offset high metabolic costs) or differences in energy allocation (trade-offs between energy storage or somatic

growth). It is possible that drifting individuals were those that had emerged most recently and thus had not fully incorporated their energy-rich yolk. Indeed, previous work has found that juveniles with larger yolks have higher mass-specific energy (Skoglund et al. 2011) and that the total energy of developing juveniles decreases over time, as the cost of growth is estimated at 35–45% of the energy content of new tissue formed (Jobling 1985; Jorgensen 1988; Brown and Srivastava 1991; Heinimaa and Heinimaa 2004; Skoglund et al. 2011). Thus, we hypothesize that the observed pattern of high energy density among drifting juveniles may be attributed to residual yolk associated with recent emergence.

An important question is whether this variable hydrologic exposure and downstream movement of juveniles is relevant at the population level. Previous extrapolations from juvenile drift data in this study system suggested that massive numbers of juveniles are transported downstream of the weir with estimates ranging from 18% (7.5 million juveniles from the 1965 brood) to 67% (2.5 million juveniles from the 2015 brood) of total production in the lower Babine River (Clarke and Smith 1972; LBNF, unpublished data). While uncertain, these estimates represent a potentially substantial loss for this population, particularly relevant given the conservation concern for Babine River sockeye (Cox-Rogers and Spilsted 2012). The Lower Babine River population has decreased by approximately 85% since the 1950s, with two counts of less than 2000 spawners in the last ten years (Department of Fisheries and Oceans Canada 2018). Further investigation of the functionality of the lake outlet and hydrological processes related to the timing of emergence and quality of rearing habitat, may contribute to further understanding of the basin-wide decreases and listed status of this at-risk population.

Given the potential linkage between hydrology and habitat connectivity, it is worth considering how the hydrology may be shifting in this system over time. Hydrograph records from the Babine River reveal changing discharge patterns in the watershed, likely due to climate variability and land use change (Fig. 6). Peak discharge date is shifting earlier since monitoring began in the early 1970s (Online Resource Fig. S1). This earlier shift is towards the timing of present-day juvenile emergence. It is unknown whether the timing of juvenile emergence is shifting such as due to shifts in spawning phenology (Online Resource Fig. S2) or incubation



**Fig. 6** Historical daily average discharge in the Lower Babine River at the outlet of Nilkitkwa Lake, British Columbia, Canada, from 1972 to 2018. Data collected at the Water survey of Canada station located approximately 50 m downstream of the adult enumeration weir. Observed period of juvenile emergence and migration generally between May 1st and August 1st. Gap in 2018 data due to inoperability of monitoring station during wildfires

temperatures. In addition, large magnitude spring freshet events have increased in frequency; specifically, peak annual discharge events above 200

$\text{m}^3 \cdot \text{s}^{-1}$  occurred only twice during the first half of the monitoring record but have occurred 7 times in the latter half. Thus, ongoing hydrologic change may increase challenges to juvenile sockeye salmon in the lake-outlet reach of Babine River. These shifts in hydrology are likely driven by a combination of climate change and land-use activities. Mean annual temperatures and precipitation in the Babine watershed have increased by 0.8 °C and 5.2%, respectively, over the past century (Foord 2016). Projections for the Babine watershed for 2055 (the Nadina sub-region within the Skeena Resource Region) estimate a further 3.2 °C increase in mean annual temperature, a 5.1% increase in mean annual precipitation, along with an 8.2% increase in spring precipitation (Foord 2016). Concurrently, industrial activities such as those associated with timber harvest and transportation infrastructure, have been expanding in the watershed, which has been shown to decrease river discharge but also increase peak flow in snowmelt-dominated watersheds (Neary 2017). In the Babine watershed, the percentage impacted area from anthropogenic land-use including transportation infrastructure, forestry, mining, and energy development is 22.8%, exceeding the high-risk threshold put forth by the Pacific Salmon Foundation's Sockeye Habitat Assessment Project (J. Pfalz, Eclipse Geomatics, unpublished data). Thus, hydrologic change, as controlled by climate and land use change, may decrease the productivity of sockeye populations in lake outlet habitats.

Species with complex life cycles rely on different habitat types at different life stages. Ontogenetic habitat shifts enable species to thrive in complex habitat mosaics. While our study focused on a single lake-outlet system and the implications of its configuration and conditions, it raises the broader challenge of understanding arrangement and connectivity in habitat complexes. We highlight that habitats may shift from bidirectional corridors to one-way travel routes; these systems may be particularly sensitive to anthropogenic perturbations and climatic change. Indeed, within complex landscapes and life cycles, the conditions and configuration of a specific location could have population-level effects. For example, key stopover habitats used by long-distance migratory birds have been shown to act as nutritional, energetic and disease-risk bottlenecks, with influence on body condition and population dynamics (e.g., survival and reproduction; Buehler and Piersma 2008).

At the intersection of landscape ecology and fish biology, understanding the dynamics of such key habitats is increasingly important in an era of global change.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10641-021-01071-1>.

**Acknowledgements** This research is part of a collaboration between Lake Babine Nation Fisheries Department and Simon Fraser University. The authors would like to thank Angel Marlowe, Fern Marlowe, Christie West, Clifford Aslin, and Peter Greene for field and logistical support. We would like to thank David Patterson and his research group, of Fisheries and Oceans Canada, for supporting laboratory analyses. We would like to thank the Lake Babine Nation Fisheries Department, Tides Canada, and the Pacific Salmon Foundation for funding this work. We also thank the Skeena Watershed Conservation Coalition, the Skeena Wild Conservation Trust, the Liber Ero Foundation, Billy Labonte and Babine Norlakes, the Salmon Watersheds Lab, and the Earth to Ocean Research Group for making this research possible.

#### Declarations

**Compliance with ethical standards** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the Canadian Council on Animal Care and the Simon Fraser University Animal Care Committee (protocols 1129B-14, 1158B-11, and 1158B-11-23).

#### References

- Adkison MD, Ward MB, Quinn TP (2014) Nest site preference and intrasexual competition in female sockeye salmon, *Oncorhynchus nerka*. *Environ Biol Fish* 97(4):385–399
- Andrew FJ, Geen GH (1960) Sockeye and pink salmon production in relation to proposed dams on the Fraser River system. *International Pacific Salmon Commission Bulletin* XI: 259p
- Armstrong JD (1997) Self-thinning in juvenile sea trout and other salmonid fishes revisited. *J Anim Ecol* 66:519–526
- Beamish RJ, Mahnken C (2001) A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Prog Oceanog* 49: 423–437
- Beamish RJ, Mahnken C, Neville CM (2004) Evidence that reduced early marine growth is associated with lower marine survival of Coho Salmon. *Trans Am Fish Soc* 133:26–33

- Buehler DM, Piersma T (2008) Travelling on a budget: predictions and ecological evidence for bottlenecks in the annual cycle of long-distance migrants. *Phil Trans R Soc B* 363:247–266
- Brannon EL (1967) Genetic control of migrating behaviour of newly emerged sockeye salmon fry. International Pacific Salmon Commission Progress report no. 16. New Westminster, Canada
- Brannon EL (1972) Mechanisms controlling migration of sockeye salmon fry. International Pacific Salmon fisheries commission. Bulletin XXI, New Westminster, Canada
- Brett JR (1971) Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am Zool* 11:99–113
- Brett JR, Hollands M, Alderdice DF (1958) The effect of temperature on the cruising speed of young sockeye and coho salmon. *J Fish Res Board Can* 15(4):587–605
- British Columbia Ministry of the Environment (BCMOE) (2009) Manual of British Columbia Hydrometric Standards. Version 1.0. British Columbia Ministry of the Environment, Science and Information Branch, for the Resource Inventory Standards Committee. Victoria, British Columbia
- Brown JA, Srivastava RK (1991) The biochemical characteristics and hatching performance of cultured and wild Atlantic salmon. *Can J Zool* 69(9):2436–2441
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference. Springer, New York
- Burnham KP, Anderson DR (1998) Model selection and inference a practical information-theoretic approach. Springer, New York
- Byrne JE (1971) Photoperiodic activity changes in juvenile sockeye salmon (*Oncorhynchus nerka*). *Can J Zool* 49: 1155–1158
- Claiborne AM, Fisher JP, Hayes SA, Emmett RL (2011) Size at release, size-selective mortality, and age of maturity of Willamette River hatchery yearling Chinook Salmon. *Trans Am Fish Soc* 140:1135–1144
- Clarke WC (1967) Observations on the migration of sockeye salmon fry in the lower Babine River. Thesis, University of British Columbia
- Clarke WC, Smith HD (1972) Observations on the migration of sockeye salmon fry (*Oncorhynchus nerka*) in the lower Babine River. *J Fish Res Board Can* 29(1):151–159
- Cooperman MS, Markle DF, Terwilliger M, Simon DC (2009) A production estimate approach to analyze habitat and weather effects on recruitment of two endangered freshwater fish. *Can J Fish Aquat Sci* 67:28–41
- Cox-Rogers S, Spilsted B (2012) Update assessment of sockeye salmon production from Babine Lake. British Columbia Can Tech Rep Fish Aquat Sci 2956:65p
- Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv Mar Biol* 26:249–293
- Department of Fisheries and Oceans Canada (DFO; Pacific Region) (2018) New Salmon Escapement Database System (NuSEDS). [internet] <https://open.canada.ca/data/en/dataset/c48669a3-045b-400d-b730-48aaf8c5ee6>
- Dunning JB, Danielson BJ, Pulliam HR (1992) Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–175
- Elliott JM (1989) The critical period concept and its relevance for population regulation in young sea trout. *J Fish Biol* 35:91–98
- Einum S, Fleming IA (2000) Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution* 54:628–639
- Fagan WF (2002) Connectivity, fragmentation and extinction risk in dendritic metapopulations. *Ecology* 83:3243–3249
- Fausch KD, Torgersen CE, Baxter CV, Li HW (2002) Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. *Bioscience* 52:483–498
- Foord V (2016) Climate patterns, trends, and projections for the Omineca, Skeena, and northeast natural resource regions, British Columbia. British Columbia Ministry of Forests, Lands and Natural Resource Operations, Omineca region. Prince George, British Columbia
- Fry FEJ (1947) Effects of the environment on animal activity. *Publ Ontario Fish Res Lab* 68:1–62
- Gibson ES, Fry FEJ (1954) The performance of lake trout, *Salvelinus namaycush*, at various levels of temperature and oxygen pressure. *Can J Zool* 32:252–260
- Gilbert CH (1913) Age at maturity of the Pacific coast salmon of the genus *Oncorhynchus*. *Ann Rep Brit Col Fish Dep* 1912: 57–70
- Griffiths JS, Alderdice DF (1972) Effects of acclimation and acute temperature experience on the swimming speed of juvenile coho salmon. *J Fish Res Board Can* 29(3):251–264
- Hartman GF, Northcote TG, Lindsey CC (1962) Comparison of inlet and outlet spawning runs of rainbow trout in loon Lake, British Columbia. *J Fish Res Board Can* 19:173–200
- Heinimaa S, Heinimaa P (2004) Effect of the female size on egg quality and fecundity of the wild Atlantic salmon in the sub-arctic river Tenö. *Boreal Environ Res* 9:55–62
- Hermoso V, Ward DP, Kennard MJ (2012) Using water residency time to enhance spatio-temporal connectivity for conservation planning in seasonally dynamic freshwater ecosystems. *J Appl Ecol* 49:1028–1035
- Hoar WS (1958) The evolution of migratory behaviour among juvenile salmon of the genus *Oncorhynchus*. *J Fish Res Board Can* 15(3):391–428
- Jobling M (1985) Growth. In: Tytler P, Calow P (eds) *Fish energetics: new perspectives*. Croom & Helm, London, pp 213–230
- Jorgensen B (1988) Metabolic costs of growth and maintenance in the toad, *Bufo bufo*. *J Exp Biol* 138:319–331
- Killick SR (1949) A study of the embryonic development and fry behaviour of sockeye salmon in the South Thompson district. Thesis, University of British Columbia
- Markle DF, Reithel SA, Crandall J, Wood T, Tyler TJ, Terwilliger M, Simon DC (2009) Larval fish transport and retention and the importance of location for juvenile fish recruitment in upper Klamath Lake, Oregon. *Trans Am Fish Soc* 138:328–347
- McDonald J, Hume JM (1984) Babine Lake sockeye salmon (*Oncorhynchus nerka*) enhancement program: testing some major assumptions. *Can J Fish Aquat Sci* 41:70–92
- McCart P (1967) Behaviour and ecology of sockeye salmon fry in the Babine River. *J Fish Res Board Can* 24(2):357–428
- Moore JW, Gordon J, Carr-Harris C, Gottesfeld AS, Wilson SM, Russell JH (2016) Assessing estuaries as stopover habitats for juvenile Pacific salmon. *Mar Ecol Prog Ser* 559:201–215

- Moss JH, Beauchamp DA, Cross AD, Myers KW, Farley EV, Murphy JM, Helle JH (2005) Evidence for size-selective mortality after the first summer of ocean growth by pink Salmon. *Trans Am Fish Soc* 134:1313–1322
- Neary DG (2017) Forest management and water in the United States. In: Garcia-Chevesich PA, Neary DG, Scott DF, Benyon RG, Reyna T (eds) Forest management and the impact on water resources: a review of 13 countries. United Nations Educational, Scientific and Cultural Organization, Paris, pp 181–198
- Pearcy WG (1992) Ocean ecology of the North Pacific salmonids. University of Washington Press, Seattle
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RC (2009) Nlme: linear and nonlinear mixed effects models. Available from <http://cran.r-project.org/web/packages/nlme/index.html>
- R Development Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org>
- Raleigh RF (1971) Innate control of migrations of salmon and trout fry from natal gravels to rearing areas. *Ecology* 52(2): 291–297
- Schlösser IJ (1995) Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia* 303:71–81
- Semko RS (1954) The stocks of West Kamchatka salmon and their commercial utilization. *Izvestiia TINRO* 41:3-109. [in Russian; English translation: fish res board can translation series no. 288, 1960]
- Skoglund H, Einum S, Forseth T, Barlaup BJ (2011) Phenotypic plasticity in physiological status at emergence from nests as a response to temperature in Atlantic salmon (*Salmo salar*). *Can J Fish Aquat Sci* 68:1470–1479
- Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *J Am Stat Assoc* 99:262–278
- Strayer DL, Findlay SEG (2010) Ecology of freshwater shore zones. *Aquat Sci* 72:127–163
- Thompson JN, Beachamp DA (2014) Size-selective mortality of steelhead during freshwater and marine life stages related to freshwater growth in the Skagit River, Washington. *Trans Am Fish Soc* 143:910–925
- Underwood AJ, Fairweather PG (1989) Supply side ecology and benthic marine ecology. *Trends Ecol Evol* 4:16–20
- West CJ, Larkin PA (1987) Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. *Can J Fish Aquat Sci* 44:712–721
- West CJ, Mason JC (1987) Evaluation of sockeye salmon (*Oncorhynchus nerka*) production from Babine Lake Development project. In: Smith HD, Margolis L, Wood CC (eds) Sockeye salmon (*Oncorhynchus nerka*) population biology and management, *Can spec pub fish Aquat Sci*, vol 96, pp 176–190
- Wiens JA (2002) Riverine landscapes: taking landscape ecology into the water. *Freshw Biol* 47:501–515
- Wood CC, Rutherford D, Bailey D, Jakubowski M (1998) Assessment of sockeye salmon production in Babine Lake, British Columbia with forecast for 1998. *Can Tech Rep Fish Aquat Sci* 2241:50p
- Zabel RW, Achord S (2004) Relating size of juveniles to survival within and among populations of Chinook Salmon. *Ecology* 85:795–806
- Zuur AF (2009) Mixed effects models and extensions in ecology with R. Springer, New York

**Publisher's note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.