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Incorporating lakes in stream fish habitat models: are we missing a key landscape attribute?

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Abstract

Although lakes and rivers are intimately connected, more effort is needed to develop conceptual approaches accounting for lake-stream interactions within the drainage network. Lakes can buffer the impacts of environmental variability in streams and facilitate stream fish recolonization processes. However, lakes have rarely been incorporated in habitat models for stream fish. We examine whether including the presence of lakes in habitat models can improve our understanding of brook trout (*Salvelinus fontinalis*) abundance in streams. We quantified brook trout relative abundance in 36 streams over three consecutive years by single-pass electrofishing. Relative abundance of brook trout in streams was greatest when lakes were present in the stream network. Lakes had greater influence on relative abundance in headwater streams than in larger streams. These results emphasize the importance of considering lakes as a critical attribute in landscape fish habitat models, many of which focus on terrestrial landscape variables. We discuss potential gains from incorporating the presence of lakes in (i) multiscale habitat models, (ii) analyses of spatio-temporal distribution of thermal refuges, and (iii) metrics of habitat connectivity in lake-stream networks.

Keywords: connectivity, environmental heterogeneity, landscape configuration, patch dynamics, riverscape.

Résumé

Bien que les lacs et les rivières soient intimement connectés, des efforts sont nécessaires pour développer des approches conceptuelles représentant les interactions lac-cours d'eau au sein du réseau de drainage. Les lacs peuvent atténuer les impacts de la variabilité environnementale dans les cours d'eau et faciliter les processus de recolonisation des poissons. Toutefois, les lacs ont rarement été incorporés dans les modèles d'habitat de poissons de cours d'eau. Nous examinons

37 si l'inclusion de la présence des lacs dans les modèles d'habitat peut améliorer notre
38 compréhension de l'abondance de l'omble de fontaine (*Salvelinus fontinalis*) dans les cours
39 d'eau. Nous avons quantifié l'abondance relative de l'omble de fontaine dans 36 cours d'eau
40 pendant trois années consécutives par des passes uniques de pêche électrique. L'abondance
41 relative de l'omble de fontaine dans les cours d'eau était supérieure lorsque les lacs étaient
42 présents dans le réseau hydrographique. Les lacs avaient une plus grande influence sur
43 l'abondance relative dans les cours d'eau de tête que dans les cours d'eau plus larges. Ces
44 résultats mettent l'accent sur l'importance de considérer les lacs comme attribut essentiel des
45 modèles d'habitat du poisson à l'échelle du paysage, dont beaucoup se concentrent sur des
46 variables terrestres du paysage. Nous discutons des gains potentiels d'incorporer la présence des
47 lacs dans (i) les modèles d'habitat multi-échelles, (ii) l'analyse de la distribution spatio-
48 temporelle des refuges thermiques, et (iii) les métriques de connectivité d'habitat dans les
49 réseaux lac-cours d'eau.

Introduction

Contrary to the first description of the river continuum concept (Vannote et al. 1980), there is now substantial evidence that spatial discontinuity in physical variables (e.g., tributary junctions, breaks in stream slopes, lentic-lotic interfaces) shapes the distribution and abundance of fish along stream and river networks (Fausch 2002; Wiens 2002; Benda et al. 2004; Fernandes et al. 2004; Winemiller et al. 2010). Although lakes and rivers are intimately connected, more effort is needed to develop conceptual approaches that account for lake-stream interactions within the drainage network (Soranno et al. 1999; Jones 2010; Wurtsbaugh et al. 2015). A first challenge is to promote integration between the divergent approaches used to study fish production in lakes and in rivers (Wurtsbaugh et al. 2015). A second challenge is to incorporate lakes in stream fish habitat models that traditionally focus on local stream variables or on terrestrial variables at larger scales. The landscape perspective inherent in approaches such as the patch dynamic and flood pulse concepts (Pringle et al. 1988; Junk et al. 1989) offers a convenient conceptual framework for describing the spatio-temporal heterogeneity and connectivity of stream and lake habitats to which fish species respond throughout the life cycle (Tockner et al. 2000; Winemiller et al. 2010).

Local environmental features are commonly used as predictors in stream fish habitat models (e.g., Bardonnnet and Baglinière 2000; Bouchard and Boisclair 2008; De Kerckhove et al. 2008; Knouft et al. 2011). At a larger spatial scale, landscape features, including land use (forest cover, agriculture, urban areas), geology (soil type) and topographical variables (stream slope, valley shape), are also commonly used as predictors of the abundance and distribution of stream fish populations (Fausch et al. 1994; Steel et al. 2004; Deschênes et al. 2007; Kanno et al. 2015). Since all of these landscape features indirectly affect production in streams via hydrological transport and storage of nutrients or sediments, these models are valuable tools for stream fish

management. However, previous studies have not placed much emphasis on the presence of lakes to explain fish abundance and distribution in stream networks. The integration of lakes in stream fish habitat models should be useful in geographical areas where lakes are natural components of the drainage network. Extensive areas within the range of brook trout (*Salvelinus fontinalis*), such as Eastern North America, have particularly high areal density of lakes (Downing et al. 2006). The presence of lakes can be particularly relevant to population persistence under harsh conditions, such as peak river flows, temperature extremes, or drought (Giller and Malmqvist 1998). In stream networks characterized by strong environmental variability (e.g., those associated with headwater streams; Schlosser 1995), lakes could act as refuges for source populations, buffering the impacts of environmental variability and facilitating fish recolonization of the stream network after disturbance (Giller and Malmqvist 1998; Adams et al. 2001; Bertolo et al. 2008). Buffering the impacts of environmental variability is particularly important in the context of climate change because extreme weather events are expected to occur more frequently in the future (Easterling et al. 2000; Acuña et al. 2014). Lakes can also increase the downstream food supply and contribute to stream fish growth and production (Haraldstad et al. 1987; Giller and Malmqvist 1998). Food subsidies from lakes may thus influence the distribution and abundance of fish at downstream sites. However, negative impacts of lakes could arise in stream-lake networks where stream fish species live in sympatry with lake predators. In this case, lakes could act as a sink by limiting recruitment or reducing adult survival (Hesthagen et al. 2015; Sandlund et al. 2016).

The main objective of our study was to determine whether the inclusion of lake presence as a landscape attribute can improve our understanding of fish abundance in streams. We use native brook trout populations in the Laurentian physiographic region where lakes are common landscape features of the drainage network (Fig. 1) and the species mainly lives in allopatry

(Pépino et al. 2012). We hypothesized that brook trout abundance should be greater when lakes are present in the stream network. Based on our results, we discuss potential gains from incorporating the presence of lakes in (i) multiscale habitat models, (ii) analyses of the spatio-temporal distribution of thermal refuges, and (iii) metrics of habitat connectivity within stream-lake networks.

Methods

The study was conducted in the Jacques-Cartier National Park and the Laurentides Wildlife Reserve (Québec, Canada), which are located at relatively high latitude (47° N) and moderately high elevation (750 m asl) in the Laurentian Plateau. This area has a humid continental climate with harsh winters (mean annual temperature: 0.3 °C; annual snowfall: 639 cm). Fish relative abundance was quantified in three consecutive years (2006-2008) at 212 stream sections distributed among 37 reaches in 36 streams (Strahler order 1-3; median stream length = 3.0 km). We defined a stream configuration variable based on the presence of lakes (surface area > 0.5 ha) in the drainage network (Fig. 2). Among the 36 streams, 11 are not connected to a lake (stream configuration coded as “SS”), 7 are lake tributaries (“SL”), 14 are lake outlets (“LS”), and 4 are both tributary and outlet (“LL”). The streams are distributed along a 157-km stretch of the 73/175 Highway (Fig. 1; Pépino et al. 2012). Fish were captured by single-pass electrofishing in an upstream direction within open stream sections. Sections were 25 m in length (mean section area = 96.2 m²). Brook trout were present in all streams, accounted for 91.9 % (10 653 individuals) of all fish captured, and were relatively small (median [25% - 75%]: 73.65mm [62.21 – 94.09mm] in SS; 77.26mm [63.97 – 78.89mm] in SL; 80.97mm [74.67 – 86.92mm] in LS; 69.81mm [58.21 – 86.69mm] in LL). Further details are provided in Pépino et al. (2012).

We used generalized linear mixed models (GLMM) to relate brook trout counts to stream configuration (Pépino et al. 2012). All models assumed an underlying negative binomial distribution, included area of the stream section (m^2 ; $\log_e$ -transformed) as an offset, and had a constant (intercept) term, as well as random terms for year, reach, and section. Use of area as an offset in the model focuses the analysis on relative population density rather than counts. We compared competing models including various combinations of stream configuration (with “SS” as reference category), mean stream width (m; standardized after $\log_e$ -transform), and an interaction between stream configuration and stream width. Comparisons were based on Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Local habitat descriptors, such as woody debris, temperature, depth, and groundwater flow, can be useful predictors of brook trout abundance in streams (Deschênes and Rodríguez 2007; Guillemette et al. 2011; Kanno et al. 2012; Kratzer and Warren 2013). Therefore, we attempted to improve the fit of the best-performing model by inclusion of local habitat descriptors (water temperature, depth, and large woody debris) as covariates. Large woody debris was defined as the number of submerged trees > 10 cm in diameter. Depth and large woody debris were $\log_e$ -transformed to reduce the influence of outliers. All variables were z-standardized to facilitate comparison of variable effects. GLMM analyses were performed using the glmmADMB package in R (R Development Core Team 2014).

Results

The best-performing model included stream configuration, stream width, and the interaction between stream configuration and stream width (model 4; Table 1). The model indicated that brook trout relative abundance was negatively related to stream width and was greater in the “SL”, “LS”, and “LL” stream configurations than in the “SS” configuration (Figs. 3 and 4). The

interaction between stream configuration and stream width showed that the effect of stream width was more pronounced when a lake was present upstream and that differences among stream configurations increased as stream width declined (Figs. 3 and 4). The best overall model was not improved by inclusion of local habitat variables, which reduced AIC by < 0.7 units (Appendix A1). Similar results were obtained for biomass (Appendix A2). Temperature was positively related to brook trout biomass and marginally improved model fit compared to the best-performing model (model 4; temperature reduced the AIC by 2.8 units).

Discussion

Our results showed that relative abundance of stream-dwelling brook trout was greatest when lakes were present in the stream network. Differences in relative abundance among configurations were greater in small streams, suggesting that lakes have greater influence on relative abundance in headwater streams than in larger ones. The negative relationship between brook trout relative abundance and stream width presumably reflects the well-known preference of brook trout for headwater streams (Petty et al. 2005; Utz and Hartman 2006). These results underscore the importance of considering lakes as a critical attribute in landscape fish habitat models, many of which currently focus on terrestrial landscape variables (Steel et al. 2004; Firman et al. 2011; but see Kanno et al. 2015). We observed that biomass, another metric of stream productivity, provided similar insights on the role of lakes for brook trout populations in the drainage network. However, full demographic analyses including biological processes such as size-structure, survival, recruitment and growth would be required to assess the sustainability of fish populations (Kanno et al. 2014a; Letcher et al. 2015; Bassar et al. 2016). Quantifying movements between streams and lakes would also contribute to understand fish population dynamics, characterise alternative life history strategies, and attain best management practices in

169 stream-lake networks (Curry et al. 2002; Addison and Wilson 2010; Landsman et al. 2011;
170 Ppino et al. 2015).

171 Connectivity between streams and lakes could confer multiple benefits on brook trout
172 populations (e.g., Cossette and Rodrguez 2004). First, lake tributaries and outlets are
173 preferential spawning habitats for lacustrine brook trout (Josephson and Youngs 1996;
174 Guillemette et al. 2011). As the spatial distribution of young-of-the-year in salmonids is mainly
175 related to that of spawning sites (Beland 1996; Hudy et al. 2010), increased brook trout
176 abundance in streams could reflect the use of streams as rearing habitat by lacustrine populations
177 that preferentially spawn in streams. Second, lake tributaries offer thermal refuge when
178 temperature rises in the littoral zone of the lake. Brook trout have been observed to emigrate
179 from the lake in mid-summer and aggregate in small inlet streams where groundwater dominates
180 base flows (Curry et al. 1997). Increased brook trout abundance in lake tributaries could
181 therefore result from behavioral thermoregulation. However, this mechanism cannot explain why
182 abundance was greater in lake outlets (“LS” stream configuration) than in streams without a
183 connection to a lake (“SS”). Third, connectivity between lake and stream environments could
184 provide ready access to better habitat for summer growth or overwinter survival in the lake at
185 low migration cost compared to an anadromous life strategy, as well as reduced predation and
186 competition from adult individuals for juveniles in stream habitats (Harvey and Stewart 1991;
187 Jardine et al. 2005; Bohlin et al. 2001; Robillard et al. 2011; Velez-Espino et al. 2013). Finally,
188 the presence of lakes in the river network could increase stream productivity downstream of the
189 lake, where stream benthic invertebrates filter plankton of lake origin (Giller and Malmqvist
190 1998). This trophic contribution, which can persist for several kilometers downstream from the
191 lake, is particularly important in small streams where autochthonous productivity is low and fish
192 feed primarily from allochthonous sources (Kawaguchi et al. 2003; Utz and Hartman 2006).

Accounting for the presence of lakes in the stream network can help attain a more complete understanding of stream-dwelling populations. Our results have potential implications for two research areas in which the role of lakes is currently underappreciated: spatio-temporal distribution of thermal refuges for cold-stenothermic fish species facing climate change and habitat connectivity metrics in stream-lake networks (Fig. 2). Most studies on spatial distribution of thermal refuges in the riverscape focus on topographic landscape metrics describing groundwater processes and identifying tributary confluences as hotspots for thermal refuges (Dugdale et al. 2015; Kurylyk et al. 2015). Inputs from groundwater and mountain streams can help stabilize thermal regimes in the face of climate change and also contribute to the spatial heterogeneity of thermal refuges within the riverscape (Kanno et al. 2014b; Snyder et al. 2015; Isaak et al. 2016). In stratified lakes, the metalimnion spans a wide range of temperatures and can act as a thermal refuge in summer as well (Goyer et al. 2014). Furthermore, lake surface temperature influences the thermal regime of the lake outlet and can stabilize stream temperature. Lake thermal responses to climate change are expected to depend on lake morphometry (Kraemer et al. 2015; O'Reilly et al. 2015); therefore, incorporating lake attributes should improve model projections of spatial heterogeneity in stream temperature (e.g., Armstrong et al. 2013; Isaak et al. 2015). Importantly, fish introductions into headwater lakes can boost the invasion of stream networks by nonnative fishes (Adams et al. 2001; Fig. 2), and may, by the same token, enhance recolonization of otherwise inaccessible portions of a stream network (Fausch et al. 2009). Connectivity indices integrating life history strategies and landscape habitat models have been developed to prioritize barrier removal in stream networks (Steel et al. 2004; Cote et al. 2009; Chelgren and Dunham 2015). However, most of these indices do not take into account the presence of lakes that provide critical habitats for migrant species and modify stream habitat suitability, as previously discussed. Incorporating lakes as key

elements of the spatial configuration of habitat suitability would improve our understanding of the role of fragmentation and dispersal in shaping the distribution of fishes in stream networks (Radinger and Wolter 2015).

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Table 1. AIC-based comparison of four candidate GLMM of stream-dwelling brook trout relative abundance. The number of model parameters (K), Akaike Information Criterion (AIC), and difference in AIC relative to the best-performing model (ΔAIC) are presented. Model terms are: SC, stream configuration (see Fig. 1); W, stream width (m; z-standardized after $\log_e$ -transform).

Model	Fixed effects	K	AIC	ΔAIC
1	W	6	4299.9	8.9
2	SC	8	4356.8	65.8
3	W + SC	9	4296.9	5.9
4	W + SC + W $\times$ SC	12	4291.0	0.0

Figure Captions

Figure 1. Map showing the position of the 36 study streams in the drainage network (Québec, Canada). Symbols refer to stream configuration (see Fig. 2 for details). Streams (light grey) and water bodies (dark) are shown. Source data: BNDTQ (Base Nationale de Données Topographiques; 1: 50 000).

Figure 2. Schematic representation of various stream configurations, from source to mouth. a) SS: no lake upstream or downstream; SL: no lake upstream but lake present downstream; LS: lake present upstream and stream confluence downstream; LL: lake present upstream and downstream. b) Influence of lakes on habitat connectivity indices. Broken lines: barrier; arrows: fish recolonization path. Rectangles represent accessible (black) and inaccessible (grey) stream habitats. Dams can be seen as a specific case of a barrier to fish passage which is adjacent to a (man-made) lake upstream of the barrier. c) Influence of lakes on the spatial distribution of thermal refuges. Rectangles represent temperature gradients (coolest: white; warmest: black). For simplicity, longitudinal variation in stream temperature in the absence of headwater lakes is not shown (see text).

Figure 3. Regression estimates for the best-performing model for brook trout relative abundance (model 4; Table 1). Lines represent one (thick) and two (thin) standard deviation intervals. SS: no lake upstream or downstream (reference category); SL: no lake upstream but lake present downstream; LS: lake present upstream and stream confluence downstream; LL: lake present upstream and downstream; W: stream width (m; standardized after $\log_e$ -transform).

466 **Figure 4.** Relationship between brook trout abundance and stream width, by stream
467 configuration. Observed values (grey crosses), fitted values from best-performing model (model
468 4; black solid lines) and 95% confidence intervals (black dotted lines) are shown. SS: no lake
469 upstream or downstream; SL: no lake upstream but lake present downstream; LS: lake present
470 upstream and stream confluence downstream; LL: lake present upstream and downstream. Mean
471 stream width is 3.9 m.

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Figure 1

Figure 2

Figure 3

Figure 4

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Appendix A1. Regression estimates for the best-performing model for brook trout abundance with further inclusion of local habitat variables. Lines represent one (thick) and two (thin) standard deviation intervals. SS: no lake upstream or downstream (reference category); SL: no lake upstream but lake present downstream; LS: lake present upstream and stream confluence downstream; LL: lake present upstream and downstream; W: stream width (m; z-standardized after $\log_e$ -transform); Temp.: temperature ($^{\circ}\text{C}$; z-standardized); Depth (m; z-standardized after $\log_e$ -transform); Wood: large woody debris index (counts; z-standardized after $(\log_e+1)$ -transform).

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Figure A1

Appendix A2. Regression estimates for the best-performing model for brook trout biomass with further inclusion of local habitat variables. Lines represent one (thick) and two (thin) standard deviation intervals. SS: no lake upstream or downstream (reference category); SL: no lake upstream but lake present downstream; LS: lake present upstream and stream confluence downstream; LL: lake present upstream and downstream; W: stream width (m; z-standardized after $\log_e$ -transform); Temp.: temperature ($^{\circ}\text{C}$; z-standardized); Depth (m; z-standardized after $\log_e$ -transform); Wood: large woody debris index (counts; z-standardized after $(\log_e+1)$ -transform). Biomass data were available for the last two years only. Biomass data were expressed in $\text{g}\cdot 100^{-1}\text{m}^{-2}$ and were $(\log_e+1)$ -transformed before analyses. All models assumed an underlying Gaussian distribution of errors and had a constant (intercept) term, as well as random terms for year, reach, and section.

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Figure A2