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ARTICLE

Optimization of temporal versus spatial replication in the development of habitat use models to explain among-reach variations of fish density estimates in rivers

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Abstract: We evaluated the effects of temporal variation of fish density estimates on the explanatory power of habitat use models. Fish density estimates were obtained using visual surveys (10 visits) in eighteen 100 m reaches over a 7-week period. Physical attributes of reaches were estimated. Field data were used to develop a simulation domain (10 000 reaches) that reflected the spatio-temporal variability of fish density estimates and physical attributes. Simulations indicated that for a sampling effort of approximately 200 surveys, the number of reaches surveyed (25 to 200) and the number of surveys per reach (1 to 8) affected the adjusted R^2 of models by 5% to 42%. The established practice of sampling a maximized number of reaches once did not appear necessarily optimal for developing habitat use models. Analysis of temporal coefficients of variation suggests that species within the same family may require a similar survey design. Hence, for salmonids, it may be more appropriate to sample more reaches once, and for cyprinids, it may be more optimal to repeatedly sample fewer reaches.

Résumé : Nous avons évalué l'effet de variations temporelles de la densité de poissons sur le pouvoir explicatif de modèles d'utilisation de l'habitat et les variables explicatives incluses dans ces modèles. Les densités d'espèces de poissons ont été estimées 10 fois dans dix-huit tronçons de 100 m durant 7 semaines de l'été 2007. Les caractéristiques physiques ont été documentées. Les données de terrain ont été utilisées pour développer un domaine de simulations (10 000 tronçons) reflétant la variabilité spatiale et temporelle des estimés de densités de poissons et la variabilité spatiale des caractéristiques des habitats. Des simulations ont indiqué que, pour un effort constant d'approximativement 200 inventaires, le nombre de tronçons échantillonnés (25 à 200) et le nombre d'inventaires par tronçon (1 à 8) ont affecté le R^2 ajusté des modèles par 5 à 42 %. Nos résultats suggèrent que la stratégie d'échantillonnage optimale diffère selon la famille d'appartenance de l'espèce. Pour certaines (salmonidés), il semble optimal d'échantillonner une seule fois un nombre maximal de sites. Pour d'autres (cyprinidés), il serait préférable d'échantillonner de façon répétée un nombre diminué de sites.

Introduction

Habitat loss has been recognized as a major threat to the survival of fish populations (Evans et al. 1996; Richter et al. 1997; Reed and Czech 2005). One objective of conservation biology is to identify key habitat attributes that should be preserved to ensure the survival of populations (Rosenfeld and Hatfield 2006). Habitat quality models are suitable tools to achieve this objective because they are, by definition, relationships between habitat use (fish presence or absence, density, biomass, etc.; Weaver et al. 1997; Rogers et al. 2005; Turgeon and Rodriguez 2005) or fitness indices (growth, survival, etc.; Brandt et al. 1992; Tyler and Brandt 2000; Boisclair 2001) and environmental conditions. Environmental conditions that explain a significant fraction of the variability of habitat quality indices (habitat use or fitness indices) are taken as key habitat attributes.

Optimal survey design to develop habitat use models explaining fish density variation among reaches should aim at maximizing the ratio of fish density variance among reaches (hereafter referred to as spatial variance) to fish density variance within reaches (hereafter referred to as temporal variance). Maximizing the spatial variance of fish density is generally achieved by maximizing the range of environmental conditions surveyed in a study area, thereby maximizing the number of reaches surveyed in this

area (Hughes et al. 2006). However, logistical constraints often imply that any reach is surveyed only once over a few months (e.g., Wiley et al. 2004; Turgeon and Rodriguez 2005) or a few years (e.g., Wang et al. 2006; Heitke et al. 2006; Infante et al. 2006). The design used by such studies presumes that it is preferable to survey a larger number of reaches once rather than a smaller number of reaches repeatedly. While this design maximizes the spatial variance of fish density, it does not provide any information about the magnitude of the temporal variance of fish density or about the effect of such variance on resulting habitat use models.

The temporal variance of fish density may be expected to depend on the size of the sampling units and on the time between two consecutive surveys. Although the temporal variance of fish density is rarely estimated, a number of studies suggest that for reaches that are within the size range often utilized by habitat use models (50–500 m reaches; Fausch et al. 2002; Hughes et al. 2006), fish density may be attributed to a variety of mechanisms operating within a few different temporal scales. Estimates of fish density and biomass obtained for a given reach may vary within a few hours because of changes in physical conditions, feeding opportunities, or predation risk (Hohausova et al. 2003; Girard et al. 2003; Bédard et al. 2005). Among-day to among-month temporal variations of fish density (Gowan et al. 1994; Schlosser 1998) may be related to physical conditions such as flow and water temper-
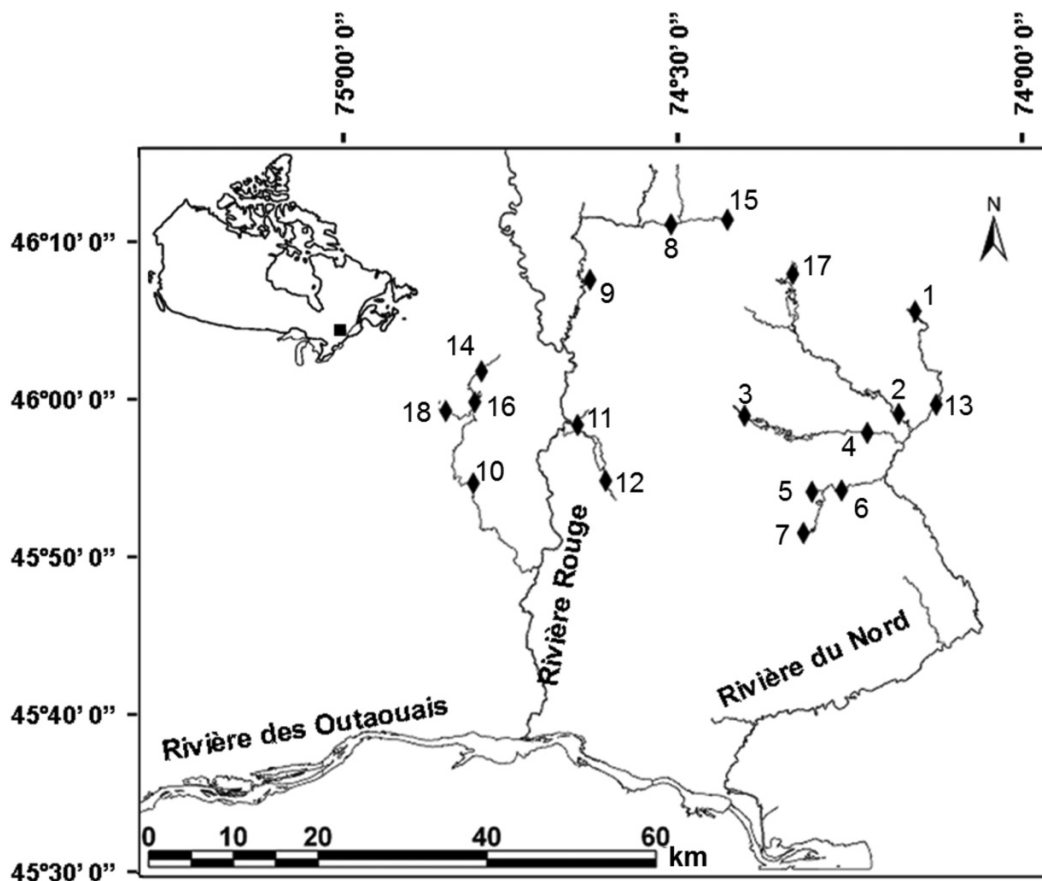
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Fig. 1. Distribution of the 18 reaches surveyed during summer 2007 in the watersheds of Rivière Rouge and Rivière du Nord, Quebec, Canada. Sites are identified by black diamonds.

ature (Grossman et al. 1998, 2010; Albanese et al. 2004) and to biological processes associated with predation and migration (Harvey 1991; Lucas and Baras 2001). Seasonal changes in fish density in reaches are generally associated with habitat shifts between summer feeding and overwintering habitats (Nickelson et al. 1992). Interactions between physical conditions and population dynamics may be invoked to explain among-year temporal variations in fish density (Lohr and Fausch 1997; Falke et al. 2010).

The temporal variance of fish density may be minimized by keeping time of day, season, year, meteorological conditions, flow conditions, and survey methods constant among surveys (Bouchard and Boisclair 2008). Despite these precautions, the temporal variance of fish density related to sampling errors and stochastic fish movements may jeopardize the development of operational statistical tools aimed at explaining variation of fish habitat use among reaches (Gowan et al. 1994; Young 1995). To date, the magnitude and the effects of temporal variance of fish density on habitat use models aimed at explaining spatial variations of fish density have never been assessed.

The objectives of this study are (*i*) to quantify the temporal variability of fish community characteristics estimated in a series of reaches surveyed under relatively standardized conditions (time of day, season, year, meteorological conditions, and survey method), (*ii*) to determine the effect of different survey designs (i.e., combinations of the number of reaches surveyed and the number of surveys per reach) on the explanatory power of habitat use models developed for different fish species to explain the spatial variation in fish density estimates (since variation of fish density estimates obtained in the field are, by definition, a combination of real fish density differences and observational errors), and (*iii*) to evaluate the effect of different survey designs on the

environmental conditions found to explain a statistically significant proportion of the variability of fish density estimates.

Materials and methods

We repeatedly surveyed fish community characteristics (10 temporal replicate estimates of fish density per species) and environmental conditions (1 to 10 times depending on the environmental condition) in 18 river reaches. The data were used for three purposes: first, to quantify the structure of the spatial and temporal variances of fish community characteristics and of environmental conditions; second, to estimate the co-variation among environmental conditions; and third, to use this information to simulate the effects on habitat use models of different trade-offs between the number of reaches surveyed (*r*) and the number of surveys per reach (*s*), for a constant total field effort (*r* × *s*).

Study area and survey reaches

Surveys were conducted in 18 reaches distributed within rivers of two adjacent watersheds (Rivière du Nord: Laurentian Region; Rivière Rouge: Outaouais Region) that flow into the Rivière des Outaouais (Fig. 1). The reaches surveyed measured 100 m along the length of the rivers. This length of reach was selected because it is commonly used to develop habitat use models in rivers (Zampella and Bunnell 1998; Diana et al. 2006; Moerke and Lamberti 2006; Bouchard and Boisclair 2008). Reaches were selected as follows. All road accesses to the rivers studied were identified and visited at random. At an access point, field crews would first walk upstream along the river over a maximum distance of 1 km (limit imposed by the need to transport equipment), and if no suitable reach was found, repeat the procedure walking 1 km downstream of the access point. A study reach was selected as the first 100 m

river section identified as relatively homogeneous. If no suitable reach was found within 1 km upstream or downstream of an access point, the reach was eliminated from the study design. Homogeneity of sites was determined using a classification of five habitat types: pool, run, riffle, glide, and cascade. To be considered homogeneous, the total length of the 100 m reach had to possess the physical characteristics of a single habitat type.

Fish community characteristics

Fish community characteristics within each reach were estimated 10 times between 16 June and 10 August 2007. Surveys for fish community characteristics were conducted between 1000 h and 1600 h and when cloud cover was ≤50% to minimize the potential effects of these variables on fish data (Bédard et al. 2005; Girard et al. 2003). Fish community characteristics were collected by underwater visual observations by three snorkelers trained continuously for at least 1 month prior to data collection to ensure accurate species identification, fish counts, and length assessment. Visual observation by snorkelers was selected as a survey method because (*i*) other methods such as seining and electrofishing could not be used in sites with high water velocities (>1 m·s⁻¹) or depths (≥150 cm), which minimizes the range of environmental conditions at which the observations could be conducted; (*ii*) electrofishing may injure or kill fish (Reynolds 1996; Cooke et al. 1998), particularly for rare species potentially present within the studied reaches (electrofishing 10 times in the same reach may exacerbate this effect and potentially affect estimates of temporal variance in fish density); (*iii*) as noted by Bayley and Dowling (1990), Reynolds (1996), Meador et al. (2003), and Kimmel and Argent (2006), electrofishing may have low capture efficiency, particularly for small fish that form the majority of the fish community that we studied; and (*iv*) numerous studies support the validity of visual surveys when estimating fish density in rivers and the existence of a strong correlation between visual and electrofishing or seining under conditions where both methods can be used (Goldstein 1978; Ensign et al. 1993; Mullner et al. 1998; Wildman and Neumann 2003; Jordan et al. 2008).

During visual surveys, one snorkeler was positioned in the thalweg (deepest part of the cross-section of the river) and the two others remained as close as possible to each shore, but at depths no shallower than 0.25 m. When no distinct thalweg could be identified, the central snorkeler was positioned in the middle of the river. Snorkelers progressed upstream to minimize fish disturbance and collected data on fish species and length observations along three transects: left shore, thalweg, and right shore. The area surveyed by the snorkelers covered 41% to 100% of the total surface of each reach (range of mean river width: 7.4–22.1 m) and was considered to encompass the complete range of environmental conditions present within a reach. Snorkelers wore white polystyrene tubes on their forearm to note the number of fish observed by species. Fish < 5 cm in total length were excluded from surveys because their density at a location was expected to be more closely associated with the presence of a spawning site rather than with habitat selection. In each reach, snorkelers noted the visible distance (by 25 cm classes), on either side, at which fish could be counted and identified with certainty and limited their observations to such distances. The sum of these distances defined the width surveyed, whereby fish species density estimates (abundances·m⁻²) were calculated for each 100 m reach.

All statistical analyses were performed using R Language (R Development Core Team 2009). A partition of variance was performed for each fish species to compare spatial and temporal variances of fish density estimates (package vegan, procedure varpart; Oksanen et al. 2010). Variances of fish density estimates were compared among species and among reaches using the spatial and the temporal coefficients of variation (CVs) of fish density estimates. CVs were used to remove the effect of different mean

fish densities on comparisons of spatial or temporal variances. To calculate the different CVs, the mean density for each species in each reach for the 10 surveys (M_S; fish·m⁻²) was used. M_S was obtained by

$$(1) \qquad M_S = \frac{\sum_{i=1}^{10} FD_t}{10}$$

where FD_t (fish·m⁻²) is the density of a species at the time of survey t, and 10 is the number of surveys conducted per reach. Mean fish density for each species across the 18 reaches (M_{FD}; fish·m⁻²) was also calculated, using the following formula:

$$(2) \qquad M_{FD} = \frac{\sum_{i=1}^{18} M_S}{18}$$

where 18 is the number of reaches surveyed. A single spatial coefficient of variation of fish density estimates (SCV) was then calculated for each species as

$$(3) \qquad SCV = \frac{SD_{FD}}{M_{FD}}$$

where SD_{FD} is the standard deviation of M_S (the 18 values of mean fish density estimates). Finally, 18 temporal coefficients of variation of fish density estimates (TCV) were obtained for each fish species as
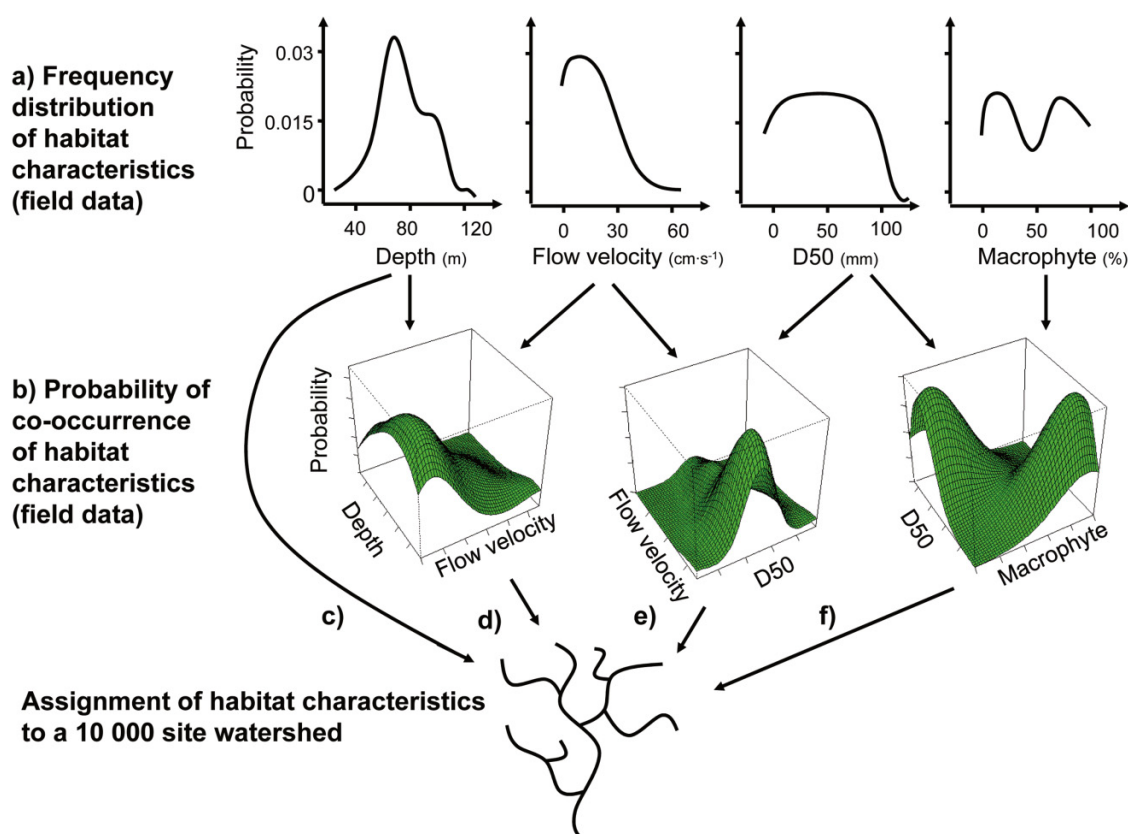
$$(4) \qquad TCV = \frac{SD_{FD_t}}{M_{FD_t}}$$

where SD_{FD_t} and M_{FD_t} (fish·m⁻²) are, respectively, the standard deviation and the mean of the ten FD_t values estimated in a reach for a given species.

Environmental conditions

Environmental conditions measured within each reach were water depth, water velocity, water temperature, substrate size, and macrophyte cover. These variables were selected because of their anticipated role in determining among-reach differences in fish community characteristics in rivers (Gorman and Karr 1978; Albanese et al. 2004; Hughes et al. 2006; Bouchard and Boisclair 2008). Environmental conditions were divided into two groups that defined how many times each would be estimated in the field. The first group comprised the "temporally dynamic environmental conditions", where variables were expected to vary within the confines of river morphology and hydrodynamics (i.e., water depth, velocity, and temperature). Water velocity was measured three times during the survey period: at the highest, lowest, and median flows recorded among the ten sampling periods in any given reach. We compared instantaneous flow measurements on the sampled rivers with flow records from 1971 to 2007 (web site of the Centre d'Expertise Hydrique du Québec: http://www.cehq.gouv.qc.ca/index_en.asp) to determine representative periods to sample for high, intermediate, and low flows. Water depth and temperature were measured at each survey period. This strategy was used to increase the probability of obtaining reach-specific mean values of temporally dynamic variables that reflected the mean field conditions experienced by fish in any given reach, therefore, adequately assessing the effects of survey designs on habitat use models aimed at explaining spatial variations in fish density estimates. The second group of variables described the "temporally stable environmental conditions", where variables

Fig. 2. Diagram of the simulation steps leading to the assignment of environmental characteristics to the 10 000 reaches of the simulation domain. (*a*) Generate a frequency distribution of physical descriptors using field data, (*b*) develop joint probability functions between physical descriptors, (*c*) randomly select and assign to each reach a depth value from the frequency distribution, (*d*) assign a water velocity to each reach, given its joint probability with water depth, (*e*) assign a value of substrate size (D50) to each reach, given its joint probability with water velocity, (*f*) assign a value of macrophyte cover to each reach, given its joint probability with substrate size.

were not expected to vary substantially during the survey period. These variables included substrate composition of the riverbed and the percentage of the riverbed covered with macrophytes. Macrophytes did grow in height during the survey period, but the surface they covered remained relatively constant over the course of the 7 weeks, and as a result, this variable along with substrate composition were estimated only once during the survey period.
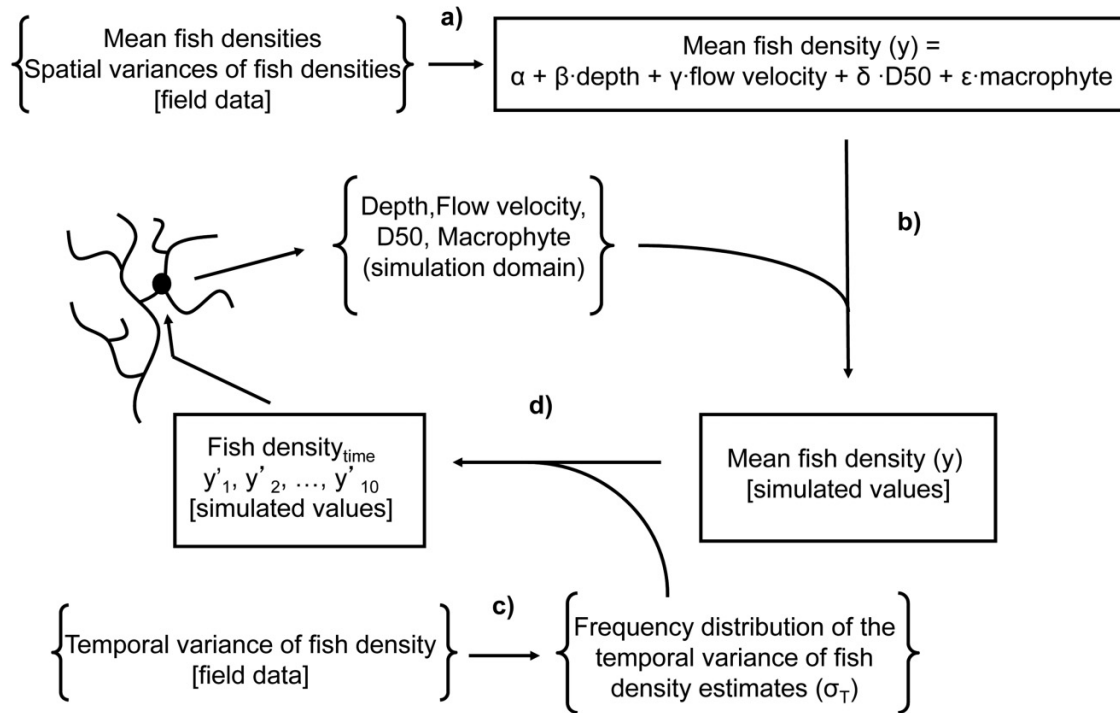
Temporally dynamic and stable environmental conditions were quantified with the following procedure. Water depth (measuring rod; ±5 cm) and water velocity (Gurley Pygmy flow meter; 30 s at 40% of the water column) were measured thrice (both shores and the thalweg) at 10 m intervals for a total of 30 measurements per 100 m reach. These 90 values of temporally dynamic environmental conditions (30 measurements per survey, with each reach surveyed three times at highest, intermediate, and lowest flows) were averaged to represent the mean environmental conditions in each of the 18 reaches surveyed. Water temperature was measured once per fish survey in the middle of the reach. Substrate composition was assessed as the percent contribution of nine particle diameter classes to the riverbed surface area (from clay to boulder; Wolman 1954). These percentages were estimated visually (Latulippe et al. 2001). Given that a particle may be represented by three axes (*A* is the shortest, and *C* is the longest), different types of substrate are defined using the length of their *B* axis. The substrate size that constituted the 50th percentile of the frequency distribution of the substrate found in a reach was obtained by sequentially adding the percent contribution of the types of substrate (starting with the finest particle size) until 50% of the riverbed surface area had been accounted for. The mean length of the *B* axis of this substrate size class was used as the D50 for a reach.

Development of a simulation domain

Studies that aim at developing habitat use models designed to explain spatial variation in fish density generally operate by surveying a large number of reaches (tens to hundreds; Hughes et al. 2006). However, because these reaches are only surveyed once (often because of logistic constraints), this strategy does not permit the estimate of temporal variance in fish density. In contrast, the sampling strategy used in the present work (10 surveys per reach) permits the estimation of the temporal variance of fish density estimates but does not provide a sample size sufficient to develop habitat use models (18 reaches). This shortcoming of our sampling strategy was circumvented by using field-derived observations to generate a framework, hereafter referred to as a simulation domain. The simulation domain consisted of 10 000 reaches in which fish density estimates had a spatial and a temporal variability, and environmental conditions had a spatial variability, similar to those observed in the rivers surveyed.

Variables used to represent the environmental conditions of the reaches of the simulation domain were water depth, water velocity, substrate size, and macrophyte cover. Substrate size within a reach was represented by D50. Environmental conditions, meant to represent the average conditions within reaches of the simulation domain, were assigned to each reach of the simulation domain following six steps (Fig. 2). First, water depth, water velocity, substrate size, and macrophyte cover data collected in the 18 reaches surveyed were used to generate a frequency distribution of these variables. Second, joint probability functions between water depth and water velocity, water velocity and substrate size, and substrate size and macrophyte cover were developed. These functions are plots of frequencies versus paired

Fig. 3. Diagram of the simulation steps leading to the assignment of fish densities to the 10 000 reaches of the simulation domain. (*a*) Develop a multiple regression predicting mean fish density estimates (one per species) in reaches, (*b*) assign to each reach a mean density for each of the five fish species, (*c*) create a frequency distribution of the temporal variance of fish density estimates using field data, and (*d*) generate 10 fish densities estimates per reach by adding temporal variance to mean densities.

coordinates and represent the probabilities of all possible values for one variable given a value for another variable. Third, depth values were randomly selected from their frequency distribution, and a depth value was assigned to each of the 10 000 reaches of the simulation domain. Fourth, a water velocity was assigned to each reach of the simulation domain given its joint probability with water depth (i.e., random selection of water velocity within the possible range given water depth). Fifth, a value of substrate size (D50) was assigned to each reach of the simulation domain given its joint probability with water velocity. Sixth, a value of macrophyte cover was assigned to each reach of the simulation domain given its joint probability with substrate size. The variables assigned to the 10 000 reaches of the simulation domain therefore respected the spatial variability of, and the correlations among, the environmental conditions estimated in the field.

Five fish species (brook trout, *Salvelinus fontinalis*; common shiner, *Luxilus cornutus*; smallmouth bass, *Micropterus dolomieu*; pumpkinseed, *Lepomis gibbosus*; and white sucker, *Catostomus commersonii*) were included in the fish community of the simulation domain. These species were chosen to represent the full range of spatial and temporal variances of fish density estimates and four of the five families observed. The assignment of 10 fish density estimates for any given fish species to the 10 000 reaches of the simulation domain proceeded following four steps (Fig. 3). First, we created a linear regression between mean fish density (*y*) and four environmental descriptors (x_1 = depth, x_2 = water velocity, x_3 = D50, and x_4 = macrophyte cover).

$$(5) \qquad y = \alpha + \beta x_1 + \gamma x_2 + \delta x_3 + \varepsilon x_4$$

The coefficients of this regression (α, β, γ, δ, and ε) were selected such that the mean density of all 10 000 reaches ($\bar{y}$) and the variance between these reaches (spatial variance, ρ_S) would reflect values that were observed in the field. Second, we used the linear regression created in the first step and the values of the four

environmental conditions assigned to any given reach of the simulation domain to assign a mean fish density (*y*) to each of the 10 000 reaches of this domain. Third, we used the 10 field-derived fish density estimates in any given reach to calculate a total of 18 values (one per reach) of the temporal variance of fish density estimates, which were used to develop a frequency distribution of the temporal variance of fish density estimates. This distribution respected the mean and the standard deviation of the observed temporal variances of fish density estimates obtained from field surveys. Randomly sampling this distribution, we assigned to each of the 10 000 reaches of the simulation domain a temporal variance (σ_T). Fourth, we generated 10 fish density estimates per reach of the simulation domain (*y′*) using the mean fish density value assigned to any given reach (*y*) and the temporal variance of fish density estimates assigned to this reach (σ_T) using eq. 6.
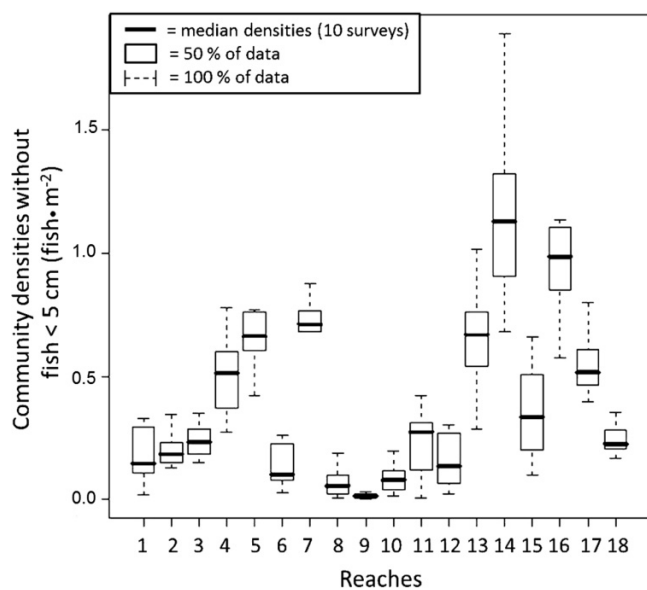
$$(6) \qquad [y'_1, y'_2, y'_3, \ldots, y'_{10}] = \mathcal{N}(\mu = y, \sigma = \sigma_T)$$

Development of habitat use models from the simulation domain

The effect on habitat use models of different combinations of the number of reaches and of the number of surveys per reach for an almost constant total field effort (($r \times s$) = 200–201) was assessed by comparing the multiple regression models developed with data obtained from the simulation domain using six survey designs. These survey designs consisted of six combinations of the number of reaches to survey and of the number of surveys to conduct per reach (*s*): 200 reaches × 1 survey per reach; 100 reaches × 2 surveys per reach; 67 reaches × 3 surveys per reach; 50 reaches × 4 surveys per reach; 40 reaches × 5 surveys per reach; 25 reaches × 8 surveys per reach.

For each ($r \times s$) combination, 10 000 models were computed after randomly selecting the proper number of reaches and surveys per reach from the simulation domain. Mean fish density estimates within each reach of the simulation domain were used as the

Fig. 4. Among-reach variation of total fish (≥5 cm) community density (fish·m⁻²).

dependent variable when survey designs involved more than one survey per reach. Fish density estimates were modelled using the four environmental conditions assigned to reaches of the simulation domain. Stepwise forward selection was used to identify the environmental conditions that were significant at $p < 0.05$ and that contributed to an increase in the R^2_{adj} of the habitat use models by >0.05 (R Language, package packfor; Dray et al. 2007). The R^2_{adj} was used as the criterion because Ohtani (2000) has shown that it is an unbiased estimator of the contribution of a set of explanatory variables for the purpose of describing the response variable in multiple regressions. The effect of different combinations of number of reaches and surveys per reach on species-specific habitat use models was estimated by comparing the R^2_{adj} and environmental variables selected during the multiple regression analyses of simulated data with the ones obtained for the species-specific reference models derived from field data.

Results

Fish community

The mean density of the complete fish community (except fish <5 cm) ranged from 0.014 (Reach 9) to 1.19 fish·m⁻² (Reach 14; Fig. 4). The relative importance of spatial and temporal variances to the total variance of fish density estimates differed among species. Spatial variance represented 63% (common shiner) to 81% (brook trout) of the total variance (Table 1), while temporal variance represented 2% (brook trout) to 19% (yellow perch, *Perca flavescens*) of the total variance. Residual variance, which could not be attributed solely to either spatial or temporal variances, represented between 9% (yellow perch) and 29% (pumpkinseed) of the total variance (Table 1).

Spatial (SCV) and temporal (TCV) coefficients of variation of fish density estimates ranged from 1.45 (brook trout) to 4.11 (golden shiner, *Notemigonus crysoleucas*) and 0.29 (brook trout) to 2.56 (common shiner), respectively (Table 1). Among reach comparisons of TCV by species showed variations from 2.51 times (smallmouth bass) to 6.5 times (rock bass, *Ambloplites rupestris*). Mean TCV across reaches ranged from 0.54 (brook trout) to 1.42 (common shiner). Ranking of mean TCV indicated that species possessing similar mean TCV also tended to belong to the same families (Table 1). The only salmonid species (brook trout) had the lowest mean TCV, followed by the three species of Centrarchidae (smallmouth bass, pumpkinseed, and rock bass), the Percidae (yellow perch), the

Catostomidae (white sucker), and the five species of Cyprinidae (cutlip minnows, *Exoglossum maxillingua*; creek chub, *Semotilus atromaculatus*; golden shiner; fallfish, *Semotilus corporalis*; and common shiner).

Environmental conditions

Mean water depth ranged from 0.38 to 1.29 m (Table 2), mean velocity ranged from 0 to 56 cm·s⁻¹, and riverbed substrate composition was highly heterogeneous among reaches. Silt and sand had the highest mean percent contribution of total riverbed composition (35.6% and 23.4%, respectively), but these types of substrate had low percent contribution to specific reaches. In contrast, pebble, cobble, and boulder had mean percent contributions that ranged from 4.9% to 13.3% of riverbed composition, yet they represented as much as 26.6% to 48.4% of the riverbed in some reaches. Macrophyte cover was also variable among reaches and ranged from 0% to 95% cover (mean = 22%).

Simulation domain

The mean explanatory power of the 10 000 models developed for the five species included in the simulation domain increased asymptotically as the number of surveys per reach increased (Fig. 5). The increase in mean R^2_{adj} of models ranged from 5% (brook trout) to 42% (common shiner) as the number of surveys per reach increased from 1 (200 reaches surveyed) to 8 (25 reaches surveyed). On average, 48% (from 40% to 68%) of the increase in the mean R^2_{adj} of models occurred as the number of surveys per reach increased from 1 to 2. The corresponding value as the number of surveys per reach increased from 1 to 3 was 67% (from 62% to 75%). Hence, most of the potential increase in mean R^2_{adj} of models occurred as the number of surveys per reach increased from 1 to 3.

The 95% simulation interval (SI; interval containing 95% of results) of the explanatory power of models developed for the five species included in the simulation domain tended to increase as the number of surveys per reach increased (Fig. 5). This situation, which may be related to the decrease in the number of reaches used to develop models (total field effort being kept constant at $(r \times s) = 200$), varied among species. The lower and the upper limits of the 95% SI for the R^2_{adj} from models developed for brook trout, using 200 reaches surveyed once, were 73% and 90%, respectively (SI = 17%). In contrast, the SI for models developed for this species using eight surveys and 25 reaches was 42%. Thus, the SI for the R^2_{adj} from models for brook trout increased by 145% ((42% − 17%)/17%) as the number of surveys per reach increased from 1 to 8. With the same parameters, the SI for the R^2_{adj} from models for other species was less affected and increased by 57% (pumpkinseed), 43% (common shiner), 42% (white sucker), and 28% (smallmouth bass). The mean SI for the R^2_{adj} from models (all species combined) increased by 33% as the number of surveys per reach increased from 1 to 2 and by 45% as it increased from 1 to 3. For most species modelled, the greatest increase in SI for the R^2_{adj} from models occurred when the number of surveys per reach increased from 3 to 8 and the number of sites surveyed decreased from 67 to 25.

The frequency of selection by multiple regressions of the four environmental variables included in the reference models tended to decrease as the number of reaches surveyed decreased and the number of surveys per reach increased (Fig. 6). This tendency varied among species. For brook trout, the frequency of selection of the variables included in the reference model decreased by 2% to 56%, depending on the variable (mean = 21%), as the number of sites decreased from 200 to 25, and as the number of surveys per reach increased from 1 to 8 (Fig. 6). Corresponding values averaged 13%, 5%, and 4% for smallmouth bass, pumpkinseed, and white sucker, respectively. Common shiner was the only species for which the selection of the four environmental variables included in the reference models was not affected by the survey design.

Table 1. Fish community characteristics for the 18 sample sites, including observed densities estimates, proportion of fish density variance attributable to space, to time, and to the interaction between space and time, and spatial (SCV) and temporal (TCV) coefficients of variation.

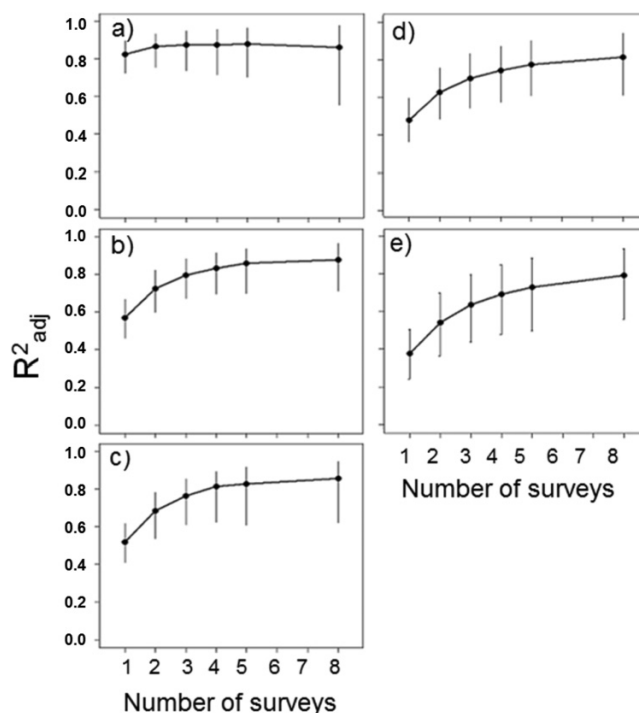| Species | Observed density (fish·m⁻²) | | | Partition of variance (%) | | | | TCV | | |
	Min.	Max.	Mean	Space	Time	Interaction	SCV	Min.	Max.	Mean
Brook trout (*Salvelinus fontinalis*)	0	0.024	0.002	81	2	17	1.45	0.29	1.02	0.54
Smallmouth bass (*Micropterus dolomieu*)	0	0.049	0.007	77	3	20	3.29	0.76	1.91	0.98
Pumpkinseed (*Lepomis gibbosus*)	0.001	0.182	0.045	68	3	29	1.55	0.38	1.92	1.03
Rock bass (*Ambloplites rupestris*)	0.001	0.093	0.019	69	4	27	1.91	0.38	2.46	1.15
Yellow perch (*Perca flavescens*)	0	0.141	0.016	72	19	9	2.13	0.92	2.36	1.17
White sucker (*Catostomus commersonii*)	0	0.068	0.009	71	12	17	2.10	0.79	2.08	1.18
Cutlip minnow (*Exoglossum maxillingua*)	0	0.144	0.017	69	5	26	2.58	0.45	2.16	1.23
Creek chub (*Semotilus atromaculatus*)	0	0.226	0.036	73	9	18	2.23	0.88	2.39	1.30
Golden shiner (*Notemigonus crysoleucas*)	0	0.294	0.021	74	5	21	4.11	0.81	2.50	1.37
Fallfish (*Semotilus corporalis*)	0	0.224	0.038	64	10	26	1.54	0.53	2.42	1.40
Common shiner (*Luxilus cornutus*)	0	0.228	0.066	63	10	27	1.60	1.03	2.56	1.42

Table 2. Mean and range of environmental conditions measured in the 18 survey reaches.

| Variables | Site descriptors | | |
	Min.	Max.	Mean
Water depth (cm)	38	129	68
Water velocity (cm·s⁻¹)	0	56	15
Water temperature (°C)	17	25	21
Substrate type (% cover)			
Clay	0	1.5	0.1
Silt	1.8	96.9	35.6
Sand	0	61.4	23.4
Gravel	0.4	26.9	12.6
Pebble	0	37.7	10.8
Cobble	0	48.4	13.3
Boulder	0	26.6	4.9
Metric boulder	0	12.5	1.0
Bedrock	0	1.6	0.2
Macrophyte cover (%)	0	95	22

Fig. 5. Mean explanatory power (R^2_{adj}) of habitat use models developed using different combinations of number of reaches and number of replicate temporal surveys per reach with a constant field effort of 200 surveys. Habitat use models were developed following 10 000 simulations for (*a*) brook trout, (*b*) smallmouth bass, (*c*) pumpkinseed, (*d*) white sucker, and (*e*) common shiner. Vertical lines represent 95% SI of R^2_{adj}.

Discussion

This study showed that fish density estimates can vary substantially (TCVs up to 2.56) among surveys to a series of 100 m reaches. It has long been recognized that fish density at a site can vary through time. However, previous studies have focused on inter-annual variation of fish density, which may be attributed to population dynamics rather than on temporal variation of fish density over shorter time intervals (Moyle and Vondracek 1985; Danehy et al. 1998; Oberdorff et al. 2001). Fish density variation over shorter time intervals (weeks to months) are often estimated for groups of species (e.g., Gorman and Karr 1978: 33% to 68% change in total fish community density between June and September; Schlosser and Ebel 1989: 6 to 10 times change in total cyprinids density between May and June). Comparisons among TCV values estimated over similar time intervals are also complicated by the negative relationship expected between TCV and the size of the sampling sites, which often varies among studies (Imre and Boisclair 2004: 10 m; Moyle and Vondracek 1985: 30–40 m; Oberdorff et al. 2001: >100 m; Danehy et al. 1998: 30 times bankfull width ≈ 90–200 m). One contribution of the current study is therefore to show that the density of individual fish species can vary substantially among surveys, despite efforts to control for the size of sampling sites (100 m reaches), the time of day (1000 to 1600), the season (7 weeks of a summer), the year (single year), the meteorological conditions (<50% cloudiness), and the survey method (visual observation by snorkelers).
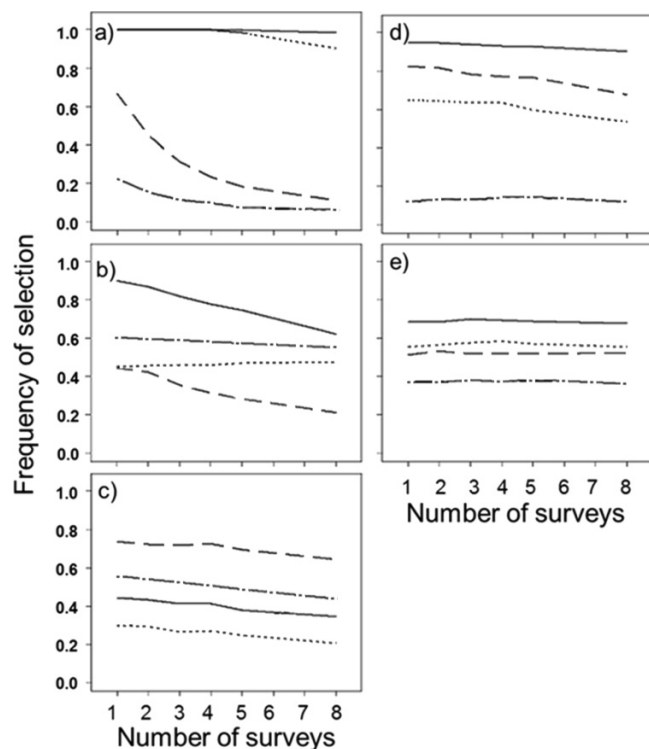
The objective of this study was not to determine the actual or specific relationship between fish density estimates and environ-

mental conditions in the watersheds that we sampled. The sampling of 18 reaches is not statistically sufficient to achieve such an objective (too many potential independent variables relative to the number of sampling sites or degrees of freedom). Our ultimate objective was to compare the relative ability of different sampling designs ($r \times s$) to retrieve a fictive relationship (created by the authors) between fish density and environmental conditions that has been imbedded in a dataset (the simulation domain) in which the spatial and temporal variance of fish density estimates mimics those obtained in the field by visiting 18 sites (providing spatial variance) on 10 occasions (providing temporal variance).

Numerous hypotheses may be invoked to explain the temporal variation of fish density estimates over a 7-week period during summer. Although this study was not designed to test hypotheses

Fig. 6. Frequency of selection of explanatory variables used in the reference models (solid line = depth; dotted line = D50; dash-dot-dashed line = water velocity; and dashed line = macrophyte cover) for habitat use models developed using different combinations of number of reaches and number of surveys per reach with a constant field effort (200 fish surveys). Habitat use models were developed following 10 000 simulations for (*a*) brook trout, (*b*) smallmouth bass, (*c*) pumpkinseed, (*d*) white sucker, and (*e*) common shiner.

about the mechanism underlying such variation, our results may be used to superficially explore some of these hypotheses. For instance, physical events such as changes in flow rates (Grossman et al. 1998, 2010) and biological processes such as seasonal mortality (Lohr and Fausch 1997; Falke et al. 2010) may have contributed to the temporal variance of fish density estimates. However, a redundancy analysis (package vegan, procedure rda; Oksanen et al. 2010), combined with an ANOVA test by permutation (package stats, procedure anova; R Development Core Team 2009) were used to test the effect of flow conditions (classification variables: high, intermediate, and low flows) on temporal variations of fish density estimates while controlling for the effect of reaches. Fallfish was the only species for which density was significantly affected by flow conditions, where the density of fallfish tended to increase as flow increased ($p = 0.035$).

Seasonal or ontogenetic shifts in habitat use may also confound comparisons between sites. Field data were collected between 16 June and 10 August 2007. A sampling period of 7 weeks (or more) is often required to collect data during stream surveys (e.g., Wang et al. 2001; Petry et al. 2003; Wilson and Xenopoulos 2008). Habitat use patterns within such a time interval may therefore vary depending on the life histories of the species. Demographic trends may also affect temporal variations within sites. To test for the presence of demographic trends within our dataset, Julian days were substituted as the explanatory variable of fish density estimates. No statistically significant relationship between fish density estimates and survey day was found for any of the species (0.08 for fallfish $< p < 0.81$ for golden shiner). These analyses suggest that for the reaches studied, within the range of flows observed, and over the 7-week survey period, flow and mortality

rates may not have been determinant drivers of temporal variations of fish density estimates. Given these results, we hypothesize that observation error (e.g., errors in counts of fish observed and in the estimation of the distance of observation) and real temporal variation (e.g., fish movements in and out of refuges and reaches) are the major and interactive drivers of temporal variations of fish density estimates.

Temporal variation of fish density estimates that we observed at a site may be generated by two sources: fish movement in and out of a site between surveys (i.e., real temporal variations of fish density) and different errors made by snorkelers on different surveys (i.e., observational temporal variations of fish density). We recognize that we cannot assess the fraction of the variance among or within reaches that is related to real temporal variation or to observation error. For the purpose of our simulation domain modelling, we assume that all of the temporal variation is due to real variation in fish density over time, rather than observational error. However, if temporal variation is mostly due to observational error, then modifications to sampling protocols that decrease observational error may obviate the benefits of repeated temporal sampling. Increasing the length of the sample reach may also reduce sampling error and the benefits of temporal replication. Nevertheless, sample reaches in excess of 100 m were not practical in our study, as longer reaches included multiple habitat types, and we required associations of fish with homogeneous habitat types for calibrating our sampling domain. However, this may not be a constraint if a survey is designed to sample multiple habitats in a representative reach. The optimal combination of replication in time and space will therefore depend both on the relative size of spatial and temporal variation and the degree to which sampling protocols can minimize temporal variation.

TCV estimated during the present study differed among species and appeared related to taxonomy. The ranking of TCV resulted in the grouping of species by families. Brook trout had the lowest mean TCV (0.54), while species of cyprinids had the largest mean TCV (1.23 to 1.42). Low TCV for the only salmonid species observed is consistent with the suggestion that this family contains species that may display site fidelity or territoriality (Bridcut and Giller 1993; Steingrímsson 1999; Bridger et al. 2001) that tends to promote a more even dispersal of individuals in space, facilitating more precise population estimates. However, the present study should not be taken as an indication that all riverine salmonids display site fidelity or territoriality and do not perform major movements. In this study, fish were not marked and their movements were not assessed. Studies designed to assess fish movements indicate that populations of Salmonidae may be composed of both mobile and sedentary individuals in variable proportions (Heggenes et al. 1991; Rodríguez 2002; Scruton et al. 2003). The present study may suggest, however, that despite potential movements, the density of brook trout may be consistently higher in certain reaches than others. The higher TCV associated with species of cyprinids may be related to observational error. The species of cyprinids present in the reaches all have small body size that make them more difficult to observe than fish belonging to other families. Small fish such as cyprinids may be more prone to cryptic, evasive, or gregarious behaviours. More aggregated distributions associated with schooling behaviour could lead to greater observation error in population estimates than for less aggregated species like brook trout. The difference between the presence and absence of a shoal of cyprinids in reaches may have a strong effect on its TCV. Notwithstanding the causes of the high TCV for cyprinids, our study suggests that accurate assessment of the density of cyprinids may require more surveys per reach than is needed for other families, or alternatively, a greater investment in effort to reduce observer error if temporal variation has a large observational component.

Simulations indicated that survey designs should not be applied broadly and that the validity of a survey design ($r \times s$) may depend

on the interaction between SCV and TCV and vary among species. Models developed for species characterized by low TCV may benefit from surveying a large number of reaches only once. For such species, distributing a specified total field effort towards the repeated survey of reaches might, in fact, have a negative impact on models. This situation is best illustrated by the analyses aimed at developing models for brook trout (lowest SCV; lowest TCV). Increasing the number of surveys per reach (and decreasing the number of reaches surveyed) produced models with marginally higher R^2_{adj} related to low TCV, but markedly larger SI for R^2_{adj} related to low SCV. The probability of developing models based on the appropriate explanatory variables also decreased as the number of surveys per reach increased (related to low TCV). This study therefore suggests that the development of models based on single surveys to a larger number of reaches may be valid for salmonids (e.g., Turgeon and Rodriguez 2005). In contrast, models developed for species characterized by high TCV may benefit from the repeated survey of fewer reaches. For instance, the R^2_{adj} of models developed for common shiner (intermediate SCV; highest TCV) increased noticeably as the number of surveys per reach increased from 1 to 3 (26%), and this with relatively small changes in SI for R^2_{adj} and the probability of selecting the appropriate explanatory variables. For species possessing similar SCV and TCV, surveying 67 reaches thrice may be preferable to surveying 200 reaches once. However, more than three surveys per reach may not be useful given that the majority of the benefits for models occurred as the number of surveys per reach increased from 1 to 3, and the majority of the disadvantages associated with such an increase (increase in SI for the R^2_{adj} related to a decrease in the number of reaches) occurred as the number of surveys per reach increased from 3 to 8. Finally, for species such as smallmouth bass (highest SCV; second lowest TCV), surveying 100 reaches twice instead of 200 sites once may increase the R^2_{adj} of models by 19% with minimal effects on SI for R^2_{adj} and the probability of selecting the appropriate explanatory variables. These conclusions need to be tempered by the observation that the trade-off between replication in space versus time will likely depend on the fixed sampling effort. If effort is fixed at only 25 surveys, for example, the benefits of replication in time may be much lower because of the need to maintain spatial variation in environmental drivers of abundance in such a small sample size.

The general applicability of these results depends on the context defined by a series of spatial, temporal, physical, biological, and methodological parameters. Spatial parameters refer to the size of the sampling units (100 m reaches) used to develop habitat use models, while temporal parameters imply the time of sampling (daytime sampling; summer; single year). Physical parameters describe river size (width and depth; Table 2) and the flow regimes, which do not vary substantially over the course of the survey period. Biological parameters refer to the fish community characteristics (fish density estimates and specific composition; Table 1). Methodological parameters refer to the survey method (underwater visual survey), the total number of reaches sampled, and the biotic index of habitat use selected for study (density). The effects of changes with respect to any of these parameters on optimal survey designs are unclear. However, we have demonstrated that the balance between the number of reaches surveyed and the number of surveys per reach may affect habitat use model performance, and we believe that such effects for different combinations of these parameters should be further explored. The linkage unveiled here among fish taxonomy, TCV, and survey designs may serve as a framework to simplify the search for solutions to one of the fundamental logistic problems associated with the development of operational and reliable habitat use models.

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