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A flexible survey design for monitoring spatiotemporal fish richness in nonwadeable rivers: optimizing efficiency by integrating gears

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Abstract: We designed a flexible protocol for monitoring fish species richness in nonwadeable rivers. Nine sites were sampled seasonally with six gears in two physiographic regions in Missouri (USA). Using resampling procedures and mixed-effects modeling, we quantified richness and compositional overlap among gears, identified efficient gear combinations, and evaluated protocol performance across regions and seasons. We detected 25–75 species per sample and 89 185 fish. On average, no single gear detected >62% of observed species, but an optimized, integrated-gear protocol with four complementary gears on average detected 90% of species while only requiring 51.9% of initial sampling effort. Neither season nor physiographic region explained low spatiotemporal variation in percent richness detected by the integrated-gear protocol. In contrast, equivalent effort with an electrofishing-only protocol was 53.5% less efficient, seasonally biased and imprecise (36.1%–82.3% of richness), and on average detected 15.9% less of observed richness. Altogether, riverine fish richness is likely underestimated with single-gear survey designs. When paired with existing wadeable-stream inventories, our customizable approach could benefit regional monitoring by comprehensively documenting riverine contributions to riverscape biodiversity.

Résumé : Nous avons élaboré un protocole souple pour la surveillance de la richesse spécifique de poissons dans les rivières non négociables à gué. Neuf sites ont été échantillonnés durant différentes saisons, avec six engins, dans deux régions physiographiques au Missouri (États-Unis). En utilisant une technique de rééchantillonnage et la modélisation des effets mixtes, nous avons quantifié le chevauchement de la richesse et de la composition entre les engins, cerné des combinaisons d'engins efficaces et évalué la performance des protocoles pour les différentes régions et saisons. Nous avons détecté de 25 à 75 espèces par échantillon et 89 185 poissons. En moyenne, aucun engin n'a, par lui-même, détecté plus de 62 % des espèces observées, mais un protocole optimisé intégrant quatre engins distincts et complémentaires a permis de détecter 90 % des espèces, tout en ne nécessitant que 51,9 % de l'effort d'échantillonnage initial. Ni la saison ni la région physiographique n'explique la faible variation spatiotemporelle du pourcentage de richesse détecté par le protocole des engins intégrés. En comparaison, un effort équivalent par un protocole comprenant seulement la pêche électrique avait une efficacité de 53,3 % plus faible, présentait un biais saisonnier, était imprécis (de 36,1 % à 82,3 % de la richesse) et, en moyenne, détectait 15,9 % moins de la richesse observée. Dans l'ensemble, la richesse des poissons fluviatiles est probablement sous-estimée par les schémas d'inventaire à un seul engin. Jumelée à des inventaires existants de cours d'eau négociables à gué, notre approche adaptable pourrait être utile pour la surveillance régionale en permettant de documenter de manière exhaustive les contributions fluviatiles à la biodiversité des paysages fluviaux. [Traduit par la Rédaction]

Introduction

Conservation entities need efficient and unbiased methods for monitoring riverine biodiversity given the many stressors altering rivers worldwide (Vörösmarty et al. 2010). Rivers influence assemblage dynamics at regional extents by providing habitat for floodplain- and channel-dependent riverine fishes (Galat and Zweimuller 2001) and corridors connecting stream-fish populations throughout river basins (McCluney et al. 2014). Consequently, rivers are pivotal to how fish assemblages respond to drivers of global change by governing interactions among species range shifts, dispersal pathways, and expanding water infrastructure (Kominoski et al. 2018). However, survey-design developments for sampling riverine assemblages have lagged behind those for other freshwater systems (Reash 1999), likely because rivers are among the most demanding aquatic systems to sample (Paukert and Galat 2010).

Fish assemblages and habitats become increasingly complex downriver (Ward et al. 2002), making riverine fishes particularly difficult to monitor (Flotemersch et al. 2011). Beyond logistics of sampling large areas, surveys can be hampered by riverine environmental conditions, including high turbidity, depth, spatiotemporally variable flows, debris, and off-channel habitats affecting observational ability and assemblage dynamics (Flotemersch et al. 2011; Gibson-Reinemer et al. 2016*a*). Assessments of local riverine fish richness (hereinafter "richness assessments") typically account for these added complexities with greater effort (Hughes et al. 2002) and multiple gears (e.g., Neebling and Quist 2011; Loisl et al. 2014; Zajicek and Wolter 2018), which can result in highly customized designs for specific rivers and reaches (McManamay et al. 2014; Gibson-Reinemer et al. 2016*a*). However, these designs may lack versatility needed for

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Table 1. Site characteristics and means (SD) of habitat variables from nine nonwadeable sites across two physiographic regions in Missouri (USA).

Site	Region	Samples	MWCW (m)	Site length (m)	Watershed area (km²)	Secchi (m)	Depth (m)	Velocity (m·s⁻¹)
L. Gasconade	Ozarks	5	92	4 600	9 025	0.9 (0.5)	1.6 (0.8)	0.3 (0.3)
L. Meramec	Ozarks	4	84	4 200	9 780	0.8 (0.4)	1.5 (0.8)	0.5 (0.4)
L. Grand	Prairie	4	78	3 900	19 615	0.3 (0.3)	2.1 (1.1)	0.4 (0.3)
U. Gasconade	Ozarks	4	75	3 750	7 245	1.8 (0.4)	1.2 (0.6)	0.5 (0.4)
Salt	Prairie	4	59	2 950	6 466	0.7 (0.6)	1.4 (0.6)	0.4 (0.4)
Black	Ozarks	4	53	2 650	3 012	1.5 (0.4)	1.4 (0.6)	0.5 (0.4)
U. Grand	Prairie	4	52	2 600	5 825	0.2 (0.1)	1.4 (0.7)	0.4 (0.3)
U. Meramec	Ozarks	3	52	2 600	3 826	1.7 (0.5)	1.0 (0.5)	0.5 (0.3)
Lamine	Prairie	4	43	2 150	2 759	0.5 (0.1)	2.0 (0.1)	0.1 (0.1)

Note: L = Lower, U = Upper, MWCW = mean wetted-channel width. Depth and velocity are indices measured from electrofishing and trawling subsamples in boatable areas. Depth was measured from side-scan sonar and velocity at approximately 60% depth with a pole-mounted digital velocity meter.

regional biodiversity monitoring of multiple rivers across varying environmental conditions.

Versatile survey designs developed for monitoring richness and assemblage composition often emulate existing wadeable-stream protocols (Reash 1999; Hughes and Peck 2008). Consequently, these designs minimize sources of sampling variation arising from greater habitat diversity in rivers by standardizing data collection to a subset of habitats with one (Hughes et al. 2002; Maret et al. 2007) or two gears (Moulton et al. 2002; USEPA 2013). For example, several riverine fish assessments mainly target large-bodied fishes by continuously electrofishing 500–1600 m of river (Gammon and Simon 2000; Lyons et al. 2001; Flotemersch and Blocksom 2005). Moreover, most of these protocols assess riverine condition (i.e., degree of alteration to natural integrity) using multimetric biotic indices that require less effort to estimate precisely than species richness (Flotemersch and Blocksom 2005; Maret et al. 2007). Although most multimetric indices incorporate richness-based metrics (Pearson et al. 2011), estimated richness often depends on limited standardized effort versus the effort needed to survey available habitats comprehensively. Over time, underreported riverine richness could manifest as data gaps within increasingly used regional, basin-wide management plans. Accurate indicators of local species richness throughout watersheds are needed to map biodiversity (Troia and McManamay 2020), designate and prioritize conservation areas (Abell et al. 2007), conduct threat assessments (Sievert et al. 2016), and monitor spatiotemporal trends in populations, assemblages, and communities (Radinger et al. 2019).

Richness assessments often need to accomplish management objectives while navigating complex logistics and limited funding and timing (Hughes and Peck 2008). Consequently, survey designs for most assessments prioritize sampling efficiency. These designs typically improve efficiency by constraining observations to the single-most effective gear or use multiple gears by identifying the most effective gear for each habitat (Utrup and Fisher 2006; Loisl et al. 2014). The second approach is more comprehensive, but many species occupy multiple habitats, thereby predisposing these species to detection by multiple gears (i.e., redundant effort). Further, a single gear is unlikely to detect all species inhabiting a habitat type, especially if inhabitants vary widely in body size (Schloesser et al. 2012*a*). Ideally, investigators could further improve efficiency by distributing effort among gears to minimize redundancy across habitats and gears, yet still comprehensively represent fish assemblages.

Natural and user-induced variability can affect inferences made from ecological assessments. For example, species-sampling relationships can vary temporally by diel period (Flotemersch and Blocksom 2005) and year (Meador and McIntyre 2003). Although surprisingly few riverine fish assessments have investigated seasonal influences, species-sampling relationships could be sensitive to high spring flows (Simon and Sanders 1999), temporary occurrences of migratory or schooling species (De Leeuw et al. 2007), and recruitment (Peterson and Rabeni 1995; Gammon and Simon 2000). In contrast with time, several studies have investigated species-sampling relationships across space. For example, sampling effort to detect the same percentage of species richness across sites can vary because of habitat heterogeneity (Angermeier and Smogor 1995), stream size (Paller 1995), and by assemblage attributes, including species rarity (Kanno et al. 2009), fish density (Paller 1995), and richness (Meador 2005). The main options for overcoming variability include increasing effort (Peterson and Rabeni 1995), standardizing data collection (Bonar et al. 2009), stratifying results (e.g., by river size; Neebling and Quist 2011), and corrective modeling (McManamay et al. 2014). Failing to account for spatiotemporal variation may limit the ability of protocols to detect trends (Meador and McIntyre 2003) and (or) bias results, which can undermine one-size-fits-all survey designs (Lindenmayer and Likens 2010).

Our goal was to develop a multigear survey design for assessing local fish species richness in medium-to-large (i.e., midsized) nonwadeable rivers. Many standardized riverine assessments were developed for regulatory purposes to monitor fish-assemblage condition in great rivers (i.e., >50 000 km² watershed areas; Guy et al. 2009), meaning there are few survey designs for smaller, and typically less-altered, rivers (Yoder and Kulik 2003). We sampled nine sites seasonally with six gears across two distinct regions in Missouri (USA). This intensive effort allowed us to quantify effectiveness of individual and combined gears while varying effort via multiple randomizations. We had five specific research questions: (1) Which gears detected the most species per unit effort? (2) Which gears were most redundant? (3) On average, what combination of gears most efficiently detected 90% of observed species richness? (4) Did the most efficient protocol that integrated effort among gears detect a consistent percentage of richness across regions and seasons? (5) Was this integrated-gear protocol more effective and consistent than traditional effort with an electrofishing-only protocol? Our study is among the first riverine fish assessments to simultaneously examine species-sampling relationships across seasons and regions with such a comprehensive survey design. Investigators may benefit from knowing the effectiveness of individual gears (question 1–2) or emulate our entire approach (questions 3–5), which optimized efficiency by integrating effort among multiple gears and then evaluated protocol performance across broad spatiotemporal environmental conditions.

Materials and methods

Study area and timing

We sampled the nonwadeable rivers linking wadeable streams to Missouri's two great rivers, the Mississippi and Missouri rivers (Table 1; Fig. 1). Northern Missouri, in the Central Lowland region (hereinafter "Prairie"), is characterized by low topographical re-

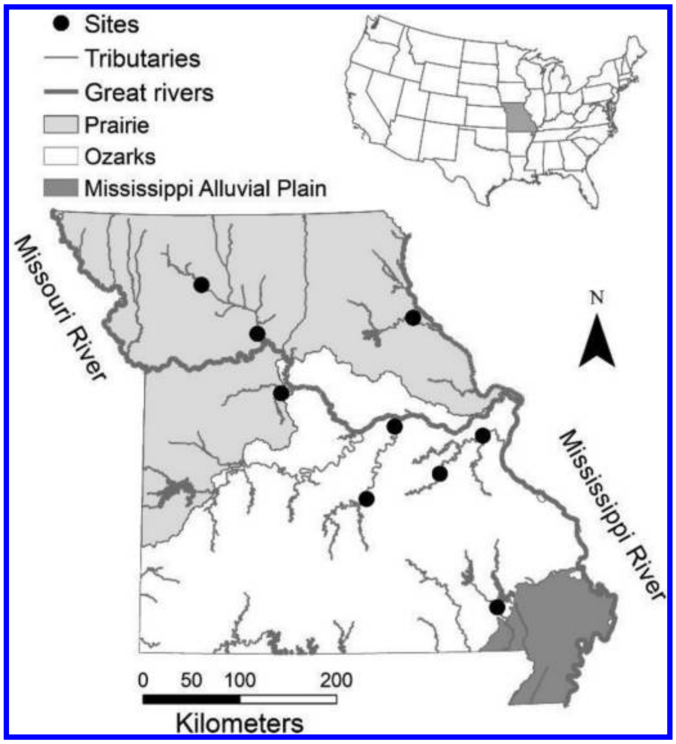


Fig. 1. Map of Missouri (USA) with nine nonwadeable sites repeatedly sampled 2014–2016. "Great rivers" are the Missouri and Mississippi rivers. Site geospatial coordinates are in Dunn et al. (2018). Shapefile sources: physiography (Missouri Resource Assessment Program), river networks (National Hydrography Dataset version 2), state boundaries (US Census Bureau).

lief and grassland–pasture (43%) or row crops (38%). Many Prairie river systems are now leveed, channelized, and otherwise engineered to limit flooding. Most Prairie rivers are low-gradient, turbid, dominated by silt and sand substrates, and vary widely in physicochemical and hydrological conditions across seasons (Sowa et al. 2007). In contrast, the Ozark Plateaus region (hereinafter "Ozarks") has pine, mixed, or deciduous forests (52%) and pasture–grassland (40%). Ozark rivers typically have higher-gradient channels that are semiconfined by bluffs, are less turbid, and have gravel–cobble alluvium and aquatic vegetation present within shallow areas (Sowa et al. 2007). Further, many Ozark rivers are groundwater-influenced, creating more seasonally stable hydrologic and physicochemical conditions.

We sampled nine sites (five Ozark, four Prairie; Table 1) between 2014 and 2016 across three seasons. State fisheries biologists preselected drainages that were accessible and geographically representative of Missouri, had few sampling restrictions posed by federally imperiled species, and had few impoundments. For example, biologists recommended the upper Meramec River drainage, so we randomly selected a sampling locality within the upper Meramec River from the six available river accesses. Our nine sites encompassed a variety of river sizes (watershed areas = 2759–19 615 km²) and environmental conditions (lowland–upland). We sampled each site three to five times (36 total samples) with at least one sample in spring (18 March – 13 June), summer (25 June – 8 September), and fall (16 September – 11 November) and at least 20 days between consecutive samples at the same site.

Survey design

Site length

Site lengths were 50 mean wetted-channel widths (MWCW) and typically encompassed at least one meander bend with multiple habitats (e.g., shoals, pools). We estimated MWCW within 5 km of a river access point by measuring wetted-channel width along 11 cross-sectional transects spaced 500 m apart using satellite imagery via Google Earth. If available, we used imagery from early spring during baseflow and leaf-off, and we used the same MWCW at sites across seasons. Finally, we randomly designated the starting point of each site as either 1 km up- or downriver of an access and extended the site in the opposite direction of the river access to limit anthropogenic influences often concentrated at accesses.

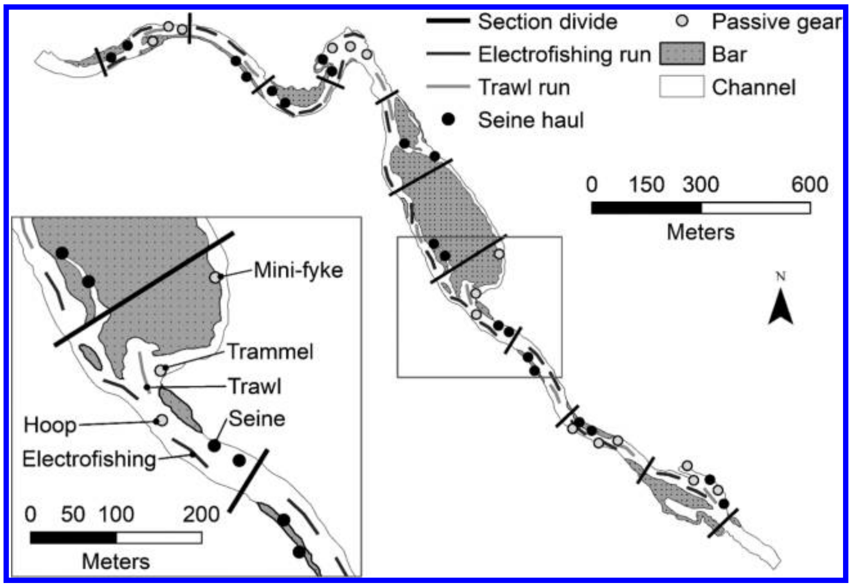
Sampling gears

Selected gears were capable of sampling all major habitats within sites. Candidate habitats included all areas with an intact main channel surface-water connection, including secondary channels, slackwaters, and other lateral units, but excluding isolated floodplain waterbodies. We primarily used benthic trawling, boat electrofishing, and seining (hereinafter "active gears"). Rather than continuously sampling with each gear, we divided effort into several discrete subsamples that could be placed in specific habitats and evenly distributed across a site. We supplemented active gears with five mini-fyke, hoop, and stationary trammel nets (hereinafter "passive gears"), which fished overnight and were placed in habitats that were difficult to sample with active gears (15 total nets per sample). Importantly, a subsample refers to a basic unit of effort by each gear (i.e., one overnight net set regardless of type, one seine haul, one 50 m electrofishing or trawl run).

Boat electrofishing sampled littoral areas (within 20 m from a bank) and shallow (0.5–1.5 m) midchannel shoals. We used a 5.2 m flat-hull aluminum boat with a 40 hp (1 hp = 746 W) jet-drive outboard motor. The electrofishing system consisted of a 5000 W generator connected to a control unit and two bow-mounted booms with "spider"-style anodes (Midwest Lake Management, Inc. Polo, Missouri). We standardized the peak power transferred to fish at 3000 W by adjusting voltage according to ambient conductivity (Miranda 2009). Our electrofishing settings broadly targeted fish assemblages and consisted of 60 Hz pulsed direct current with 25%–35% duty cycle (Guy et al. 2009). Electrofishing effort was divided into discrete 50 m downstream runs (= one subsample) lasting 189 ± 61 s (mean ± SD). An operator maneuvered the boat perpendicular to the shoreline while two crewmembers netted stunned fish using dipnets with 46 cm deep bags and 6.4 mm mesh. If swift water velocities (>0.70 $m \cdot s^{-1}$) in midchannel shoals prevented lateral movements during the initial run, we made a second 50 m run adjacent to the first run but facing the opposite bank. The effectiveness of electrofishing was limited in shallow (<0.5 m) habitats by navigability and likely at depths ≥ 1.8 m by vertically diminishing voltage needed to immobilize fish.

We used four seining techniques and two different seines (depending on habitat) to target small-bodied fishes inhabiting shallow areas with little structure. We sampled ~65 m² per subsample regardless of technique and spaced subsamples at least 25 m apart to minimize spatial dependency among subsamples. We primarily used a 9.1 m × 1.8 m bag seine with a 1.8 m bag and 6.4 mm delta knotless mesh netting (Guy et al. 2009) and a quarter-seine haul technique in areas with slow to moderate water velocities along riverbanks or a purse method to secure the bag in wadeable areas where the seine could not be beached. Alternatively, we used a 4.5 m × 1.5 m straight (bagless) seine with 6.4 mm netting to drag the seine downriver along steeply sloped shorelines where wading was restricted, with drag length compensating for allowable seine width from the bank. In swift, shallow areas (<0.3 m), we used a kick-net technique with the straight seine to conduct adjacent kick nets while dislodging benthic fishes from substrates. We considered two adjacent kick nets as equivalent to one seine haul by the other techniques.

Fig. 2. Example of a georeferenced sample of a 2.65 km site (= 50 mean wetted-channel widths (MWCWs)) in the Black River, Missouri (USA) in fall 2015. The inset details subsamples in main and secondary channels. Note MWCW is 53 m, sections (thick black lines) are 265 m (five MWCWs), total electrofishing distance = 1 km (50 m run × 20; thin black lines), trawling distance = 500 m (50 m run × 10; gray lines), and seining distance = 200 m (10 m seine haul × 20; black circles). Passive gears (light gray circles) include hoop, mini-fyke, and stationary trammel nets. Shapefile depicting river habitats was derived from 2012 National Agriculture Imagery Program, US Department of Agriculture.



Benthic trawling was used in deep, midchannel habitats. We used a modified mini-Missouri trawl with a 6.4 mm outer mesh and 38 mm inner mesh ("Gerken Siamese Benthic Trawl"; Innovative Net Systems, Milton, Louisiana). The trawl was 2.5 m long with a 2.5 m floated headrope and a weighted 3 m footrope. We interchanged three sizes (50, 61, and 76 cm) of otter boards depending on water velocity and adjusted towlines to approximate a 7:1 ratio of towline length to average river depth. The trawl was towed off the bow while reversing downriver with a subsample beginning once the towlines and the trailing buoy line were taut and ending after sampling 50 m (= one subsample; trawl subsample = 65 ± 16 s (mean ± SD)).

Five nonbaited mini-fyke nets were set per sample primarily in habitats not effectively sampled by seining, including low-velocity, structurally complex habitats (vegetation, debris, boulders) and off-channel areas. Mini-fyke nets with two 0.6 m × 1.2 m frames were bisected by a 4.5 m lead extending to a riverbank or other structure and a cod end with two steel hoops. Nets had 3.1 mm green-treated nylon bar mesh. Each mini-fyke net was set overnight for 18–24 h (= one subsample).

Five nonbaited hoop nets were set per sample targeting large-bodied fishes inhabiting deep habitats (>1.5 m) that could not be effectively sampled by electrofishing. Hoop nets were 1.2 m in diameter and 4.9 m long with 3.8 cm bar mesh (Guy et al. 2009). Each net had seven fiberglass hoops with finger throats attached to the second and fourth hoops and were set overnight for 18–24 h (= one subsample).

Five stationary trammel nets were set per sample at the bottom of deep low-velocity habitats to target large-bodied fishes. Trammel nets were 15.2 m long × 1.8 m deep with 20.3 cm and 9.5 cm bar mesh for outer and inner panels, respectively, and held in place by attaching float- and lead-line ends to vertically suspended lines at each end. We deployed each trammel net overnight for ~12 h (= one subsample).

All sampling was permitted by the Missouri Department of Conservation and performed under University of Missouri Animal Use and Care Protocol 8532. Sampled individuals that could not be field identified were preserved and subsequently identified. We limited passive-gear bycatch of non-fishes by using passive-set trammel nets rather than gill nets, limiting soak times to 12–24 h (versus multiple days), and only partially submerging mini-fyke nets.

Scaling sampling effort to river size

The sizes of our sites varied nearly sevenfold (watershed areas = 2759–19 615 km²), so we scaled sampling effort with active gears according to each site's total length to ensure similar proportions of habitat were sampled at each site (Fig. 2; also refer to online Supplementary material 1[1]). We sampled ~40% (20 MWCWs), 25% (12.5 MWCWs), and 7% (3.5 MWCWs) of each site's length with electrofishing, trawling, and seining, respectively. These site-length percentages balanced our field time among active gears during the initial phase of protocol development. We achieved these percentages by summing the lengths of subsamples, with each electrofishing and trawling subsamples equaling 50 m and seining subsamples approximating 10 m. We distributed sampling effort across a site by apportioning active-gear subsamples among 10 equally sized sections (one section = five MWCWs; Fig. 2). We used eq. 1 to calculate the number of subsamples per section for each active gear (i) and then rounded to the nearest subsample per section:

$$\text{Subsamples}_i \times \text{Section}^{-1} = \frac{\text{Site length (m)} \times \text{Target percentage}_i}{100 \times \text{Sections} \times \text{Subsample length (m)}_i} \tag{1}$$

For example, in the 53 m wide Black River (50 MWCWs = 2650 m), we conducted two 50 m electrofishing runs in each section, totaling 1000 m electrofishing (electrofishing length based on target percentage (40% site extent) = 1060 m; Fig. 2). Balancing active effort among sections enabled a randomization procedure to

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[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0315.

identify optimal effort by resampling equal-effort sections (see Statistical analyses for question 3). Passive-gear effort was not scaled to river size because passive effort was not in terms of distance, and the habitats sampled by these gears were often restricted (e.g., secondary channels, pools > 2 m deep).

We distributed effort within sections by dividing sections into fourths or sixths depending on river size, and then we randomly selected an area to sample with each gear using a random-number generator on a ruggedized tablet computer. If a gear could not be used effectively in habitats within the selected area, another area within the same section was randomly selected. Similarly, if a gear could not be used effectively in a section, an adjacent section was sampled. This process was repeated for each active gear and in each of the 10 sections. The sequence of gears varied by sample, but we avoided sampling sections after electrofishing on the same day to limit interference among gears. Overall, our design scaled effort by active gears across river sizes, supplemented active effort with passive gears, and balanced sampling effort spatially within sites. Hereinafter, we refer to our original design as our “full-effort” protocol.

Statistical analyses

We initially quantified pairwise species richness (question 1) and overlap (question 2) among gears by subsample rather than by cumulative effort (pooled subsamples) for two purposes. First, each subsample required a comparable crew investment to complete and process regardless of gear (20–35 min), whereas cumulative effort varied widely among gears (e.g., five mini-fyke nets ≈ 3 h versus ≥1 km electrofishing ≈ ≥8 h). Second, it is instructive to demonstrate with two gears that total species richness detected by multigear designs depends on the interplay between effectiveness and overlap of constituent gears before presenting the same concept with combinations of six gears (question 3).

Question 1: Which gears detected the most species per unit effort?

We used generalized linear mixed-effects models to determine whether fish species richness per subsample varied by gear (e.g., one 50 m electrofishing run, one mini-fyke net, etc.). The candidate model set included a global model with a three-way interaction among the fixed effects gear (six), region (Prairie, Ozark), and season (spring, summer, fall), nested models with gear effects, and a null intercept-only model (12 candidate models). Interactions enabled richness by gear to depend on seasons and regions. Our 36 samples were nested within nine sites, and both factors were treated as random effects in all models. We used a negative binomial error distribution to account for overdispersion and inspected residuals for nonindependence and heteroscedasticity (Supplementary material 2[1]). Finally, we evaluated the relative support of candidate models with Akaike’s information criterion (AIC) and gauged model accuracy with pseudo-R^2 statistics that estimated variation explained by fixed effects (marginal: R^2_{M}) and fixed + random effects (conditional: R^2_{C}) (Nakagawa et al. 2017).

Question 2: Which gears were most redundant?

We used Sørensen’s similarity coefficient to quantify the average compositional overlap in species (presence or absence) among subsamples within (six gears) and among gears (30 gear combinations). Sørensen’s coefficients were metrics for redundant sampling effort that excluded joint absences and could range from 0 (= no shared species) to 1 (= identical species; Anderson et al. 2011). We implemented a resampling procedure to estimate average subsample overlap for each combination. For example, overlap between electrofishing and seining within each sample was estimated by calculating Sørensen’s coefficient from one randomly selected electrofishing subsample and one seining subsample. We also noted the cumulative species richness within these two subsamples. When calculating overlap between subsamples from the same gear, we sampled without replacement to avoid pairing identical subsamples. We replicated these steps 999 times and averaged coefficients and subsample richness across replicates and samples.

Question 3: What combination of gears most efficiently detected 90% of observed species richness?

We identified the most efficient protocol that on average detected 90% of observed richness across samples, which is a common benchmark in richness assessments (Flotemersch et al. 2011). We hypothesized efficiency could be further improved by minimizing redundant effort within and among gears. Therefore, we developed a resampling procedure to estimate the average richness that would have been detected during each sample by each of the 287 496 candidate protocols nested within the full-effort protocol (total protocols = $\prod_i^6 x_i$, where x equals 11 and 6 for each active and passive gear i, respectively). For example, the procedure randomly selected without replacement two mini-fyke nets and three sections worth of trawling subsamples for a protocol requiring two mini-fyke nets and 30% of the full trawling effort (i.e., three sections = three of 10 trawl subsamples for a 40 m wide river; six of 20 subsamples for an 80 m wide river). Then richness was calculated from these subsamples. These steps were replicated 999 times, and we obtained final estimates of percent richness for each candidate protocol by averaging richness across replicates (see Supplementary material 3 for code[1]).

Richness was standardized across samples by converting the estimated richness detected by each candidate protocol to the percentage of richness observed in each sample (hereinafter “percent richness”). Then we selected the protocol requiring the least effort (fewest combined sections and nets) that detected ≥90% of species per sample (hereinafter “integrated-gear protocol”) and examined its performance in further analyses (see below). Ours and most other richness assessments report percent **observed** richness rather than percent **theoretical** richness (observed species + unobserved species). For clarity, Chao’s (1987) incidence-based estimator of theoretical richness indicated the full-effort protocol detected on average 86% ± 9% (mean ± SD) of species at sites per sample, meaning our reported percentages of richness is slightly lower than theoretical richness (Table 2).

Question 4: Did the most efficient protocol detect a consistent percentage of richness across regions and seasons?

After formalizing the most efficient gears into the integrated-gear protocol, we examined the protocol’s consistency across regions and seasons, which might be important if broadly using the protocol within regional monitoring programs. Rather than expecting investigators to emulate our exact scaling scheme in the field (i.e., eq. 1), we simplified the integrated-gear protocol by categorizing rivers into two groups (Small Rivers: <65 m wide, $n = 5$; Large Rivers: ≥65 m wide, $n = 4$). The number of subsamples corresponded to the average MWCW of sites within each category (average MWCW of Small Rivers = 52 m, Large Rivers = 82 m). Consequently, Small and Large rivers required 34 and 50 subsamples, respectively, in further randomizations (see Results for expanded section on integrated-gear subsample requirements).

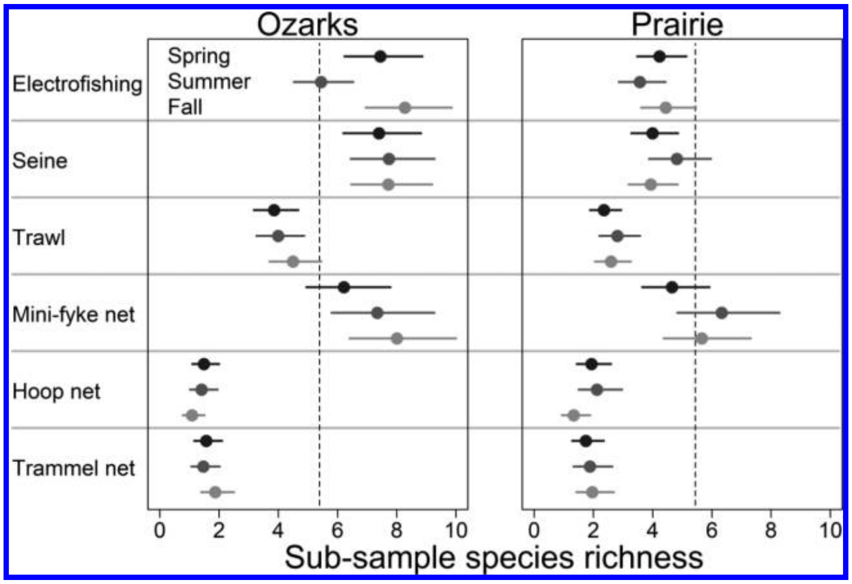
The spatiotemporal variability of the integrated-gear protocol was visualized by plotting the relationship between sampling effort and percent observed richness for samples (i.e., species-accumulation curve (SAC); Gotelli and Colwell 2001). We constructed a SAC for each sample using a resampling procedure to ensure its form was insensitive to any specific sampling sequence. The procedure first calculated observed richness of a randomly selected subsample from a pool of all subsamples available to the integrated-gear protocol. Next, the procedure conducted 999 replicates and averaged richness across replicates. These steps were repeated while incrementally increasing the number of subsamples by one without replacement until reaching 34 and 50 subsamples for Small and Large rivers, respectively. Next, we examined

Table 2. Mean (SD) species richness per sample within nine nonwadeable sites across 36 samples in Missouri (USA).

River	Observed	Min.	Max.	Theoretical	IG, 90%	IG, *n* = 20	E, *n* = 20
Black	67 (6)	61	75	85 (20)	60 (6)	52 (5)	40 (8)
L. Gasconade	60 (3)	55	64	65 (4)	54 (4)	43 (4)	35 (8)
L. Grand	33 (3)	29	35	39 (6)	29 (3)	23 (3)	16 (1)
L. Meramec	69 (1)	68	70	77 (4)	62 (3)	48 (3)	40 (4)
Lamine	40 (4)	36	45	46 (5)	35 (3)	31 (3)	22 (8)
Salt	47 (2)	45	50	52 (5)	43 (2)	38 (2)	34 (5)
U. Gasconade	52 (4)	47	55	68 (17)	47 (2)	37 (2)	31 (2)
U. Grand	29 (4)	25	34	40 (8)	25 (3)	21 (2)	18 (3)
U. Meramec	46 (3)	43	48	52 (3)	42 (3)	38 (3)	25 (5)

Note: L = lower, U = upper, IG = integrated-gear, *n* = subsamples, E = electrofishing. Theoretical richness values are estimates of total (observed + unobserved) species obtained from Chao's (1987) incidence-based estimator. Richness (IG, 90%) is from the integrated-gear protocol. Richness (IG, *n* = 20) is from 20 subsamples via the integrated-gear protocol (multiple gears). Richness (E, *n* = 20) is from twenty 50 m electrofishing subsamples.

Fig. 3. Predicted subsample richness ± 95% confidence interval by gear, region, and season (*n* = 2900 subsamples). Dashed vertical lines signify the reference condition in the best-supported model (intercept = summer electrofishing in Ozark rivers).



whether the maximum observed percent richness (= response variable) varied by season and (or) region by fitting four linear mixed-effects regression models: intercept-only, region-only, season-only, and region + season. We included a site-level random effect in all models to account for nonindependence of multiple samples per site and used $\mathrm{AIC_c}$ and R^2_{M} to evaluate relative support for competing models.

Question 5: Was the integrated-gear protocol more effective and consistent than traditional effort with an electrofishing-only protocol?

We compared SACs constructed from the integrated-gear protocol and a traditional fish richness assessment requiring 1 km of electrofishing using the resampling procedures described immediately above. Curves were constructed by incrementally increasing subsamples from 1 to 20 since each electrofishing subsample was 50 m (20 subsamples = 1 km). Next, we linearly regressed the percent species richness after 20 subsamples (= response) to one of nine models. These models evaluated whether (*a*) integrated-gear and 1 km electrofishing protocols detected different percentages of species richness (i.e., effect of protocol), (*b*) percentages varied by season and (or) region (effects of season and (or) region), and (*c*) one protocol was more sensitive to season and (or) region than the other (interactions between protocol and season or region). We also included MWCW as a covariate in all models because both protocols required 20 subsamples rather than scaling effort to river size. The 1 km electrofishing protocol was nearly twice as variable as the integrated-gear protocol (SD of 1 km electrofishing = 9.9%, integrated-gear = 5.4%), so we used generalized least squares regression to estimate separate variances for the two protocols. We also forced multiple observations from the same sites to have identical errors via a compound symmetry error structure and evaluated relative support for competing models with $\mathrm{AIC_c}$ and a pseudo-R^2 statistic from R package "piecewiseSEM" (Lefcheck 2016).

Results

We detected 89 185 individual fish and 140 species across 36 samples. Observed species richness per sample ranged from 25 to 75 (Table 2). Mean (±SD) richness per sample by region equaled 59.6 ± 9.2 species (Ozarks) and 37.1 ± 7.8 species (Prairie). By comparison, the historically (1970–2010) reported average species richness per sample (excluding samples with ≤5 species) in Ozark (*n* = 371) and Prairie (*n* = 141) river sites (drainage area ≥ 1000 km²) was 24.1 ± 9.5 species and 16.8 ± 6.9 species, respectively (Missouri Department of Conservation, unpublished fish assemblage database). Among historical surveys, 93% used one (28%) or two (65%) gears, with electrofishing and seining being predominant gears.

Question 1: Which gears detected the most species per unit effort?

Mini-fyke nets, seining, and electrofishing detected the most species per subsample, but the relative efficacy of gears varied

Table 3. Ranked competing models explaining subsample richness (n = 2900) from 36 samples in nine nonwadeable sites in Missouri (USA).

Rank	Model	K	LL	ΔAIC	w_i	R^2_M	R^2_C
1	G + R + S + G × R + G × S + R × S	26	−6895.8	0.0	0.98	0.37	0.42
2	G + R + S + G × R + G × S + R × S + G × R × S	36	−6889.5	7.5	0.02	0.37	0.42
3	G + M + G × M	12	−6929.7	40.0	<0.01	0.35	0.40
4	G + R + S + G × R	14	−6928.3	41.1	<0.01	0.35	0.40
5	G + R + S + G × S	19	−6932.7	60.0	<0.01	0.36	0.41
6	G + S + G × S	18	−6937.6	67.6	<0.01	0.28	0.41
7	G + R	7	−6965.1	100.8	<0.01	0.34	0.40
8	G + R + S	9	−6963.7	101.9	<0.01	0.34	0.40
9	G + R + S + R × S	11	−6961.9	102.3	<0.01	0.35	0.39
10	G	6	−6970.1	108.6	<0.01	0.27	0.40
11	G + S	8	−6968.5	109.5	<0.01	0.27	0.40
12	Intercept-only (null)	1	−7409.3	977.1	<0.01	<0.01	0.13

Note: Also included are the number of fixed-effects (K), log-likelihoods (LL), ΔAkaike information criteria (AIC), model weights (w_i), and marginal (M) and conditional (C) R^2 statistics. G = Gear, R = Region, S = Season. All models included random effects for site and sample. Estimated fixed-effects in model 1 are in the online Supplementary material 4[1].

slightly among seasons and regions (see Fig. 3 for estimated richness per subsample by gear). The best-supported model explaining subsample richness included all main effects and three two-way interactions among season, region, and gear (w_1 = 0.98; R^2_M = 37%; Table 3; see Supplementary material 4 for effect sizes[1]). All effect sizes reference summer electrofishing in Ozark rivers. Overall, predicted subsample richness ranged from 1.1 to 8.3 species and was mainly structured by gear (gear-only model, R^2_M = 27%) and region (gear + region model, R^2_M = 34%), but not season (gear + season model, R^2_M = 27%). Although two-way interactions indicated effect sizes interdependently varied by gear, season, and region, predicted subsample richness was generally consistent with the signs of main effects, making predictions more interpretable and generalizable. For example, predicted subsample richness by gear was almost always higher in Ozark rivers than in Prairie rivers, but to varying degrees depending on gear and season. Notable exceptions resulting from the gear × region interaction were for hoop (mean predicted species = 1.3 in Ozarks, 1.8 in Prairie) and trammel nets (= 1.6 in Ozarks, 1.9 in Prairie) when subsample richness was slightly higher in Prairie rivers. The effect of season was also notable with electrofishing subsample richness in spring (mean predicted species = 7.4 in Ozarks, 4.2 in Prairie) and fall (= 8.3 in Ozarks, 4.4 in Prairie) being slightly higher than that in summer (5.4 in Ozarks, 3.6 in Prairie).

The ranked order of subsample richness by gears was generally consistent across seasons in Ozark (Spearman's $\rho > 0.77$) and Prairie ($\rho > 0.89$) sites. For example, the most species were caught via mini-fyke nets (range of predicted richness per subsample = 4.7–8.0 species), seining (3.9–7.3 species), and electrofishing (3.6–8.3 species), whereas hoop (1.1–2.1 species) and trammel nets (1.5–2.0 species) consistently detected the fewest species, and trawling was intermediate (2.4–4.5 species).

Question 2: Which gears were most redundant?

All Sørensen's coefficients within and among gears were <0.50, indicating fish species in subsamples were compositionally more dissimilar than similar (Fig. 4). The six highest coefficients (Sørensen's coefficient > 0.27; i.e., most redundant) were multiple subsamples from the same gears (e.g., two electrofishing runs). In contrast, the lowest compositional overlap (Sørensen's coefficient < 0.10; least redundant) was between gears targeting large-bodied fishes (hoop and trammel nets) and those targeting small-bodied fishes (seining and trawling). Coefficients were intermediate for gear combinations targeting similarly sized species, but in different habitats.

Greater overlap within gears than among gears meant certain combinations of gears detected more species than two subsamples from the single-most effective gear (mini-fyke nets). For example, two mini-fyke nets on average detected slightly fewer cumulative species (10.2) than three other gear combinations (electrofishing + mini-fyke = 11.3 species, electrofishing + seine = 11.1 species, mini-fyke net + seine = 10.8 species; Fig. 4).

Questions 3–4: What gear combination most efficiently detected 90% of observed richness, and did this protocol detect a consistent percentage of richness across regions and seasons?

The average SAC constructed from subsamples from the full-effort protocol across 36 samples showed most species were detected by <20% of effort (Fig. 5). Only 2.0% of species (0.5–1.5 species) were detected on average with our final 10% of effort (i.e., 2.5–4.0 h of additional sampling). On average (mean ± SD), detecting 90% of species required 59.5% ± 3.3% of our original, full effort. No single gear detected on average 90% of observed species: electrofishing = 62.7% ± 10.1%, seining = 57.6% ± 10.9%, mini-fyke nets = 34.5% ± 10.9%, trawling = 29.5% ± 8.9%, trammel nets = 11.9% ± 6.6%, hoop nets = 11.1% ± 6.1%. Instead, detecting 90% of species required ≥2 gears and was achieved by 69 698 (24%) of candidate protocols. The most efficient protocol (fewest subsamples) that detected on average 90% of species required 51.9% of our original effort. This protocol featured 70% of the original electrofishing effort, 60% of original seining effort, 30% of original trawling effort, and five mini-fyke nets, while excluding hoop and trammel nets. Accordingly, integrated-gear protocols for Small and Large rivers required 34 and 50 total subsamples, respectively (Small River subsamples = 14 electrofishing runs, 12 seine hauls, three trawl runs, five mini-fyke nets; Large River subsamples = 21 electrofishing runs, 18 seine hauls, six trawl runs, five mini-fyke nets; Supplementary material 1[1]). A sample with these integrated-gear protocols would likely require 2–4 days with a three-person crew.

Species-accumulation curves from the integrated-gear protocol were similar across seasons and regions (Fig. 6). For example, the integrated-gear protocol on average achieved 90% of observed species richness with low variation (SD = 1.6%). Moreover, no models were better supported than the null model (w_1 = 0.64), with the region-only model having the second most, but only marginal, support (ΔAIC_c = 1.6; w_2 = 0.28; R^2_M = 3%; Table 4).

Question 5: Was the integrated-gear protocol more effective and consistent than traditional effort with an electrofishing-only protocol?

Percentages of observed richness varied widely with the 1 km electrofishing protocol (range among samples = 36.1%–82.3%) compared with the integrated-gear protocol (64.0%–86.6%). The

Fig. 4. Left: heat plot displaying the average compositional overlap (species presences or absences with Sørensen's coefficients) between two subsamples within and among gears (n = 2900 subsamples). Higher coefficients (darker boxes) have greater overlap in species composition. Subsamples were from 36 samples in nine nonwadeable sites in Missouri (USA). Right: average cumulative richness from two subsamples from different gear combinations. E-fish = electrofishing, M-Fyke = mini-fyke net.

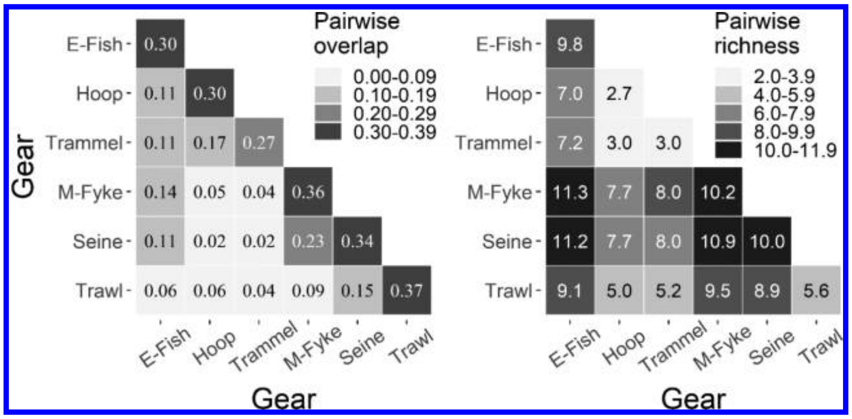
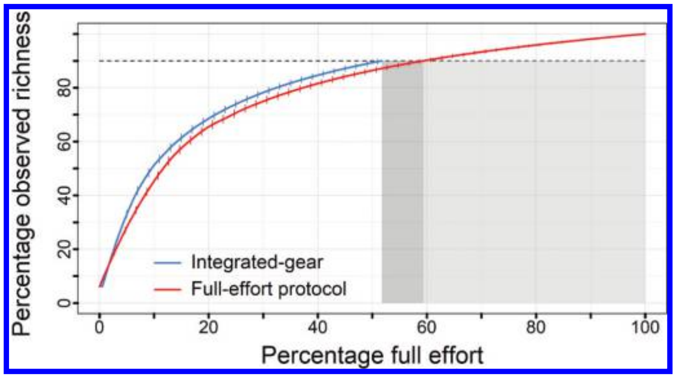


Fig. 5. Mean species-accumulation curves (±95% confidence intervals) from 36 samples for full-effort and integrated-gear protocols in Missouri (USA). Light and dark gray boxes depict the 40.5% and 7.6% of effort saved by only targeting 90% of species and minimizing redundant effort among gears, respectively. [Colour online.]



best-supported model explaining variation in percent richness included effects of protocol type, season, region, a protocol × season interaction, and MWCW (pseudo-R^2 = 62%; w_1 = 0.59; Table 5; Fig. 7). Protocol type had the largest effect size ($\hat{\beta}_{\text{Integrated}}$ = 20.2, SE = 5.9). For example, 20 subsamples with the integrated-gear protocol on average detected 15.9% (4–12 species) more of the fish assemblage than the 1 km electrofishing protocol (mean ± SD; integrated gear = 74.4% ± 5.4%; 1 km electrofishing = 58.5% ± 9.9%). If 58.5% of richness is acceptable for monitoring purposes, then the integrated-gear protocol on average required only 10.7 subsamples (i.e., 53.5% efficiency improvement over 1 km electrofishing). In fact, SACs between protocols were only similar in the Salt River, a flow-regulated river where fish congregated in effectively electrofished shallow pools during frequent periods of artificially low discharge (Fig. 7*f*).

The protocol × season interaction indicated electrofishing-only protocols performed inconsistently across seasons compared with the integrated-gear protocol, especially from fall to summer ($\hat{\beta}_{\text{Integrated-Fall}}$ = –7.8, SE = 3.8). On average, the electrofishing-only protocol detected only 53.6% of species in summer compared with 62.7% in fall. In contrast, sampling with the integrated-gear protocol had little among-season variation (average percentage of species by season = 74.2% in spring, 73.7% in summer, 75.2% in fall; Fig. 7*j*). The effect of region was small, imprecise ($\hat{\beta}_{\text{Prairie}}$ = 2.2, SE = 2.7), and equivocal based on moderate support for a model without a region effect (ΔAIC_c = 1.1; pseudo-R^2 = 62%; w_2 = 0.34) but still controlled for spatial variation. Finally, a precisely estimated effect for MWCW ($\hat{\beta}_{\text{MWCW}}$ = –0.3, SE = 0.1) indicated the fixed 20-subsample effort detected lower percentages of richness as river size increased. Overall, SACs between the two protocols revealed the electrofishing-only protocol was more variable, less efficient, seasonally biased, and detected fewer species than comparable effort with the integrated-gear protocol.

Discussion

Our study was among the first to evaluate the performance of an intensive multigear survey design for sampling riverine fish assemblages across seasons and regions. The intensity and extensiveness of sampling provided rare insights into richness and fish-sampling dynamics. For example, we documented at least 23 new distributional accounts (Dunn et al. 2018) and rediscovered multiple imperiled species presumed extirpated from specific subdrainages or statewide. Overall, our sampling indicated rivers likely support more species than historically reported per sample, but detecting high percentages of richness requires an optimized design that distributes effort across complementary gears.

Subsample richness and gear redundancy

Boat electrofishing and seining were the most effective individual active gears across regions and seasons. Several gear-evaluation studies spanning broad geographical areas and river types have found electrofishing to be the single-most effective and versatile gear for sampling riverine fishes (Neebling and Quist 2011; Gibson-Reinemer et al. 2016*a*; Zajicek and Wolter 2018). In contrast, the effectiveness of seining often varies by study (Simon and Sanders 1999; Lapointe et al. 2006), and we suspect these disparities partly reflect the availability of easily seined habitats among studies. For example, similar to Neebling and Quist (2011), our seining subsamples in Prairie sites detected fewer species than electrofishing (mean predicted species, seining = 4.3, electrofishing = 4.7), but in our Ozark sites, seining subsamples detected more species than electrofishing (seining = 7.6, electrofishing = 7.1). Unlike most Prairie rivers, Ozark rivers are largely unchannelized and retain many shallow margins that may be inhabited by small-bodied species and juveniles that can be effectively seined. Nonetheless, our results indicate electrofishing and seining were both relatively effective individual gears.

The effectiveness of passive effort varied considerably among gears. Riverine richness assessments often exclude passive gears because of additional retrieval costs, meaning there is limited information on the comparability of passive versus active gears. Although hoop and trammel nets targeted areas that were not easily sampled by other gears, neither gear detected many species

Fig. 6. Mean (±95% confidence intervals) species-accumulation curves from 36 samples in Missouri (USA) for the integrated-gear protocol across regions and seasons. [Colour online.]

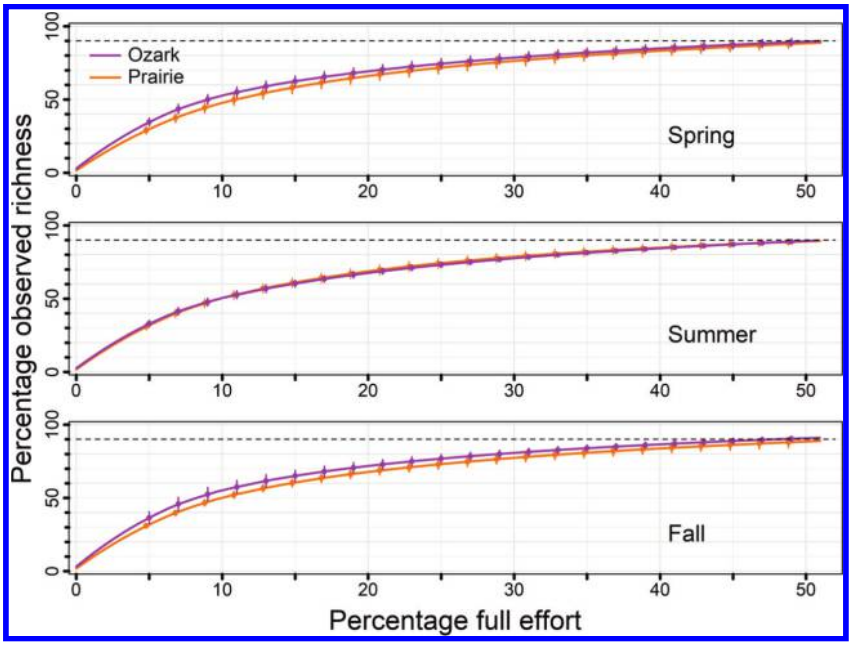


Table 4. Ranked competing models explaining the percentage of observed fish species richness detected with the integrated-gear protocol ($n = 36$ samples) in nine nonwadeable sites in Missouri (USA).

Rank	Model	K	LL	ΔAIC_c	w_i	R^2_M	R^2_C
1	Intercept-only (null)	1	78.1	0.0	0.64	0.00	0.00
2	R	2	78.6	1.6	0.28	0.03	0.03
3	S	3	78.3	4.9	0.06	0.01	0.01
4	R + S	4	78.7	6.9	0.02	0.04	0.04
5	R + S + R × S	6	79.1	12.7	<0.01	0.05	0.05

Note: Also included are the number of fixed effects (K), log-likelihoods (LL), ΔAkaike information criteria corrected for small sample size (AIC_c), model weights (w_i), and marginal (M) and conditional (C) R^2 statistics. R = Region, S = Season. All models included a random effect for site. The estimated fixed-effect in model 1 is in the online Supplementary material 4[1].

Table 5. Ranked competing models explaining the percentage of observed richness detected with integrated-gear and 1 km electrofishing protocols from 36 samples in nine nonwadeable sites in Missouri (USA).

Rank	Model	K	LL	ΔAIC_c	w_i	pseudo-R^2
1	P + R + S + P × S + MWCW	8	−218.0	0.0	0.59	0.62
2	P + S + P × S + MWCW	7	−219.9	1.1	0.34	0.62
3	P + R + S + P × R + MWCW	7	−222.1	5.4	0.04	0.59
4	P + R + S + MWCW	6	−224.4	7.3	0.02	0.59
5	P + S + MWCW	5	−226.3	8.6	0.01	0.59
6	P + R + P × R + MWCW	5	−227.1	10.1	<0.01	0.57
7	P + R + MWCW	4	−229.4	12.2	<0.01	0.57
8	P + MWCW	3	−231.3	13.6	<0.01	0.57
9	MWCW (null)	2	−244.8	38.2	<0.01	0.14

Note: Rankings were based on ΔAkaike information criteria corrected for small sample size (AIC_c). Also included are the number of fixed-effects (K), log-likelihoods (LL), and model weights (w_i). P = protocol, R = Region, S = Season, MWCW = mean wetted-channel width. All models accounted for nonindependence of multiple samples per site and allowed variance to vary by protocol. Estimated fixed effects in model 1 are in the online Supplementary material 4[1].

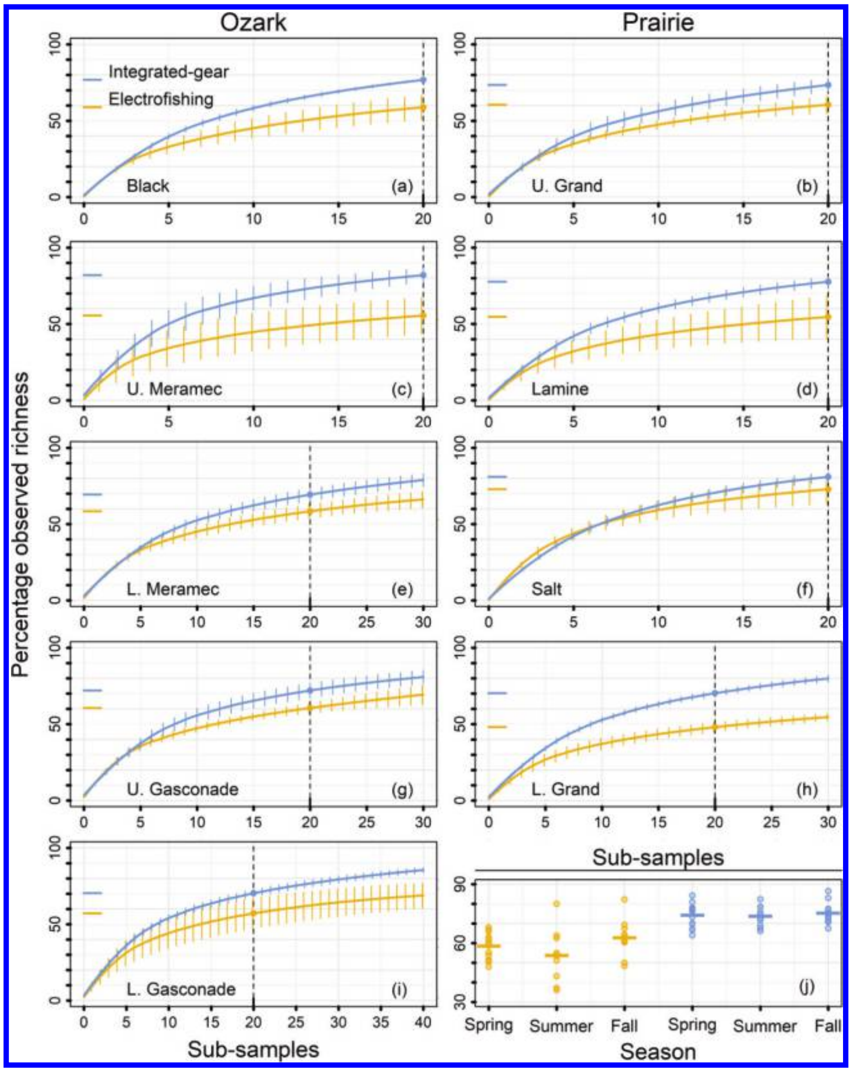
on average per net (<2.5 species), which is consistent with Pugh and Schramm (1998) and Lapointe et al. (2006). Moreover, despite Ozark sites supporting on average 23 more species, the mean predicted subsample richness of both gears was slightly higher in Prairie sites (hoop = 1.8 species; trammel = 1.7 species) than in Ozark sites (hoop = 1.3 species; Ozark = 1.6 species). Consequently, neither gear would have provided an informative index of underlying fish richness if only used at low effort levels. In contrast, subsample richness for mini-fyke nets reflected regional differences in richness and on average detected the most species per subsample among all gears across spatiotemporal settings (mean predicted subsample richness = 6.4 species). Standard or mini-fyke nets are frequently used to sample fish assemblages within lentic and (or) floodplain waterbodies (e.g., Fischer and Quist 2014), but their use is comparatively rare in riverine fish richness assessments (but see Schloesser et al. 2012*b*; Braun et al. 2016). Our findings indicate mini-fyke nets may be undervalued options for assessing riverine richness, especially if used in structurally complex and (or) lateral low-velocity habitats.

The most efficient path to documenting high species richness is one that minimizes redundant effort, and compositional overlap among subsamples signifies redundant sampling. Overlap was always lower among gears than within gears, which likely reflected the high habitat and taxonomic diversity of our study systems. For example, low overlap could have resulted from species- and life-stage-specific selection of the many different habitats within sites and gear-specific detections for certain fish morphologies and behaviors (Schloesser et al. 2012*a*). Consequently, our results using basic sampling units (subsamples) indicate use of individually effective and complementary gears across habitats helps minimize redundant sampling effort, thereby more efficiently representing the high biophysical diversity of rivers.

Integrated-gear protocols

On average, we reduced our original sampling effort based on subsamples by 48.1% by targeting only 90% of species and combining complementary gears. Difficult-to-detect species are often rare and require disproportionate effort to capture (Angermeier and Smogor 1995; Kanno et al. 2009). For example, SACs from our full-effort protocol indicated detecting 90% of species on average required 59.5% of effort. Similarly, Kanno et al. (2009) examined eight fish datasets across North America encompassing multiple stream sizes and noted detecting 90%–95% of observed richness required on average 58.0% of each study's full sampling effort. Other riverine fish assessments report similar findings (i.e., de-

Fig. 7. Mean species-accumulation curves (±95% confidence intervals) based on subsamples from electrofishing-only (50 m run) and integrated-gear (multiple gears) protocols from 36 samples at nine sites (panels *a*–*i*) in the Ozark and Prairie regions of Missouri (USA). Lower right panel (*j*) is percent richness grouped by season with 20 subsamples equaling either 1 km of electrofishing or a combination of gears (electrofishing, trawling, seining, mini-fyke nets) with the integrated-gear protocol. [Colour online.]



tecting 90% of species requires 54%–65% of full effort; Lapointe et al. 2006; Van Liefferinge et al. 2010; Neebling and Quist 2011). However, we saved on average another 7.6% of sampling effort by optimally integrating effort among effective gears and eliminating ineffective gears altogether. For example, our integrated-gear protocol mainly featured the three most individually effective gears (electrofishing, seining, and mini-fyke nets), eliminated the two least-effective gears (hoop and trammel nets), and used only enough trawling to detect the subset of benthic, midchannel species at sites. Our design could provide a practical means for comprehensively assessing riverine richness, but investigators could similarly optimize protocols to detect lower percentages of richness when logistics only afford rapid assessments.

Our approach also generated numerous alternative sampling protocols (287 496) that could provide flexibility for accomplishing multiple, competing sampling objectives. This flexibility could allow protocol development to operate within structured decision-making frameworks that identify implicit sampling objectives from protocol users (Gregory et al. 2012). Beyond optimizing efficiency, protocols could be customized simultaneously for additional objectives including sampling specific taxa, functional guilds, or multimetric indices of riverine condition. Moreover, alternative protocols could circumvent anticipated sampling constraints, such as eliminating passive gears in rivers with unpredictable flow regimes and increasing trawling effort in lieu of seining in deeper sites. Customizable protocols may be especially suited for regional monitoring programs requiring versatility and (or) richness assessments wishing to integrate gears used to inventory main and off-channel components of riverine landscape diversity (Erős et al. 2019).

Spatiotemporal sampling variation

Species-sampling relationships were surprisingly similar with the integrated-gear protocol in Ozark and Prairie rivers despite different environmental conditions and assemblages. This finding was unexpected given several factors that cause species to accumulate more slowly are associated with Prairie rivers, including lower fish densities (Angermeier and Smogor 1995), lower habitat diversity (Fischer and Paukert 2009; Van Liefferinge et al. 2010), and greater anthropogenic disturbance (Hughes et al. 2002). However, species can also accumulate more slowly in species-rich sites (Meador 2005), which might have slowed accumulation rates in Ozark rivers, thereby equalizing SACs across both regions.

We also found SACs were similar across seasons with the integrated-gear protocol. This finding was similar to Erős et al. (2008), who noted SACs constructed from littoral fish assemblages in the Danube River (Hungary) were more sensitive to fine-grain spatial and diel influences than seasonal influences. However, many fish species richness assessments do not investigate species-sampling relationships across seasons and instead limit sampling to specific seasons (late summer – early fall; Reash 1999). Although we caution that assemblage composition and other metrics could vary seasonally (Simon and Sanders 1999; Wolter and Bischoff 2001), our protocol offers a less restrictive sampling window if solely monitoring changes in species richness. This flexibility could prove valuable when conducting emergency impact assessments, avoiding critical periods for sensitive species, and accommodating overburdened field schedules.

In contrast with the integrated-gear protocol, the electrofishing-only protocol was more variable and seasonally biased, especially from summer to fall. One kilometre of electrofishing in summer detected 36.1%–80.0% of richness, which we suspect resulted from varying fish behavior and available habitats among sites. For example, our electrofishing effort mainly sampled littoral areas, which can be temporarily occupied by fish depending on flow and temperature (Wolter and Bischoff 2001; Erős et al. 2008), life stage (Wolter et al. 2016), and behavior (De Leeuw et al. 2007). Especially in summer, many species are restricted to deep areas during daylight that are inaccessible to electrofishing (Simon and Sanders 1999; Flotemersch and Blocksom 2005). The prevalence of these areas varied across our focal rivers spanning a nearly sevenfold difference in river size, which may have contributed to low percentages of richness and high summer variability. In contrast, the integrated-gear protocol was less sensitive to these influences for at least two reasons. First, variability in species-accumulation data decreases as higher percentages of richness are detected (Angermeier and Smogor 1995), and equal effort with the integrated-gear protocol detected more species than electrofishing (mean with 20 subsamples = 74.4% with multiple gears, 58.5% with electrofishing). Second, the four gears within the integrated-gear protocol sampled multiple habitats, thereby detecting species regardless of varying habitat use across seasons and sites. Consequently, less sampling variability should result in greater power to detect trends in species richness, which might be more cost-effective for monitoring over time (Wagner et al. 2013).

Increasing sampling effort at sites often detects additional species and reduces variability in assemblage indicators, especially multimetric indices of riverine ecological condition (Flotemersch and Blocksom 2005; Maret et al. 2007). Many fish richness assessments increase effort by lengthening sampling distances, thereby also expanding the longitudinal extent of their sites (Flotemersch et al. 2011). These designs originated in small streams where a pass with a single gear (i.e., electrofishing) often samples most available areas (e.g., Lyons 1992; Angermeier and Smogor 1995), meaning conflating sampling effort with stream length is unavoidable. However, lengthening sites also accumulates rare species by incorporating additional habitats into sites from longitudinal gradients, which may induce sampling variability, causing investigators to lengthen sites further. Because riverscapes are continuous and unique species are distributed throughout river networks (Fischer and Paukert 2009), there may not be a finite site length for entirely sampling assemblages. For example, the recommended site lengths from fish assessments reexamined by Kanno et al. (2009) were mostly proportional to each assessment's initial sampling length. In contrast with longitudinally expanding designs, we controlled effort by varying sampling intensity, allowing us to focus on available within-site habitat diversity (i.e., subsamples per 50 MWCWs). Sampling intensity-focused designs, such as ours, may be especially relevant for large rivers with diverse, laterally and vertically distributed habitats.

Adaptations and future applications

Our survey design distributed effort across sites with multiple gears using a scaling scheme proportional to river size. The design's main benefits are comprehensively sampling available habitats and, at a species level, potentially providing information on habitat use, detection, and density from subsamples. Moreover, the comprehensiveness of the survey design could help validate emerging molecular techniques (environmental DNA, metabarcording) for biodiversity monitoring (Pont et al. 2018). Our general design could be adapted for different objectives and rivers. For example, investigators could eliminate the scaling scheme (eq. 1) by developing separate protocols for different river size classes beforehand (e.g., Neebling and Quist 2011) or applying identical effort across river sizes (Bayley and Peterson 2001). Our design could also likely be adapted to provide abundance- and (or) guild-based metrics needed for most riverine multimetric indices. For example, investigators could calibrate catch-per-effort data among gears using clustered subsamples within sections (Peterson and Paukert 2009) and (or) combine effort across subsamples via several techniques (Gibson-Reinemer et al. 2016*b*). Alternatively, investigators could designate certain gears for specific biotic metrics (De Leeuw et al. 2007). Regardless, multiple gears and the hierarchical design afford flexibility for making inferences at site and subsample grain sizes.

Conclusion

Our approach and intensive sampling provided several findings relevant to riverine fish assessments. Electrofishing, seining, and mini-fyke nets detected the most species with comparable effort across three seasons in rivers spanning two distinct regions. However, a protocol integrating effort among complementary gears that targeted different habitats was more effective than any single gear. Similarly, compared with a traditional electrofishing-only protocol, an integrated-gear protocol consistently detected more species with greater precision regardless of season and region.

Protocols that accurately assess riverine fish species richness may be needed as freshwater species and management organizations cope with rapidly changing environments. Kanno et al. (2009) noted that the main goal of most fish assessments has been monitoring assemblage condition, rather than documenting richness and species distributions. Traditional monitoring designs and condition-based assessments are critical tools for documenting fish-assemblage responses to changing waterbody condition (USEPA 2016). However, their restricted focus on specific taxa might underestimate local richness, especially in diverse and difficult-to-sample systems and, therefore, distort reported diversity patterns at riverscape scales. Our approach may provide a template for improving the comprehensiveness of surveys, which could help conserve riverine biodiversity by clarifying distributions of declining or introduced species and informing riverscape biodiversity planning and prioritization.

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USGS. Although the software has been subjected to rigorous review, the USGS reserves the right to update the software as needed pursuant to further analysis and review. No warranty, expressed or implied, is made by the USGS or the US Government as to the functionality of the software and related material nor shall the fact of release constitute any such warranty. Furthermore, the software is released on condition that neither the USGS nor the US Government shall be held liable for any damages resulting from its authorized or unauthorized use. The computation for this work was performed on the high performance computing infrastructure provided by Research Computing Support Services and in part by the National Science Foundation under grant number CNS-1429294 at the University of Missouri, Columbia, Missouri.

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