Comparing electrofishing and snorkelling for characterizing fish assemblages over time and space

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Comparing electrofishing and snorkelling for characterizing fish assemblages over time and space

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26 Abstract

27 Environmental processes and dispersal movements occurring over long distances (10
28 to 100 km) continually influence local stream fish assemblages. However, electrofishing
29 protocols are classically implemented in short reaches (~1km) and are not suited for frequent
30 characterization of assemblages over long distances. We developed a new sampling
31 protocol (SPA: Snorkelling Point Abundance) for characterizing fish assemblages over long
32 distances, using series of sampling points, as often applied in electrofishing (PASE: Point
33 Abundance Samples by Electrofishing). Nine pairs of PASE and SPA surveys, repeated in a
34 narrow and in a wide stream, were compared. Greater species abundance, occurrence and
35 richness were found on PASE, but relative species abundance were comparable between
36 protocols. Assemblages were highly variable over time (between-surveys) on both protocols.
37 The spatial structure of point assemblages (within-survey) was consistent between protocols
38 and related to species' habitat use (depth, current velocity). For several species, the
39 longitudinal distribution of abundance along reaches was comparable between protocols
40 when surveys were pooled. Overall, SPA could be an alternative to electrofishing for
41 analysing spatial structure over long distances.

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44 **Key-words:** sampling efficiency, electrofishing, underwater observation, abundance count,
45 freshwater fish, STATIS.

Résumé

La dispersion des individus et les processus environnementaux agissant sur de longues distances (10-100 km) influencent continûment les assemblages de poissons en rivière. Les protocoles d'échantillonnage par pêche électrique, essentiellement utilisés sur des petits tronçons (~ 1km), ne permettent pas de caractériser les assemblages sur de longues distances. Nous avons développé un nouveau protocole d'échantillonnage basé sur des observations régulières de points en plongée (SPA), semblable au protocole standard de pêche électrique par points (PASE). Nous avons comparé neuf paires de campagnes (PASE et SPA) dans une petite et une grande rivière. La pêche électrique estime une plus grande abondance, occurrence et richesse spécifique. Les assemblages étaient variables dans le temps (inter-campagnes) indépendamment du protocole. Les points d'échantillonnage ont présenté des structures spatiales (intra-campagnes) comparables entre protocoles et liées à l'habitat utilisé par les espèces. Après regroupement des campagnes, la répartition longitudinale de l'abondance de certaines espèces le long des tronçons était comparable entre protocoles. Globalement, la plongée est une alternative aux pêches électriques par points pour analyser des structures spatiales sur de grandes distances.

Mots-clefs : efficacité d'échantillonnage, observations en apnée, comptage, poissons d'eau douce, STATIS.

Introduction

Fish metacommunities (Wilson 1992, Leibold et al. 2004) are groups of local communities connected by dispersal and influenced by series of regional and local environmental filters (Angermeier and Winston 1998, Jackson et al. 2001, Heino et al. 2009). Understanding the influence of environmental processes and dispersal and the changes they undergo (e.g., alterations in habitat and connectivity) on fish metacommunities requires observation at the scale of the dispersal processes (Fausch et al. 2002). Dispersal frequently occurs over 10-100 km distances for holobiotic fish populations (Persat et al. 1994), and over hundreds of kilometres for diadromous populations (Groot and Margolis 1991, Persat et al. 1994). Conventional sampling techniques such as electrofishing (Cowx et al. 2009, Copp 2010, Tomanova et al. 2013) are often difficult to implement over such distances, due to logistical limitations. Direct observation by snorkelling, frequently used in marine environments (Fowler 1987, Kulbicki et al. 2010, Bozec et al. 2011), is an alternative sampling method in freshwaters when great distances need to be covered (Torgersen et al. 2006, Brind'Amour et al. 2011, Brenkman et al. 2012).

Comparisons of fish abundance estimates in rivers or lakes by electrofishing versus snorkelling often reported lower total abundance estimates with snorkelling, but results depended on the species/family considered (Brosse et al. 2001, Macnaughton et al. 2014). Studies also showed that fish abundance estimates with the two sampling protocols were strongly correlated (e.g., from 0.50 to 0.90 for salmonids: Hankin and Reeves 1988, Wildman and Neumann 2003). However, they also suggested that comparison could be influenced by habitat characteristics (e.g., water depth, current velocity, flow rate), species size and behaviour (e.g., schooling or cryptic species) and observer bias (Joyce and Hubert 2003, Persinger et al. 2004, Macnaughton et al. 2014).

A frequent limitation of these methodological comparisons was their short sampling units (length < 2 km for rivers; Heggenes et al. 1990, Chamberland et al. 2014); most comparisons used observations made along transects shorter than 100 m (Chamberland et

al. 2014, Weaver et al. 2014). In addition, many comparisons were not repeated between years or seasons to evaluate temporal stability (Hankin and Reeves 1988, Persinger et al. 2004). Finally, only a few studies compared abundance estimates at community level (Brind'Amour and Boisclair 2004, Persinger et al. 2004, Chamberland et al. 2014, Weaver et al. 2014, Macnaughton et al. 2015), while many others compared sampling protocols on less than three target species, generally salmonids (Hankin and Reeves 1988, Heggnes et al. 1990, Ensign et al. 1995, Joyce and Hubert 2003, Wildman and Neumann 2003).

A literature search retrieved only two studies comparing electrofishing and snorkelling with similar sampling designs for both protocols (Brosse et al. 2001, Weaver et al. 2014). In a lake-based study, Brosse et al. (2001) used series of independent points, as frequently applied in electrofishing in medium to large rivers (PASE sampling: Point Abundance Sample with Electrofishing; Nelva et al. 1979, Copp 2010). They concluded that abundance estimates of lacustrine fish obtained by electrofishing were higher, but may be more strongly biased by fright and disturbance of fish assemblages. In rivers, Weaver et al. (2014) used predetermined open sampling grids (no block nets) and counted fish first by snorkelling then by electrofishing. They concluded that snorkelling provided adequate estimates of fish density, especially when other methods are difficult to apply or electrofishing risks harming or killing protected species. Nevertheless, they advised comparing efficacy between snorkelling and other methods before implementation.

The present study provides an extensive comparison of electrofishing and snorkelling surveys made in two stream reaches, one narrow and one wide. The originality lays in studying medium to long reaches (2.5 and 14 km), paired sampling at repeated time points (n=9 surveys) and many fish species (n=23), with similar sampling designs for both electrofishing and snorkelling. We describe a new snorkelling protocol (SPA: Snorkelling Point Abundance) for characterizing fish assemblages over long distances, using series of regular point observations as often applied in electrofishing (PASE). The study objectives were (1) to describe and compare estimates of density and occurrence between electrofishing and snorkelling; (2) to compare spatial and temporal variations in fish

community structure between the two protocols; and (3) to compare the longitudinal distribution of species abundance between protocols.

Methods

Study reaches

Snorkelling and electrofishing protocols were compared in two rivers with contrasting habitat conditions: a wide river (Ain River: total length 190 km) regulated for hydropower and subject to hydropeaking, and a narrow unregulated phreatic tributary (Seymard River: 15 km long), in south-eastern France (Fig. 1). The study reach in the Ain River was 14 km long, ~70 m wide, with mean annual discharge of $\sim 100 \text{ m}^3 \cdot \text{s}^{-1}$ (Fig. 1). The Seymard River reach was 2.5 km long, ~10 m wide, with mean annual discharge of $\sim 1 \text{ m}^3 \cdot \text{s}^{-1}$. The Seymard reach was situated immediately upstream of the confluence with the Albarine, an intermittent stream that joins the Ain River about 400 m downstream (Fig. 1).

Fish sampling protocols

Five pairs of surveys were conducted in the Ain River and four pairs in the Seymard River, in spring or autumn, between 2012 and 2013 (Table 1). Each pair comprised a PASE (electrofishing) and a SPA (snorkelling) survey, at a maximum 12 days' interval (Table 1). For both protocols, surveys consisted of a series of sampling points chosen along the reaches, moving downstream. The exact location of sampling points could differ between protocols for a given paired survey.

The PASE protocol was implemented from a motorboat (or by wading in shallow areas), attempting to reduce fish fright as much as possible by a stealthy approach to the sampling points. A long anode was immersed and held steady at each sampling point, and all fish around the anode were captured with a landing net. The electrical generator was set at each survey according to water conductivity, so as to sample with a current of 400-500 V and 1.5 A. The protocol involved a team of three or four operators. The surface area of each

sampling point was $\sim 7 \text{ m}^2$, corresponding to an average attraction radius of 1.5 m around the anode, although that could depend on fish size (Régis et al. 1981). Each fish captured was identified to species level and released. Mortality was low and not recorded.

The SPA protocol design was based on PASE, and involved sampling-point observation by a scuba-diver experienced in fish detection and identification, swimming slowly downstream to limit fright responses. The diver was followed by a second operator, walking along the bank, diving or in a small boat, who helped to locate sampling points and recorded observations (using a waterproof recorder). A total of five experienced divers contributed to sampling. At each point, all fish observed within an average radius of 1.5 m around the diver (i.e., the approximate effective radius of electrofishing) were identified to species level and counted. Underwater visibility was estimated as the distance at which snorkelers could see bright flippers, and surveys were postponed when visibility was $< 2 \text{ m}$.

Sampling points and environmental characteristics

For both protocols, sampling points were regularly spaced longitudinally and randomly selected laterally (on cross-sections). Longitudinal spacing was pre-defined as 80 m along the 14 km reach of the Ain River reach and 30 m along the shorter 2 km Seymard River reach, for ~ 200 points in the Ain and ~ 90 points in the Seymard in each survey. However, during the last PASE survey in the Seymard River, only the upstream 2000 m. was sampled, and consequently, for the last paired survey, only data from the upper Seymard reach were used (Table 1). The lateral position of each point had been selected in the lab by randomized codes between 1 (= right shore) and 6 (= left shore). Sampling exactly the same two points in a paired survey is difficult in practice; therefore, the paired surveys used similar sampling designs, with fixed longitudinal spacing and random lateral positioning, but with different sampling points.

Point positions (recorded by GPS: WGS 84) were projected in a Lambert II extended system for analysis, and distance from the most upstream point of the section (curvilinear

distance, in metres) was calculated in the lab using curvilinear coordinates (i.e., along the centre of the channel).

At each sampling point, current velocity (m.s^{-1}), wetted width (m), water depth (m) and dominant substrate size over the observed area (mm) were estimated visually; although rough, these visual estimates provided a sufficient description of habitat characteristics for the purposes of the study, given the very wide range of values observed in the reaches (e.g., estimated velocities ranged between 0 and 3 m.s^{-1}). Some widths were measured to calibrate the visual estimates, and current velocities were assessed by observing the drift of suspended material (e.g., leaves, or the divers themselves). The morphologic unit (riffle, run or pool; Jowett 1993) to which the point belonged and the presence of woody debris were also recorded. The hourly discharge rate of the Ain River (Fig. 2) was continuously recorded by a gauging station (managed by DREAL Rhône-Alpes, regional agency for the environment) 800 m downstream of the study reach. Water temperature in the Ain was measured on each survey, 800 m downstream of the Albarine River confluence (data provided by Électricité de France). Discharge in the Seymard River (Fig. 2) is ungauged and less variable than in the Ain River due to its phreatic origin; it was estimated from the daily groundwater level close to the Seymard at Saint-Maurice-de-Rémens, using a regression model calibrated from punctual discharge measurements ($N = 934$, $R^2 = 0.87$). Water temperature was estimated from the daily air temperature at the Ambérieu-en-Bugey weather station (located 5 km east of the Seymard; data provided by Météo France), using a regression model calibrated from punctual measurements of daily water temperature of the Seymard River between 6 April and 26 September 2013 ($N = 174$, $R^2 = 0.83$).

Data analysis

Comparison of species density and species occurrence

To determine whether the two protocols provided similar fish counts and/or presence-absence, species density and occurrence, averaged across surveys, were first compared. Mean density, transformed as $\log(1 + \text{density})$ per survey and averaged across surveys, was

defined as the number of individuals per species per 1000 m² in the survey. Mean occurrence was transformed as $\log(1 + \text{percentage of points where the species occurred})$ per survey and averaged across surveys. The log-transformations were used in order to reduce heterogeneity of variance.

Model II regressions (major axis method: Legendre and Legendre 1998) were used for these comparisons, because the two protocols were expected to provide estimates with comparable variance of error. Firstly, to determine whether PASE and SPA estimates correlated significantly, we tested whether the observed correlation coefficient (r) was significantly greater than by chance. Secondly, to determine whether PASE and SPA estimates differed significantly, we tested whether the slope differed significantly from 1. Both tests were based on random permutations of PASE and SPA sampling points per survey ($N = 999$, significance threshold $P = 0.05$).

Small (adult length < 10 cm) and thin fish with benthic behaviour and benthic feeding should be more difficult to observe by snorkelling (Bozec et al. 2011). In contrast, electrofishing efficiency was expected to be more homogeneous between species, due to limited fright bias (Thevenet and Statzner 1999). Therefore, a synthetic variable was defined to describe expected underwater species observability, varying between 0 and 8 and equalling the sum of scores for four species traits considered to influence underwater observability (total length, body shape, benthic behaviour and feeding habitat: Persat et al. 1994, Lamouroux et al. 1999, Buisson and Grenouillet 2009; Table 2). We tested if the residuals of our regressions (comparison of density and occurrence between protocols) were related to the expected observability by Spearman correlation tests.

Comparison of community structure variation in time and space

Fish community structure estimates were compared between the two protocols by STATIS analysis (Escoufier 1985, Lavit et al. 1994). STATIS is a multivariate multi-table analysis commonly used to compare temporal or spatial series of data sets that share similar characteristics (e.g., sampling sites and/or sampling variables; Gaertner et al. 1998, Muiño et

al. 2003, Abdi et al. 2012, Blackett et al 2014). Here, STATIS was used to compare species abundance data tables (with the same species list) obtained with the two protocols. STATIS performed simultaneous principal component analysis (PCA) of the two tables, searching for common factorial axes (i.e., compromise structure for the two protocols), giving a correlation coefficient (RV) varying between 0 and 1 depending on the similarity between the compromise structure and the initial tables (Robert and Escoufier 1976). In the present study, RV values near 1 indicate similarity of fish assemblage structures sampled with PASE or with SPA.

To compare the variations in fish community structure estimated by electrofishing and snorkelling in time (between-survey variation) and space (between sampling points: within-survey variation), two STATIS analyses were performed. To assess similarity in temporal variations in community structure, analysis was first performed on abundance data averaged by survey (between-survey analysis). To assess the similarity in spatial variation in community structure, a second analysis was performed on the point abundance data after subtracting average abundance per survey (within-survey analysis). This second analysis searched for a compromise in assemblage variations between sampling points: i.e., eliminating temporal variations and focusing on spatial variations. For both STATIS analyses, the significance of the RV coefficient was tested using random permutations ($N = 999$, threshold: $P = 0.05$) on the rows and columns of the PASE tables. Point abundances were $\log(1+x)$ transformed before the two STATIS analyses to reduce the scatter of fish point abundance values (Vaudor et al. 2011).

Finally, to facilitate interpretation of spatial (within-survey) analysis, relationships between STATIS factorial axes and environmental characteristics of sampling points (water depth, current velocity, dominant substrate size, presence of woody debris, and morphological units) were investigated. Cluster analysis was performed on sampling point scores on the factorial axes (k-means procedure with Calinski criterion: R Core Team 2014), and variation in sampling point environmental characteristics between clusters was assessed (Kruskal-Wallis tests, threshold $P = 0.05$, with all environmental variables considered as

ordinal). Cluster analysis on factorial scores was preferred over correlation analysis between factorial scores and environmental characteristics, because species abundance generally responds non-linearly to the environment (Lamouroux et al. 1999).

Comparison of the longitudinal distribution of individual species

Finally, we designed a permutation test to analyse whether the longitudinal distributions of individual species along the curvilinear reach coordinates were consistent between the two protocols. For this purpose, we calculated the cumulative distribution curve, along the curvilinear coordinate (Fig. 3a, Fig. 3b), of the relative abundance of the species (i.e., point abundance divided by total abundance). The area between the two cumulative distributions (two protocols) was computed; this area decreases as consistency between the longitudinal distributions of relative abundance increases. The random permutations tested whether the area was smaller than expected by chance (i.e., after random permutations of observed abundance between points). Importantly, longitudinal distribution of abundance was compared in two ways: firstly, between longitudinal distributions estimated from pooled data for all surveys; and secondly, for longitudinal distributions within paired surveys, with cumulative distribution per survey and areas between the two cumulative distributions summed across surveys. These comparisons of longitudinal distribution were restricted to species observed on both SPA and PASE and with abundance > 2 individuals. All analyses were performed for the Ain River and Seymard River separately, using R software (R Core Team 2014).

Results

Sampling points and corresponding environmental characteristics

Mean discharge rate in Ain River surveys was $81.8 \text{ m}^3 \cdot \text{s}^{-1}$ (range, $18.6 \text{ m}^3 \cdot \text{s}^{-1}$ to $221 \text{ m}^3 \cdot \text{s}^{-1}$; Fig. 2); mean water temperature was 15.1°C (range, 11.4° to 18.0°) in spring and 13.3°C (range, 12.0° to 15.1°) in autumn. A mean 195 points were sampled with PASE

(range, 178 to 210) and 213 with SPA (range, 183 to 249; Table 1). The proportion of points at which fish occurred was 29.8% with PASE and 18.6% with SPA. Environmental characteristics at sampling points were comparable on PASE and SPA surveys (mean width ~70 m and mean depth ~1 m; Table 3). However, current velocities (0.57 vs. 0.33 m.s⁻¹), substrate size (97.7 vs. 211.9 mm) and percentage points with woody debris (5.74% vs. 2.03%) were greater in SPA than PASE samples (Table 3). Substrate size estimates showed wide standard deviations between surveys (Table 3). For both protocols, most points were in run (> 66 %) or riffle (> 25 %) habitats (Table 3).

Mean discharge rate in Seymard River surveys was 0.9 m³.s⁻¹ (range, 0.2 m³.s⁻¹ to 1.3 m³.s⁻¹; Fig. 2); mean water temperature was 14.9°C (range, 14.7° to 15.2°) in spring and 12.6°C (range, 12.3° to 13.0°) in autumn. A mean 93 points were sampled with PASE (range, 56 to 108) and 75 with SPA (range, 58 to 91; Table 1). The proportion of points at which fish occurred was 57.3% with PASE and 37.7% with SPA. Environmental characteristics at sampling points were comparable on PASE and SPA surveys (mean width ~9.5 m, mean depth ~0.5 m, mean current velocity ~0.14 m.s⁻¹, substrate size ~14 mm, and percentage points with woody debris ~7 %; Table 3). For both protocols, most points were in run (> 60 %) or riffle (> 17 %) habitats (Table 3). Underwater visibility ranged between 3 and 5 m in both rivers.

Comparison of species density and species occurrence

More fish were counted with SPA ($N_{\text{Ain}} = 17,267$; $N_{\text{Seymard}} = 3,775$) than with PASE ($N_{\text{Ain}} = 6,494$; $N_{\text{Seymard}} = 1,249$) in both rivers, but this was essentially due to higher numbers of the abundant *Phoxinus phoxinus* estimated with SPA (proportion of *Phoxinus phoxinus* in the Ain: SPA = 86% and PASE = 74%; in the Seymard: SPA = 93% and PASE = 61%). For most other species, mean abundance was greater with PASE (Table 4). In addition, 43% of species observed with PASE in the Ain River were not observed with SPA (*Alburnus alburnus*, *Blicca bjoerkna*, *Gobio gobio*, *Tinca tinca*, *Gasterosteus aculeatus*, *Lepomis gibbosus*, *Pseudorasbora parva*, *Rhodeus amarus*, *Esox lucius* and *Ameiurus melas*; Table 4,

Fig. 4), and 25% in the Seymard River (*Alburnoides bipunctatus*, *Ameirus melas*, *Tinca tinca* and *Alburnus alburnus*; Table 4, Fig. 4).

Mean species density estimated with PASE and SPA was significantly correlated in both the Ain ($r = 0.89$; $P < 0.001$) and the Seymard ($r = 0.71$; $P < 0.001$), suggesting consistent estimation between protocols (Fig. 4). These results were influenced by the relative predominance of *Phoxinus phoxinus*, the most abundant species in both rivers and both protocols (from 500 to 1000 individuals per survey); nevertheless, omitting *Phoxinus phoxinus*, estimates with PASE and SPA remained correlated in both the Ain ($r = 0.81$; $P < 0.001$) and the Seymard ($r = 0.45$; $P < 0.001$).

The regression slope between species abundance on PASE and SPA did not differ from 1 in the Ain River (slope = 0.93; $P > 0.1$, Fig. 4) but differed from 1 in the Seymard River (slope = 0.83; $P < 0.005$). However, omitting *Phoxinus phoxinus*, the slope differed from 1 in both the Ain (slope = 1.42, $P < 0.005$) and the Seymard (slope = 3.54, $P < 0.001$). Density estimates were higher with PASE for many species (e.g., *Barbatula barbatula*, *Alburnoides bipunctatus*, *Barbus barbus* and *Squalius cephalus* in the Ain; *Barbatula barbatula*, *Gasterosteus aculeatus*, *Leuciscus leuciscus* and *Salmo trutta* in the Seymard; Fig. 4). Regression also indicated much higher density estimates with SPA for *Phoxinus phoxinus* in both rivers.

No correlation was observed between expected observability and residuals from regressions ($P > 0.05$). However, the species most underestimated by SPA compared to PASE in both rivers was *Barbatula barbatula*, which also had the lowest expected observability (score = 1; Table 2, Table 4). Similarly, in the Ain River, *Gobio gobio* had the lowest expected observability (score = 1; Table 2, Table 4) and was not observed with SPA. Some species with high expected observability (score > 5) had low abundance on both protocols (*Tinca tinca*, *Esox lucius*, *Perca fluviatilis*, *Salmo trutta*; Table 2, Table 4).

Comparison of species occurrence (Fig. 4) led to very similar results, except that regression slopes differed from 1 in both the Ain (slope = 1.40; $P < 0.001$) and the Seymard (slope = 1.52; $P < 0.001$). This was due to higher estimated occurrence of frequent species

with PASE than with SPA. Therefore, other results involving occurrence are not further detailed here.

Comparison of fish community structure variation in time and space

In both rivers, between-survey STATIS analysis revealed no significant common temporal structure between the two protocols (Ain River: correlation coefficient $RV = 0.12$, $P > 0.05$; Seymard River: correlation coefficient $RV = 0.07$, $P > 0.05$). Accordingly, survey scores on the factorial axes of the compromise PCA (shown for the Ain River only in Fig. 5) revealed that temporal variation between surveys was mainly due to the position of one PASE survey (2013_autumn in Fig. 5a) and one SPA survey (2012_autumnB in Fig. 5a) conducted on different sampling dates; species scores on the factorial axes (Fig. 5b) indicated which species were more abundant in these particular surveys than in others; these surveys were both made at discharge rates below $50 \text{ m}^3 \cdot \text{s}^{-1}$ in the Ain River (Fig. 2) and both belonged to survey pairs (PASE and SPA) conducted over two consecutive days (Table 1).

In contrast, and again in both rivers, within-survey STATIS analysis revealed a significant common spatial structure between the two protocols (Ain: $RV = 0.39$, $P < 0.05$; Seymard: $RV = 0.64$, $P < 0.05$): i.e., similar fish assemblages were found in similar habitat on both protocols. In both rivers, few sampling points had high scores along the F1 axis of the compromise PCA (Fig. 6a, 6c), along which most species also had positive scores (Fig. 6b, 6d). Therefore, these points corresponded to sampling points with higher abundance of many species. In both rivers, the position of sampling points along the F2 axis (Fig. 6a, 6c) was determined by different assemblages of species with scores of opposite signs on the F2 axis (Fig. 6b, 6d). Therefore, the position of sampling points along the F2 axis was essentially due to differences in relative species abundance.

Significant links between factorial scores and environmental characteristics along the within-survey axes (Fig. 6) indicated that sampling-point fish assemblages were environmentally dependent, although differently between the two rivers. In the wide Ain River, sampling points with low abundance (cluster CI4, low F1 scores; Fig. 6a) had very

great velocity and depth and no woody debris, whereas in the narrower Seymard River they (cluster CI5; Fig. 6c) were generally shallower with no woody debris. In both rivers, species such as *Telestes souffia*, *Leuciscus leuciscus* and *Alburnoides bipunctatus* had close scores on the factorial axes and high scores on F1, (i.e., often co-occurred in abundant points). In the Ain River, sampling-point position along the F2 axis depended on combinations of velocity, depth and woody debris. In particular, points in cluster CI1 (shallow and fast-flowing habitat without woody debris; Fig. 6a) had higher densities of species such as *Barbatula barbatula*, *Cottus gobio* and *Barbus barbus* and lower densities of *Perca fluviatilis* and *Rutilus rutilus* compared to the other clusters with abundant fish (CI2-CI3; Fig. 6a). In the Seymard River, the F2 axis discriminated a couple of deep sampling points where large species such as *Barbus barbus* and *Squalius cephalus* were abundant.

Comparison of longitudinal distribution of individual species

Comparison of the cumulative distributions of relative species abundance pooling all survey data (Table 4) revealed consistent longitudinal distributions for 1 of the 13 species with more than 2 individuals per survey in the Ain River (*Phoxinus phoxinus*) and 3 of the 6 species with more than 2 individuals per survey in the Seymard River (*Leuciscus leuciscus*, *Phoxinus phoxinus*, *Telestes souffia*). On pairwise survey comparison, 2 of the 13 Ain species but only 1 of the 6 Seymard species had consistent longitudinal distributions.

Discussion

The objective of the present study was to compare a snorkelling protocol, SPA, with an electrofishing protocol, PASE (Nelva et al. 1979), based on similar strategies (series of sampling points) in two different rivers. In each of nine paired surveys, electrofishing provided higher estimates of species richness than snorkelling and generated a higher proportion of points at which fish occurred. The expected underwater observability, based on species traits (i.e., total length, body shape, benthic behaviour and feeding habitat) did not

explain these differences, except maybe for *Barbatula barbatula* (a cryptic species generally living under the substrate) and *Gobio gobio* (a species that shares several traits with *Barbatula barbatula*). It is possible that several species with high expected observability but low occurrence (*Tinca tinca*, *Esox lucius*, *Perca fluviatilis*, *Salmo trutta*) complicated our understanding of the role of expected observability on the results. It is also likely that our coding of observability could be improved, although tests involving individual trait scores (not shown here) were inconclusive.

The presence of many species with low occurrence/abundance may also explain the underestimation of richness on SPA. Indeed, many points at which fish occurred had high abundance of several species, aggregated in schools. Snorkelers may have difficulty picking out rare individuals (i.e., individuals from species with low total abundance) among individuals of abundant species. This underestimation of richness by snorkelling is consistent with results in other rivers (Macnaughton et al. 2014). However, species richness estimates by snorkelling may be improved with block-nets, preventing fish from moving out of sampling sites (Chamberland et al. 2014), although closing sampling sites often leads to increased efficiency for both methods (Peterson et al. 2005). We found that richness was underestimated by snorkelling more in the wide Ain River than in the narrow Seymard, possibly due to the presence of more rare species and/or larger individuals with greater flight distance in the wider river.

Species density estimates were also lower with snorkelling for most species, but strong correlations between electrofishing and snorkelling estimates confirmed that electrofishing and snorkelling can provide consistent estimates of relative species density (Hankin and Reeves 1988, Ensign et al. 1995, Wildman and Neumann 2003, Chamberland et al. 2014, Macnaughton et al. 2014). Moreover, species densities estimated in the Ain and Seymard rivers were within the range of densities estimated with electrofishing in six reaches of the nearby Rhône River (Daufresne et al. 2015). The highly abundant, schooling *Phoxinus phoxinus* was the only species in which abundance was estimated to be much greater on SPA. One explanation is that the abundance of schools containing hundreds of small fish is

difficult for snorkelers to estimate, while many individuals escape during electrofishing (Kimmel and Argent 2006). It is also possible that groups of some fish species are attracted by snorkelers (Kulbicki et al. 2010). In contrast, schooling behaviour was not found to bias abundance estimation in marine studies (Kulbicki et al. 2010, Bozec et al. 2011), maybe due to an overall higher observability and lower density.

Snorkelling and electrofishing provided inconsistent estimates of temporal variations in fish community structure. In the Ain River, these inconsistencies were due to two surveys with distinctive fish assemblages, one by electrofishing and the other by snorkelling, on different sampling dates. These distinctive surveys did not show extreme discharge rates, turbidity or conductivity, and were therefore probably distinguished for reasons that we failed to identify: e.g. temporal variation in fish community activity between consecutive days, variation in snorkelling efficiency, or random variations associated with the choice of sampling points. Short-term variations in fish behaviour probably explain the differences in density estimates, even between consecutive days (Weaver et al. 2014). This is particularly true in rivers subject to hydropeaking (e.g., Fig. 1), where feeding periods may be short and fish may frequently seek flow refuges (Taylor and Cooke 2012).

Although Kulbicki et al. (2010) argued that operator effects between four snorkelers were weak in their marine study, they may be greater in rivers, where fish are more active, water is more turbid and current velocity complicates observation (Thurow et al. 2006, Orell et al. 2011). In the present study, five snorkelers contributed to snorkelling samples, several to each survey. Unfortunately, the number and design of surveys were not suitable for quantifying operator effects. The five snorkelers had participated in electrofishing surveys, had trained together, had good knowledge of the reaches and were familiar with the species occurring in them. It therefore seems likely that the observed temporal variation in fish assemblages was due more to actual temporal variation than to an operator effect.

Temporal variations in fish assemblage may also explain why the longitudinal distributions of individual species were more frequently consistent between electrofishing and snorkelling when survey data were pooled by protocol. Similarly, temporal variation may also

explain the large uncertainty of species density estimates (cf. standard errors in Fig. 4). More generally, point sampling or other subsampling techniques in rivers and lakes provide uncertain estimates of fish density due to a combination of spatial overdispersion (Vaudor et al. 2011) and temporal variations in density (Gido et al. 2013, Vaudor et al. 2015). Consequently, powerful assessment of freshwater fish community structure and its changes over long distances (> 10 km) requires pooling repeated survey data, whatever the sampling strategy (Brind'Amour et al. 2005, Vaudor et al. 2015).

Spatial patterns (fish point assemblage structure, longitudinal species distributions) estimated by snorkelling and electrofishing were generally consistent. Firstly, spatial (within-survey) analysis of point assemblages indicated that similar types of point assemblage were observed by both protocols. Secondly, the shared structure had similar characteristics in both rivers, despite their contrasting environmental characteristics. In particular, in both rivers, point assemblage structure was due to the small number of points with abundant fish, and indicated frequent co-occurrence of species (*Telestes souffia*, *Leuciscus leuciscus* and *Alburnoides bipunctatus*) that are often found together in the fast-flowing and/or deep conditions of midstream habitats (Lamouroux et al. 1999, Daufresne et al. 2015). Finally, despite temporal variations, the longitudinal distribution of several abundant species was similar according to both protocols, suggesting that snorkelling is useful over large spatial scales (e.g. scale of fish dispersal) for describing longitudinal species distributions.

Furthermore, most associations between point assemblages and environmental factors revealed by spatial analysis (within-survey) analysis were consistent with general knowledge of species habitat preferences, although differing between the two rivers. In particular, the different environmental characteristics of points with little abundance in the two rivers were probably due to different habitat availability in the rivers. In the faster-flowing Ain River, fish often avoid deep points (e.g., > 1.5 m, Fig. 6a) with very high velocity (e.g., > 0.7 m.s⁻¹, Fig. 6a). This is consistent with the frequent use of shallow, low-velocity habitats by freshwater species (Lamouroux et al. 1999). Such fast-flowing habitats are not found in the Seymard River, where fish tend to avoid shallows (e.g., < 0.7 m, Fig. 6a). In both rivers,

points with woody debris or vegetation tend to have higher fish densities (Brind'Amour and Boisclair 2004, Thurow et al. 2006). Accordingly, woody debris is associated with increased habitat heterogeneity and provides refuge for fish (Jackson et al. 2001). In sampling points on the Ain River with intermediate velocity, species are organized along a water depth gradient, in agreement with their well-documented preferences (Spillmann 1961, Lamouroux et al. 1999), with the benthic *Barbatula barbatula*, *Cottus gobio* and *Barbus barbus* in shallower habitats than the pelagic *Perca fluviatilis* and *Rutilus rutilus*. In the slower-flowing Seynard River, the larger species, *Barbus barbus* and *Squalius cephalus*, were occasionally found in deeper habitats. These two species are typical species of the wider and deeper Ain, and their presence in the Seynard may be due to dispersal from the Ain (Fig. 1).

The consistency of patterns of spatial variation in fish communities between electrofishing and snorkelling suggests that both protocols are appropriate for studying microhabitat preferences. Although differences in habitat use have been reported according to snorkelling and electrofishing in lakes (Brosse et al. 2001) and rivers (Persinger et al. 2004), the authors suggested that some degree of fright response to electrofishing in lakes, the mechanical influence of electrofishing on vegetation during consecutive sampling, or differences in sampling designs between the two protocols may have influenced their results. Snorkelling reduces mechanical disturbance of habitat and misinterpretation of habitat use. In particular, substrate size was sometimes difficult to estimate on electrofishing, potentially explaining differences with respect to snorkelling results. However, studying habitat use by snorkelling would require more precise measurement of habitat characteristics than the rough visual estimates of the present study.

Persinger et al. (2004) and Chamberland et al. (2014) suggested using a combination of electrofishing and snorkelling data to better estimate fish richness. The present results, however, suggest that snorkelling is not very appropriate for estimating richness, at least in rivers with many rare species. Nevertheless, for the other species, snorkelling and electrofishing provided similar estimates of relative fish density and spatial assemblage structure. Finally, the study was limited to reaches of less than 15 km, to enable comparison

with electrofishing; but snorkelling alone could be particularly attractive for assessing fish metacommunities over dozens of kilometres and in river networks with limited accessibility (Torgersen et al. 2006, Brenkman et al. 2012).

Given the variety of distances covered by individuals of many species during their lifespan (up to several dozen km: Radinger and Wolter 2014), understanding the effects of dispersal on metacommunity dynamics and studying fish resilience to environmental disturbance would require repeated assessment of community structure over a variety of spatial scales. The very wide temporal variation in estimates of community structure also indicates that studying metacommunity dynamics will require multiple repeated samples. Therefore, the simplicity of large-scale implementation of snorkelling makes this method particularly suited for better understanding fish metacommunity organization. Moreover, the protocol proposed here could be improved (e.g., by recording fish seen between points) and adapted to studies of behavioural ecology (e.g., by recording feeding activities or interactions between individuals; White et al. 2014). Snorkelling could be also further developed for studies of individual personalities, due to the importance of personality variations for ecology and evolution (Wolf and Weissing 2012).

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Table 1. Characteristics of surveys: survey date, number of days between PASE and SPA sampling events (ΔD), number of points (N), proportion of points where fish occurred (P, in %) and species richness (R).

	ΔD		Ain River						Seymard River					
	Ain	Seymard	PASE			SPA			PASE			SPA		
	River	River	N	P	R	N	P	R	N	P	R	N	P	R
2012_spring	2	-	203	33.5	15	219	32.0	11	-	-	-	-	-	-
2012_autumnA	4	1	190	25.8	15	249	10.8	7	108	64.8	11	62	53.2	6
2012_autumnB	1	1	210	22.4	14	208	18.8	11	105	50.5	10	86	52.3	5
2013_spring	12	1	178	32.0	16	183	18.6	8	101	54.5	11	91	13.2	3
2013_autumn	1	9	192	35.9	21	204	13.8	5	56	75.0	12	58	89.7	7
All surveys	-	-	973	29.8	23	1063	18.6	13	370	57.3	16	297	37.7	12

708 **Table 2.** Species counted and traits used to rank species observability. Underlined species were not sampled in the Seymour River.

Family	Species	Code	Species observability traits				
			Total Length	Body Shape	Benthic behaviour	Feeding Habitat	Expected Observability
Balitoridae	<i>Barbatula barbatula</i>	BaBa	1	0	0	0	1
Centrarchidae	<u><i>Lepomis gibbosus</i></u>	<u>LeG</u>	1	3	1	1	6
Cottidae	<u><i>Cottus gobio</i></u>	<u>CoG</u>	1	2	0	0	3
Cyprinidae	<i>Alburnoides bipunctatus</i>	AIB	1	3	1	1	6
	<i>Alburnus alburnus</i>	AIA	1	1	1	1	4
	<i>Barbus barbus</i>	BaBu	3	1	0	0	4
	<u><i>Blicca bjoerkna</i></u>	<u>BIB</u>	2	1	1	0	4
	<u><i>Chondrostoma nasus</i></u>	<u>ChN</u>	2	2	1	0	5
	<u><i>Gobio gobio</i></u>	<u>GoG</u>	1	0	0	0	1
	<i>Leuciscus leuciscus</i>	LeL	2	1	1	1	5
	<i>Phoxinus phoxinus</i>	PhP	0	1	1	1	3
	<u><i>Pseudorasbora parva</i></u>	<u>PSP</u>	0	3	1	1	5

	<i>Rhodeus amarus</i>	RhA	0	3	1	1	5
	<i>Rutilus rutilus</i>	RuR	2	3	1	1	7
	<i>Squalius cephalus</i>	SqC	3	1	1	1	6
	<i>Telestes souffia</i>	TeS	1	1	1	1	4
	<i>Tinca tinca</i>	TiT	2	3	1	0	6
Esocidae	<i>Esox lucius</i>	EsL	3	1	1	1	6
Gasterosteidae	<i>Gasterosteus aculeatus</i>	GaA	0	2	1	1	4
Ictaluridae	<i>Ameiurus melas</i>	AmM	2	2	0	0	4
Percidae	<i>Perca fluviatilis</i>	PeF	2	3	1	1	7
Salmonidae	<i>Salmo trutta</i>	SaT	2	3	1	1	7
	<i>Thymallus thymallus</i>	ThT	2	1	1	1	5

Nota: Species traits categories: Total Length (cm) categories are: 0: <10; 1: 10-20; 2: 20-40; 3: >40. Body Shape (ratio of total body length in cm to maximum body depth in cm) categories are: 0: ≥ 5.6 ; 1: 5.6-4.78; 2: 4.78-4.35; 3: < 4.35. Benthic behaviour categories are: 0: yes; 1: no. Feeding Habitat categories are: 0: Benthic; 1: Pelagic. Adapted from Persat et al. (1994), Lamouroux et al. (1999) and Buisson and Grenouillet (2009). The expected observability is the sum of species trait categories.

709 **Table 3.** Environmental characteristics of sampling points of PASE and SPA protocols (mean ± standard deviation among surveys).

	Ain River			Seymard River		
	PASE		SPA	PASE		SPA
Wetted width (m)	72.58	± 8.02	70.79 ± 4.27	9.38	± 0.95	10.12 ± 3.67
Water depth (m)	1.04	± 0.12	1.03 ± 0.05	0.52	± 0.07	0.49 ± 0.08
Current velocity (m.s ⁻¹)	0.33	± 0.09	0.57 ± 0.09	0.14	± 0.03	0.14 ± 0.04
Dominant substrate size (mm)	97.74	± 35.65	211.92 ± 79.14	15.10	± 5.86	13.03 ± 3.31
Woody debris (%)	2.03	± 2.20	5.74 ± 3.47	7.05	± 2.53	6.95 ± 4.96
Morphological units						
% Pool	1.05	± 0.88	3.33 ± 2.33	9.68	± 4.97	18.32 ± 20.58
% Run	73.24	± 6.53	65.93 ± 8.91	72.98	± 8.98	63.82 ± 19.42
% Riffle	25.70	± 7.14	30.73 ± 6.94	17.34	± 7.95	17.84 ± 14.71

710 **Table 4.** Total abundance, occurrence and results (P-values) of comparison of longitudinal distribution of some species between protocols.
 711 These tests were made for all surveys pooled (pooled) or for paired surveys (paired). Underlined species were not sampled in the Seymard
 712 River. For species codes see Table 2.

Code	Ain River						Seymard River					
	Abundance		Occurrence		P		Abundance		Occurrence		P	
	PASE	SPA	PASE	SPA	Pooled	Paired	PASE	SPA	PASE	SPA	Pooled	Paired
BaBa	140	13	75	5	> 0.1	> 0.1	192	1	90	1	-	-
<u>LeG</u>	1	0	1	0	-	-	-	-	-	-	-	-
<u>CoG</u>	13	7	10	6	> 0.1	> 0.1	-	-	-	-	-	-
AIB	246	586	37	6	> 0.1	> 0.1	3	0	3	0	-	-
AIA	6	0	5	0	-	-	4	0	4	0	-	-
BaBu	227	95	98	30	> 0.1	> 0.1	23	11	4	2	-	-
<u>BIB</u>	248	0	6	0	-	-	-	-	-	-	-	-
<u>ChN</u>	53	81	6	2	> 0.1	> 0.1	-	-	-	-	-	-
<u>GoG</u>	10	0	7	0	-	-	-	-	-	-	-	-
LeL	49	1174	11	10	> 0.1	> 0.1	67	92	23	15	<0.005	<0.005
PhP	4802	14833	166	143	< 0.001	< 0.05	761	3497	109	90	<0.05	>0.1
<u>PsP</u>	2	0	2	0	-	-	-	-	-	-	-	-
<u>RhA</u>	1	0	1	0	-	-	-	-	-	-	-	-

RuR	82	7	6	2	> 0.1	> 0.1	1	10	1	1	-	-
SqC	205	79	59	22	> 0.1	> 0.1	19	40	7	10	>0.1	>0.1
TeS	326	316	24	14	< 0.1	< 0.1	84	88	21	11	<0.05	>0.1
TiT	5	0	5	0	-	-	1	0	1	0	-	-
EsL	2	0	2	0	-	-	2	2	2	2	-	-
GaA	11	0	8	0	-	-	50	27	36	3	>0.1	>0.1
AmM	2	0	1	0	-	-	1	0	1	0	-	-
PeF	13	27	8	3	> 0.1	> 0.1	4	1	3	1	-	-
SaT	20	27	14	12	> 0.1	> 0.1	29	1	20	1	-	-
ThT	30	22	29	16	> 0.1	< 0.05	8	5	4	4	>0.1	>0.1

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Figure 1. Location of the study river reaches (grey bold lines) on the Ain and Seymard Rivers. BD TOPO® <http://professionnels.ign.fr/bdtopo>

Figure 2. Hourly discharge ($\text{m}^3 \cdot \text{s}^{-1}$) in the Ain River reach and daily discharge ($\text{m}^3 \cdot \text{s}^{-1}$) estimated in the Seymard River reach from June to November, in 2012 and 2013. Grey bars indicate sampling events.

Figure 3. (a) Map of the abundance of *Leuciscus leuciscus* obtained with PASE (black squares) and SPA (black circles) protocols in the Seymard River; (b) cumulative longitudinal distributions (for PASE and SPA, all surveys pooled) as a function of curvilinear distance. The grey area between curves decreases with the consistency of longitudinal distribution between protocols. It is lower than expected by chance for this example ($P < 0.001$; Table 2).

Figure 4. Model II regressions (major axis method; black lines) relating mean species density among surveys (individuals per 1000 m^2 , log scale, left) estimated by PASE vs. SPA in the Ain River (a) and in the Seymard River (b). Dotted lines associated to species represent the standard error between surveys, vertically for PASE and horizontally for SPA. Grey lines represent the 1:1 relationships. Only species observed on SPA were labelled. (c) and (d) are similar plots for mean species occurrence (log scale). See Table 2 for species code.

Figure 5. Factorial map of the STATIS between-survey analysis of PASE (black) and SPA (grey) data in the Ain River. (a): survey scores, with links between paired surveys, (b): species scores. See Table 2 for species code.

Figure 6. Factorial map of the STATIS within-survey analysis of sampling points. (a): factorial scores in the Ain River and associated clusters. (b): species scores in the Ain River. (c): factorial scores in the Seymard River and associated clusters. (d): species scores in the Seymard River. See Table 2 for species code. For significant associations between point clusters and environmental variables (V: current velocity in m.s^{-1} ; D: water depth in m; W: presence of woody debris; S: dominant substrate size in mm; L: wetted width in m; $P < 0.05$), the 75% (100% for CI3 and CI7) percentile of the environmental variable corresponding to each cluster is shown: 25% of point values are above this percentile.

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Figure 1. Location of the study river reaches (grey bold lines) on the Ain and Seymard Rivers. BD TOPO® <http://professionnels.ign.fr/bdtopo>

912x551mm (150 x 150 DPI)

Figure 2. Hourly discharge (m³.s⁻¹) in the Ain River reach and daily discharge (m³.s⁻¹) estimated in the Seymard River reach from June to November, in 2012 and 2013. Grey bars indicate sampling events.

520x318mm (150 x 150 DPI)

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448x520mm (150 x 150 DPI)

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520x490mm (150 x 150 DPI)

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512x322mm (150 x 150 DPI)

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493x518mm (150 x 150 DPI)