Leibniz-Institute of Freshwater Ecology and Inland Fisheries

The gain of additional sampling methods for the fish-based assessment of large rivers

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The gain of additional sampling methods for the fish-based assessment of large rivers

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Abstract
Fishes serve as indicators in ecological assessments of European large rivers. Electrofishing is the standard fishing method although it is restricted to the shallow littoral shoreline. Fish occurring in the open water zone of the main channel remain consequently underestimated. Additional sampling methods that cover the mid-channel of rivers could close the electrofishing-gap, but strengths', weaknesses and gains of both electrofishing and additional sampling methods for fish-based assessments of large rivers have not been contrasted yet. We analyzed a unique dataset consisting of 2,693 fish samplings in European large rivers and compared electrofishing with the additional sampling methods trawling, seining, and drift-netting. We compiled fish metrics commonly used in fish-based assessments yielded by the different gears and highlight the differences in fish species, biodiversity metrics (Shannon Index, Evenness, Simpson Index), the Fish Region Index (FRI) and densities of fish in selected guilds (eurytopic, rheophilic, lithophilic, phytophilic, psammophilic, potamal) that are considered indicative for the degradation of habitats in large rivers. Electrofishing yielded overall highest numbers of species, biodiversity metrics and densities of fish guilds, except for the number of migratory and Habitat Directive species, the FRI and densities of potamal fish. The additional gears, predominantly trawling, captured additional rheophilic and lithophilic species. Trawling also assessed most migratory and Habitat Directive species and yielded higher densities of potamal fish as well as larger fish than electrofishing. Trawl catches further estimated higher biodiversity compared to seining, while the latter yielded higher densities of eurytopic, rheophilic, lithophilic and phytophilic fish. Drift-netting yielded the lowest estimates overall but sample size was very low. We suggest that electrofishing is an appropriate method to assess and evaluate the effects of hydromorphological degradation and rehabilitation on fish, and to guide river management. It sufficiently well represents the typical fish assemblage of large rivers despite its restriction to the shoreline. In contrast, assessing specifically Habitat Directive, migratory and rare species, as well as obtaining complete species inventories, e.g., for biodiversity assessments, requires complementary sampling of the mid-channel of large rivers by additional gears such as trawling.

Keywords: Fishing gear comparison, trawl, seine, drift-net, electrofishing

Highlights:

- Shorelines and the mid-channel form two distinct meso-habitats in large rivers
- Electrofishing is applied at the shoreline but well represents the fish assemblage
- Electrofishing estimated higher biodiversity and density of habitat-sensitive fish
- Additional gears that cover the mid-channel captured additional species
- Trawling applied in the mid-channel captured higher densities of potamal fish

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1. Introduction

Representative sampling is a crucial challenge in ecological assessments of large rivers (De Leeuw et al., 2007; Poikane et al., 2014), i.e., in rivers with a catchment size >10,000 km² (Berg et al., 2004). Challenges arise from the pure size of the water body (Flotemersch et al., 2011), the complexity of the riverine ecosystem (Ward et al., 2002) with its variety of habitat structures (Loisl et al., 2013), the varying suitability and selectivity of different sampling methods and the diversity of fish assemblages with broad requirements on specific habitats (Penczak and Jakubowski, 1990). The shoreline and the open water zone of the main channel are two distinct meso-habitats of large rivers. The littoral shoreline is rather shallow and therefore has a great variety of differently structured micro-habitats such as sand banks, gravel bars or areas loosely to densely colonized by emerged or submerged vegetation (Erős et al., 2008; Lechner et al., 2014). Complex structures such as large wood provide refuge, both for fish and prey organisms (Lynch and Johnson, 1989) and also aquatic vegetation and can strongly influence fish community dynamics (Casselman and Lewis, 1996; Jacobsen and Perrow, 1998; Weaver et al., 1997). Hence, highest fish production and diversity are observed at the shoreline (Randall et al., 1996). The open water zone of the main channel is rather unstructured with higher flow velocities, greater depths and it further covers the major part of the river by both area and water volume (Szalóky et al., 2014). Though Wolter et al. (2004) have shown that the open water zone of the main channel has distinct fish assemblages, its importance as an relevant meso-habitat for riverine fishes (Loisl et al., 2013; Szalóky et al., 2014), especially for potamal species (Wolter and Bischoff, 2001) has long been neglected (Dettmers et al., 2001b; Galat and Zweimüller, 2001).

Electrofishing is a standard method to sample fish, even in large rivers (e.g., Beier et al., 2007; Dußling, 2009; Aparicio et al., 2011). Electrofishing efficiency is however limited to shallow areas (Bohlin et al., 1989) and decreases even in small streams with increasing river width (Kennedy and Strange, 1981). It is well suited to sample complex habitat structures such as aquatic vegetation or large wood, which harbor high concentrations of fish (Erős et al., 2008; Lewin et al., 2014), but may be obstacles for most other sampling methods. However, fish occurring in the open water zone of the main channel are underestimated by electrofishing.

Additional methods such as trawling (e.g., Wolter et al., 2004), seining (e.g., Neebling and Quist, 2011), gill-netting (e.g., Goffaux et al., 2005), drift-netting (e.g., Fladung, 2002), and long-lining (e.g., Loisl et al., 2013) can be applied in the open water zone of the main channel and could therefore be beneficial for the fish-based assessment of large rivers (Flotemersch et al., 2011). However, besides long-lining, these fishing gears are prone to entanglements and therefore less suitable for application in complex, structured habitats.

Biodiversity measures enhance understanding of the complex components driving ecosystems (Morris et al., 2014). Biodiversity can however be biased because abundance of species and densities of fishes can change in identical habitats during ontogeny (Blondel, 2003), between seasons (Dettmers et al., 2001a; Wolter and Bischoff, 2001) and even between day and night (Erős et al., 2008; Wolter and Freyhof, 2004). Many fish species are further either stationary or mobile throughout their lifecycle (Radinger and Wolter, 2014). Composition of fish assemblages is accordingly variable even within identical habitats, which makes assessments aiming to compare fish communities across large spatial extents rather challenging.

Multiple sampling of identical sampling sites is beneficial (Dußling et al., 2004a; Kucera-Hirzinger et al., 2008) to increase sample size and to minimize natural and temporal variation due to, for example, sampling methodology, migration or habitat patterns (Wolter et al., 2004). Repeated samplings over time (Magurran and Henderson, 2003) and over large spatial extents (Tokeshi, 1993) further decrease sampling error and increase estimates of species richness. On the other hand, repeated samplings lead to some challenges in statistical analyzes

(Poikane et al., 2014). Different approaches regarding sampling or analytical methodology combined with variable fish traits can result in contrasting conclusions on ecological states (Heino et al., 2013), requiring a certain standardization, especially when large-scale data are considered.

The main objectives of this study were to evaluate commonly used fish sampling methods and identify the gain of additional methods for the fish based assessment of large rivers while accounting for the heterogeneity due to field sampling data. To achieve our objectives, we:

(i) compiled a dataset of 2,693 fish sampling occasions in European large rivers and calculated various fish assemblage metrics commonly used in fish-based assessments;

(ii) compared fish metrics based on electrofishing with those based on trawling, seining, and drift-netting in a first analysis comprising 849 fish samplings. Further, we tested electrofishing against each additional method in three independent comparisons standardized to similar sites sampled by both gears;

(iii) identified strengths, weaknesses and gains of applying additional sampling gears in large rivers; and

(iv) evaluated whether electrofishing is sufficient for the fish-based assessment of large rivers

We hypothesized that fish metrics depend on the sampling method used and that even though additional sampling methods constitute valuable tools, the application of electrofishing is superior for the fish-based assessment of large rivers. We further hypothesized that additional sampling gears capture additional species and therefore complete the species inventory, specifically concerning potamal fish. Thus, selection of sampling gears and use of complementary sampling methods strongly depend on the study objectives. While obtaining complete species inventories probably requires applying several sampling methods, the evaluation of a rehabilitation structure in the littoral zone of a large river may not.

2. Methods

2.1 The Large River Database (LRDB)

The LRDB has been compiled within the EU project "Improvement and Spatial Extension of the European Fish Index (EFI+, EC 044096) and further completed since. It consists of 2,693 sampling occasions from 358 sampling sites located in 16 European large rivers, i.e., rivers with a catchment size >10,000 km² (Berg et al., 2004). The LRDB is structurally comparable to the Fish Database of European Streams, described in detail by Beier et al. (2007). In contrast to the latter, it contains multiple samplings of identical sampling sites using different gears, which allows for analysis of the improvement of fish metrics by applying additional gears in large rivers.

The LRDB contains rivers Aller, Danube, Elbe, Ems, Havel, Ijssel, Lek, Meuse, Narew, Oder, Rhine, Saale, Spree, Tisa, Vistula and Weser. River Danube and its tributary river Tisa drain into the Black Sea. All other rivers drain into the North Sea or the Baltic Sea (Fig. 1). Rivers were sampled in the main channel, in backwaters and in mixed locations (i.e., covering both the straight channel and oxbows) across an average length of 2,221 m, 866 m and 951 m, respectively. Assessments took place over several years (1996-2010), during different seasons and a few samplings were conducted at night. The most frequent sampling methodology was electrofishing (E: 1862) and trawling (T: 710), followed by seining (S: 48) and drift-netting (D: 47). The remaining 26 samplings using gill-netting (23), long-lining (2) and fyke-netting (1) had to be excluded from further analyses due to a lack of comparability. Fished length and fished width had been recorded for each sampling occasion for electrofishing, trawling and drift-netting and fished area is given for seining which allowed determining species densities assessed by each method. Further, total length of captured fish had been recorded for some samplings and species, which allowed to considering size selectivity between electrofishing and trawling for frequently captured species.

2.2 Data standardization protocol

To standardize data, we selected only sampling occasions:

A. located in rivers draining into the North Sea and Baltic Sea. Rivers draining into the Black Sea were excluded because they contain too distinct and more species-rich fish communities biasing the comparisons;
B. covered a fished length of at least 400 m for electrofishing, trawling and drift-netting to ensure that at least 95% of the species inventory were captured (Wolter et al., 2004). Seining covered an area of at least 4000 m²;
C. captured at least 100 fish to fulfill national sampling standards (Dußling et al., 2004a) while maintaining reasonable sample sizes for the gear comparisons;
D. conducted during daytime; and
E. conducted in the main channel.

The remaining dataset consisted of 849 samplings at 159 sites in 14 rivers. Electrofishing (59.7%) and trawling (35.5%) were the most commonly applied gears followed by seining (4.5%) and drift-netting (0.2%). This dataset was used for a preliminary pairwise comparison between all gears. Further, three independent standardized datasets were created to compare electrofishing with each additional gear:

1. trawling (ET; samplings: 446; sites: 17; rivers: 5; assessed 1997-2008);
2. seining (ES; samplings: 78; sites: 4; rivers: 1; assessed 1997-2004); and
3. drift-netting (ED; samplings: 10; sites: 1; rivers: 1; assessed 1997-2000).

The key condition for each of these three datasets was, in addition to standardization steps A – E, that both methods compared were applied at least once at each sampling site. At the single locations this ensures that the same fish assemblage was sampled and that observed differences between gears might be attributed to method. Fig. 1 shows the locations of all sampling sites. However, each of these three final datasets still consisted of inhomogeneous sample sizes and contains confounding effects due to pseudo-replication, violating the assumption of independence (i.e., clustered and nested data as well as repeated measurements; Zuur and Ieno, 2016), which had to be accounted for in the statistical analyzes. These were repeated samplings at same sampling sites, in different rivers (ET comparison only), during different seasons and in different years.

2.3 Data analyzes

Gear contribution to the sampling results was assessed using fish assemblage metrics commonly applied in fish-based assessments of rivers referring to species, biodiversity and selected ecological guilds (Noble et al., 2007). All catches were standardized according to length / area sampled as individuals per 100 m² for each sampling occasion prior to data analysis. The standardized fish densities were used to calculate densities of ecological guilds and the Fish Region Index of the whole sample according to Dußling et al. (2004b).

In addition to the total number of fish species (including lamprey species) captured in all sampling occasions (= species inventory), we highlight the number of species that were captured exclusively by the different gears. We further analyzed numbers of species and proportions of fish in the total catches (PROP) that are migratory, protected or Habitat Directive species (Council Directive 92/43/EEC, 1994), referred to as 'HD species'. The very few reported hybrids between species were excluded from all analyses.

Species richness S as basic measure of biodiversity (Spellerberg and Fedor, 2003) was determined for each sampling occasion. Further common biodiversity measures calculated here were the Shannon Index and Evenness (Spellerberg, 2008) and the Simpson Index (Somerfield et al., 2008). Each index was calculated for each sampling as follows:

Species richness S

$$S = number\ of\ species$$

Shannon Index H

$$H = -\sum \left(\frac{n_i}{N}\right) \log \left(\frac{n_i}{N}\right)$$

Evenness e

$$e = \frac{H}{\log S}$$

Simpson diversity Index D

$$D = 1 - \sum \left(\frac{n_i}{N}\right)^2$$

where n_i = number of individuals of a species i; N = number of all individuals of all species.

We further analyzed the whole sample Fish Region Index (FRI_{total}), referred to as FRI further on, which is a fish-specific index for differences between river and stream regions (Dußling et al., 2004b). It characterizes fish species by means of their probabilities of occurrence in different river regions (Wolter et al., 2013) within the longitudinal river zonation (Illies, 1961) and takes values from three to eight (Dußling, 2009). For instance, a FRI of 7.00 corresponds to typical fish species of the metapotamal river region, respectively the common bream region (Dußling et al., 2004b). The FRI_{total} relates to the entire fish assemblage at a site and is particularly valuable for the assessment of large rivers because it rather sensitively indicates hydromorphological impacts related to river regulation, impoundments, but also rhithralisation effects (Wolter et al., 2013). The FRI_{total} was determined for each sampling occasion as:

Fish Region Index $FRI_{(total)}$

$$FRI_{(total)} = \frac{\sum_{i=1}^{S} \left(FRI_i \frac{n_i}{S^2 FRI_i}\right)}{\sum_{i=1}^{S} \frac{n_i}{S^2 FRI_i}}$$

where n_i = number of individuals of species i; FRI_i = FRI of species i; S^2FRI = variance of the FRI of species i. FRI_i and S^2FRI were retrieved from the literature (given below).

We selected the eurytopic and rheophilic habitat guilds as well as the lithophilic, psammophilic and phytophilic reproduction guilds and considered those as indicative guilds for environmental change (Welcomme et al., 2006) and hence valuable for assessments. The eurytopic guild represents generalist species and therefore mostly serves as indicator for degradation. In contrast, rheophilic species prefer running waters with higher flow patterns, i.e., benefit from natural flow dynamics. Rhithralisation can therefore also indicate degradation of the stagnant flow dynamics of the potamal regions of large rivers by decreased densities of eurytops and increased densities of rheophils. Lithophilic and psammophilic species essentially depend on spawning substrates that are maintained by hydromorphological processes and require coarse and fine substrate, respectively. Phytophilic species are obligate plant spawners depending on aquatic vegetation.

The assignment of fish species to guilds and to the species-specific FRI and S^2FRI (Table S1, supplementary information) primarily followed the classification provided by Scharf et al. (2011). We used Dußling et al. (2004b) and EFI+ Consortium (2009) for the remaining species. The calculation of FRI and S^2FRI of single species is provided in Wolter et al. (2013). We further analyzed the potamal guild as it represents species inhabiting primarily the open water zone of the main channel (Wolter and Bischoff, 2001). Species numbers and PROP were determined and densities of fish analyzed for each guild.

Within the standardized comparisons of ET and ES, we also analyzed fish densities of single species that were captured in at least 50% of all samplings with each gear (referred to as common species: *Abramis brama*, *Gymnocephalus cernuus*, *Leuciscus idus*, *Perca fluviatilis* and *Rutilus rutilus*). Within the ET comparison, we further analyzed size selectivity of electrofishing compared to trawling based on the total length of all measured fish of each common species. No length measurements of fish were available for the seine and drift-net catches.

2.4 Statistics

Mixed effects models were used for statistical analyses because they are robust to inhomogeneous samples inherent in most field data and because they allow account to be taken of random effects and unequal sample sizes (Zuur et al., 2009). Random effects resemble potential confounding effects from stratified sampling in time or space that violate the assumption of independence (Gonzales and Griffin, 2004). Random effects were site (ES comparison), site nested in river (ET comparison) and season nested in year. Method was treated as fixed factor in each model. Models' goodness of fit was assessed using the Akaike Information Criterion (AIC, Akaike, 1981). Separate mixed effects models were fitted for each ecological guild and biodiversity index. This resulted in 33 models, i.e., 11 preliminary models comparing all gears amongst each other (ETSD, Table S7), 11 models for the standardized ET comparison (Table S10) and 11 models for the standardized ES comparison (Table S12). The standardized ED comparison was not considered for statistical analyzes due to a small sample size (Table S13). P-values of ETSD models were adjusted using Tukey post hoc tests (Tukey, 1949) for multiple comparisons (Table S8). For each model, marginal R^2 and conditional R^2 were calculated as the amount of explained variance by the fixed effect (i.e., the method) and by the fixed and all random effects, respectively (Nakagawa and Schielzeth, 2013). Additional models were applied as described above within the ET (5 models, Table S15) and ES (5 models, Table S17) comparisons to test for differences in densities of common species. Differences in the total length of common species within the ET comparison were tested accordingly (five models, Table S19), but also included the sampling occasion as an additional random effect to account for sampling-based stratification of length measurements.

Data were analyzed in R 3.3.1 (R Development Core Team, 2016). We used the function *lmer* in the R package *lmertest* (Kuznetsova et al., 2016), which depends on package *lme4* (version 1.1-12; Bates et al., 2015) for fitting linear mixed models. Response variables were log-transformed when non-normality or heteroscedasticity was observed in residual plots. All response variables were modeled with a Gaussian error. Tukey post hoc tests were applied using function *glht* in the R package *multcomp* (version 1.4-5; Hothorn et al., 2016). The function *r.squaredGLMM* in the R package *MuMIn* (version 1.15.6; Barton, 2016) was used to determine marginal and conditional R^2. Statistical figures were plotted using the function *lineplot.CI* in the R package *sciplot* (version 1.1-0; Morales et al., 2012). Fig. 1 was drawn using ArcMap, version 10.2.2.

3. Results

3.1 Preliminary comparison of all gears

849 samplings at 159 sites in 14 large rivers yielded 503,593 fish of 66 species (including three lamprey species, referred to as fish in the following; Table S2). Most common fish were generalist species belonging to the eurytopic guild and represented >71% of the total catch. Electrofishing estimated highest total numbers of all species. Additional gears estimated higher PROP of eurytopic, phytophilic and potamal species and trawling captured one migratory species more than electrofishing (Table 1).

Electrofishing estimated significantly higher (Table S8) species richness, Shannon Index, Evenness, and Simpson Index and lowest FRI (Fig. 2) as well as significantly higher densities of eurytopic, rheophilic, lithophilic and psammophilic fish (Fig. 3, Table S6). Density of phytophilic fish was significantly higher for electrofishing compared to trawling. Trawling and seining estimated significantly higher densities of potamal fish than electrofishing. Trawling yielded significantly higher estimates of species richness, the Shannon Index, Evenness, the Simpson Index compared to seining and drift-netting and further higher densities of psammophilic fish compared to seining. Seining yielded significantly higher densities of eurytopic, lithophilic and phytophilic fish compared to trawling.

3.2 Standardized gear comparisons

The ET comparison yielded 249,040 fish of 47 species (Table 1). All six species captured exclusively with trawling were rheophilic and lithophilic (Table S3). Trawling captured more rheophilic, lithophilic, migratory and HD species than electrofishing (Table 1). The ES comparison yielded 39,389 fish of 33 species (Table 1). Seining captured two specimen of *Salmo salar* that was not captured with electrofishing (Table S4). The ED comparison yielded 4,192 fish of 18 species (Table 1). Drift-netting captured one specimen of *Abramis ballerus* that was not captured with electrofishing (Table S5). PROP of eurytopic, phytophilic and potamal fish were higher for all additional gears compared to electrofishing (Table 1).

Electrofishing led to the highest total numbers of species, of species exclusively caught by one method, the significantly highest species richness, Shannon Index, Evenness and Simpson Index and lowest FRI (Fig. 4) as well as significantly highest densities of eurytopic, rheophilic, lithophilic, phytophilic and psammophilic fish (Fig. 5) compared to trawling (Table S10) and seining (Table S12). Identical trends were indicated compared to drift-netting (Table S13). Trawling estimated significantly higher densities of potamal fish than electrofishing.

Trawling and seining assessed significantly higher densities of the potamal species *Abramis brama*, whereas densities of all remaining common species were significantly higher for electrofishing (Fig. 6) compared to trawling (Table S15) and compared to seining (Table S17). Total lengths of the common species *Abramis brama*, *Leuciscus idus*, *Perca fluviatilis* and *Rutilus rutilus* were significantly higher when captured with trawling as compared to electrofishing (Fig. 6, Table S19).

4. Discussion

Our study revealed that electrofishing captured most (94%) species across 849 samplings and clearly outperformed the other gears by 30% (trawling), 48% (seining) and 80% (drift-netting). Standardized comparisons validated that electrofishing captured more species than any other gear as well as the highest number of species exclusively caught by a single method. These findings clearly underline the well-known importance of the littoral zone for fish (reviewed by Strayer and Findlay, 2010), combined with the superior efficiency of electrofishing therein. Nevertheless, all fishing gears indicated typical fish assemblages of the metapotamal river region that was characterized by generalist species and a FRI of around seven (Dußling et al., 2004b).

The littoral zone along the shorelines provides integral resources for fish to reproduce (diverse spawning substrates), hatch (reduced flow patterns), feed (diverse terrestrial and aquatic food and prey items) and shelter (diverse physical structures). Most fish species are therefore encountered at the littoral zone, at least during some parts of their life-cycle. Biodiversity and fish density (Randall et al., 1996), also as a result of higher productivity (Lewin et al., 2014), are therefore substantially higher in structured littoral habitats compared to the structure-free open water zone. Therefore, the higher efficiency of electrofishing compared to the additional gears demonstrated here does not only reflect differences in selectivity between the compared gears, but rather differences between the meso-habitats sampled by the gears. Thus, although electrofishing left a gap concerning the sampling of the mid-channel, it well represented typical assemblages of large rivers by species numbers and biodiversity and it also captured highest densities of fish guilds that are indicative for hydromorphological degradation. As hydromorphological enhancements of the littoral zone constitute key rehabilitation measures to restore degraded habitats for riverine fishes (Kail and Wolter, 2011), electrofishing is likely more suitable to assess their success than other fishing methods that are applied within the mid-channel.

Concomitantly to the shoreline, the mid-channel also constitutes a unique meso-habitat of large rivers that provides a vast refuge for potamal species (Wolter and Bischoff, 2001).

Further, the mid-channel line typically provides higher flow velocities that constitute important guiding currents for upstream migrating fish (Benitez et al., 2015) such as anadromous salmonids (e.g., Kemp and O'hanley, 2010). The main currents in the mid-channel are also utilized by drifting fish larva (Lechner et al., 2016; Zitek et al., 2004) as well as downstream migrating species such as *Anguilla anguilla* when navigating to the sea (Piper et al., 2015). Correspondingly, additional gears applied in the mid-channel estimated higher PROP of potamal fish than electrofishing and also contributed additional migratory species to the total species inventory. Additional gears are hence likely more suitable for the assessment of management measures that target the restoration of longitudinal connectivity to promote fish migration (e.g., Fullerton et al., 2010; Kemp and O'hanley, 2010).

All other gears captured additional species to electrofishing in standardized comparisons. Species richness further showed that a high sampling effort is required with any gear to capture the whole species inventory of large rivers (Dembkowski et al., 2012), because species richness was relatively low for each sampling occasion compared to the total number of species captured across all samplings with each method. Therefore, a combination of sampling gears is highly beneficial to capture more species and to complete the species inventory (Gutreuter et al., 1995; Clark et al., 2007; Eggleton et al., 2010). Assessments aiming to determine the species inventory should accordingly apply various fishing gears covering both the shoreline and the mid-channel of the main channel and also extent sampling effort.

Trawling was the only fishing gear that estimated higher densities of the potamal guild and that captured most additional species to electrofishing in standardized gear comparisons. It seems therefore more suited than seining or drift-netting to be applied in addition to electrofishing to assess the entire species inventory, the density of potamal fish and to specifically capture rare and migratory species. Higher PROP and densities of potamal fish in trawl catches further underline that potamal fish preferably move within the mid-channel during daytime and are therefore less represented in daytime-electrofishing catches. Trawling further captured larger fish of common species (except the small-growing *Gymnocephalus cernuus*) than electrofishing. Both the meso-habitat and the gear-based selectivity of electrofishing and trawling (e.g., Wolter and Freyhof, 2004) contribute to predominantly larger fish captured by trawling because larger fish rather utilize the mid-channel section of the main channel (Wolter and Bischoff, 2001) and to predominantly smaller fish captured by electrofishing. Electrofishing however assessed higher densities of all common species, except the potamal *Abramis brama*. Consequently, trawling estimates lower densities of larger fish whereas electrofishing rather estimates higher densities of smaller fish. Trawling would further also capture older fish of large-growing species whereas electrofishing would underestimate the abundance of large fish in general and of older fish of large-growing species. Both the meso-habitat and gear-based size-selectivity have further implications for the assessment of biomass as rather many fish captured with electrofishing would have a lower biomass than rather few fish captured with trawling. Further benefits of additional methods such as trawling applied in combination with electrofishing are accordingly complementary size and age spectra (Goffaux et al., 2005; Porreca et al., 2013; Wiley and Tsai, 1983) as well as biomass estimates of fishes and fish assemblages.

Seining partly covered both the littoral and open water zone of the main channel, which was well reflected in the fish metrics estimated. However, in Iowa's (USA) nonwadeable rivers Neebling and Quist (2011) assessed sampling effort and resulting species numbers estimated with electrofishing, trawling and seining and concluded that seining was ineffective. Seining was found to underestimate species numbers, abundances and catch per unit effort in small streams (Poos et al., 2007; Wiley and Tsai, 1983) and to capture lower numbers of rare species than electrofishing in a small river (Poesch, 2014). Our findings support the lower suitability of seining to assess the species inventory of large rivers. Biodiversity estimates obtained by seining were lower compared to both electrofishing and trawling. However, seining may be valuable for assessing densities of eurytopic, rheophilic, lithophilic and phytophilic fish within the littoral zone, especially in the absence of complex habitat structures.

Drift-netting yielded consistently the lowest estimates of each fish metric assessed. These findings might be not representative at all, because only two drift-netting samples from the same day could be used in our analyses. However, 94% of the 47 drift-net samplings in our database had to be excluded from the analyses because they captured less than 100 fish (median area sampled 85.000 m²). This indicates that drift-netting captures rather low numbers of fish. Nevertheless, drift-netting captured one additional migratory species compared to electrofishing though its rare application in the standardized comparison which shows that drift-netting can also have gains for the assessment of biodiversity and migratory species. Apart from the low catch rates, the application of drift-netting is also restricted due to typical uses of the river channel such as inland navigation. Most large rivers serve as navigable waterways and intense ship traffic prevents the application of a floating net within the fairway.

Densities, biodiversity and fish size were shown to largely depend on the meso-habitat sampled and the sampling method applied therein. Therefore, researchers and managers should carefully select meso-habitats and sampling gears according to the research objectives (De Leeuw et al., 2007; Flotemersch et al., 2011) and explicitly refer to the meso-habitat sampled as well as account for the benefits and limitations of the sampling gears used. In case of applying complementary sampling gears in both meso-habitats, each meso-habitat should be addressed separately to e.g., describe density, size and biomass of fish within the mid-channel and at the shorelines while number of captured species can be pooled to characterize the whole species inventory of large rivers.

Differences in selectivity caused by physico-chemical parameters between the compared gears were not explicitly tested in this study (but accounted for in statistical analyzes by including random effects) as fishing gears were not applied under experimental conditions and as fishing gears were applied in different meso-habitats. Poos et al. (2007) did however not find any indications for turbidity, dissolved oxygen and conductivity to account for selectivity differences between electrofishing and seining in a small river. Nevertheless, each fishing gear has potential selectivity restrictions associated with environmental conditions during sampling. For instance, Lyon et al. (2014) reported that efficiency of electrofishing decreased with turbidity caused by higher river discharge. Further, the application of trawling is restricted within dry years if water levels are too low. Seine nets on the other hand are difficult to handle if velocities are too high, generally restricting their application to low flow conditions. Environmental variation can be minimized by selecting identical seasons and time of the day for the sampling and further by repeating the sampling multiple times within a season. From the analytical perspective, statistical methods such as mixed effects models (Zuur et al., 2009) that allow to account for stratification of the samples (e.g., per year, season, river, site or sample) help to reduce the accompanying uncertainties stemming from e.g., varying environmental conditions that are inherent in field samplings covering large spatio-temporal scales.

4.2 Management recommendations

The availability of two distinct meso-habitats in large rivers has far reaching implications for the assessment of large rivers. Appropriate sampling strategies largely depend on the research questions (De Leeuw et al., 2007; Flotemersch et al., 2011) and should follow clearly-defined objectives as they constitute an integral part for the evaluation of river restoration (Morandi et al., 2014). Gears that can sample complex structures and that are applied at the shoreline of large rivers such as electrofishing are consequently more likely to capture more fish and more species but smaller fish. Electrofishing is therefore well suitable to reflect the typical fish assemblage of large rivers and performs superior to additional methods in evaluating the success of hydromorphological restoration projects along the banks. Complementary sampling gears applied in the mid-channel section are more likely to capture fish and species that specifically utilize currents for navigation and dispersal as well as larger fish. Additional gears may perform better than electrofishing in assessing the success of projects aiming for the reestablishment of large migratory species, the restoration of longitudinal connectivity or the facilitation of fish migration and dispersal. Any combination of sampling gears covering both the shoreline and the main channel will perform superior over single fishing methods (Gutreuter et al., 1995; Clark et al., 2007; Eggleton et al., 2010) when assessments aim for a complete inventory of all species present at a site (biodiversity) or for recording rare, endangered and migratory species (Lintermans, 2016) as well as to obtain complementary size, biomass and age spectra. Trawling appeared as a more beneficial addition to electrofishing than seining and drift-netting to capture specifically migratory and rare species and potamal fish and hence to estimate biodiversity. However, each method requires considerable sampling efforts to capture a substantial proportion of the species inventory (Neebling and Quist, 2011). To facilitate large scale assessments, sampling gears need to be applied consistently (Goffaux et al., 2005) within similar meso-habitats and under comparable environmental conditions.

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Tables

Table 1. Species numbers and ratios of fishes captured with each gear (E = electrofishing; T = trawling; S = seining; D = drift-netting) for the preliminary comparison of all gears and for standardized comparisons of electrofishing versus each additional gear. Sam, Sp, Excl and Fi = total numbers of samplings, of species, of exclusive species and of captured fish (=total catch), respectively. EURY, RH, LITH, PHYT, PSAM and POT = eurytopic, rheophilic, lithophilic, phytophilic, psammophilic and potamal guilds, respectively. MIG = migratory species and HD = species listed in annexes of the Habitat Directive. "n" refers to the number of species and "PROP" refers to the ratio of fishes in the total catch captured with the respective gear

					EURY		RH		LITH		PHYT		PSAM		POT		MIG		HD	
	Sam	Sp	Excl	Fi	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]
Gear		Preliminary comparison of all gears																		
E	512	62	22	304155	20	71.8	32	27.5	19	9.7	13	6	4	5.7	6	6.9	15	15.7	14	2.8
T	297	40	3	177924	16	90.3	21	9.7	13	0.2	8	14.5	2	2.1	5	64.2	16	8.3	9	0.3
S	38	26	1	21219	11	90.3	11	9.3	5	2.5	8	21.5	2	3.3	4	74.0	6	1.9	6	1.9
D	2	8	0	295	6	99.3	2	0.7	0	0	1	90.8	0	0	4	93.2	1	0.3	0	0
		Standardized gear comparisons																		
E	162	41	7	74393	17	69.5	17	30.1	7	2.8	11	6.5	3	1.5	5	5.1	12	20.1	7	3.1
T	284	40	6	174647	16	90.7	21	9.3	13	0.2	8	14.5	2	2	5	64.3	16	8.1	9	0.3
E	56	30	13	30238	13	66.7	15	33.1	7	7.5	9	8.3	4	5.6	5	15.1	7	11.1	5	2.3
S	22	20	1	9151	10	93.8	9	6.2	4	2.3	4	28	2	0.1	4	71.4	5	2.3	2	1.9
E	8	17	10	3897	9	66.1	8	33.9	4	6.1	2	3	2	5.4	4	7.3	5	10.9	3	3.6
D	2	10	1	295	6	99.3	2	0.7	0	0	1	90.8	0	0	4	93.2	1	0.3	0	0

Figures

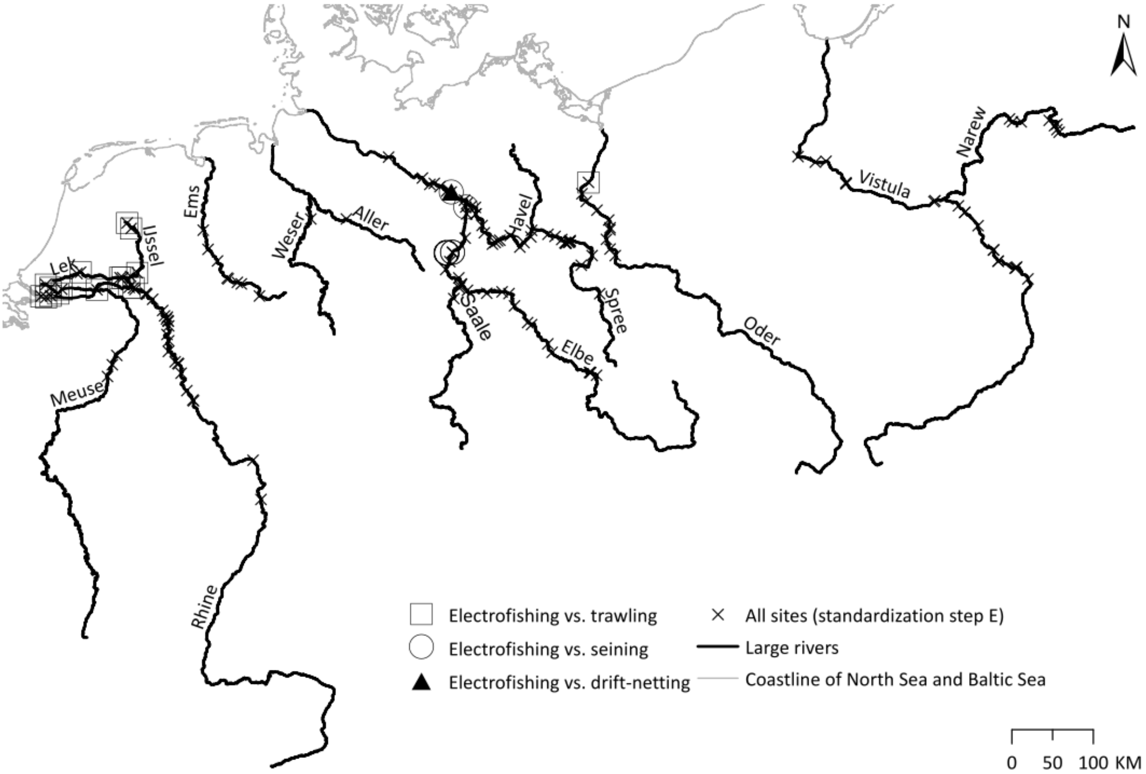

Figure 1. Location of sampling sites

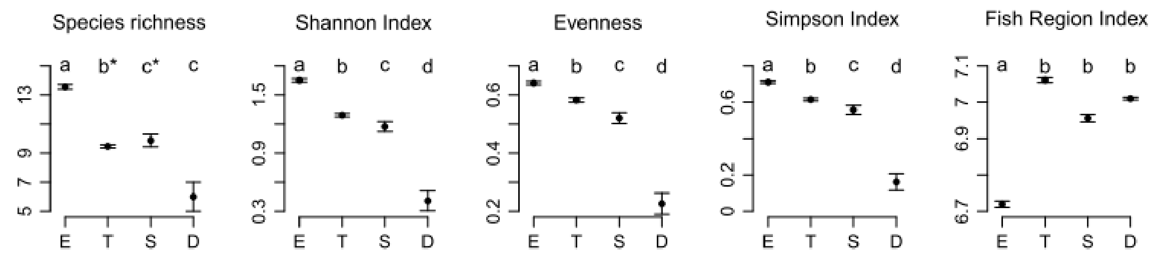

Figure 2. Biodiversity as estimated across 849 samples in European large rivers (E = electrofishing [512 samples]; T = trawling [297], S = seining [38], D = drift-netting [2]). Different lower case letters indicate significant differences; *note that species richness estimated by T is significantly higher compared to S when accounting for unequal sample sizes and random effects in a mixed effects model. D has a little sample size which requires cautious interpretation. Y-axis is log-scaled, mean and +/- standard errors (Table S6) are shown

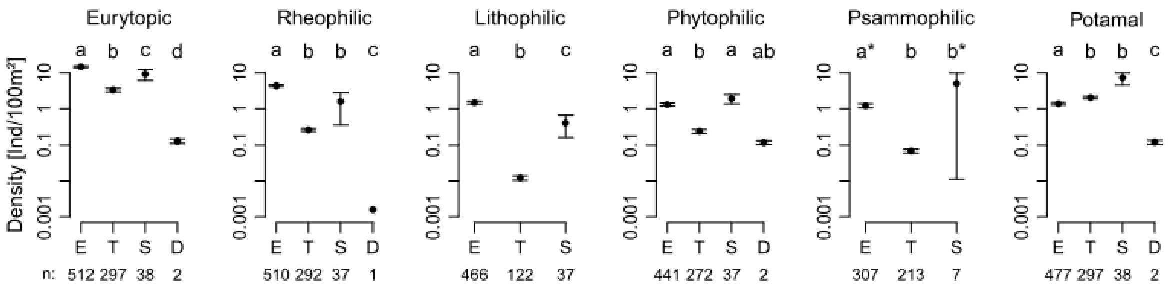

Figure 3. Densities of selected guilds as estimated across 849 samples in European large rivers (E = electrofishing [512 samples]; T = trawling [297], S = seining [38], D = drift-netting [2]; sample sizes (n) differ between guilds and same gears due to non-catches of fish in some samplings). Different lower case letters indicate significant differences. *Note that the high average value for the psammophilic density determined with S is biased due to one outlier and log transformed density estimated with electrofishing is significantly higher as estimated with seining for the psammophilic guild when also accounting for unequal sample sizes and random effects in a mixed effects model. Y-axis is log-scaled, mean and +/- standard errors (Table S6) are shown. D has a little sample size which requires cautious interpretation and no species belonging to lithophilic and psammophilic guilds were caught with D

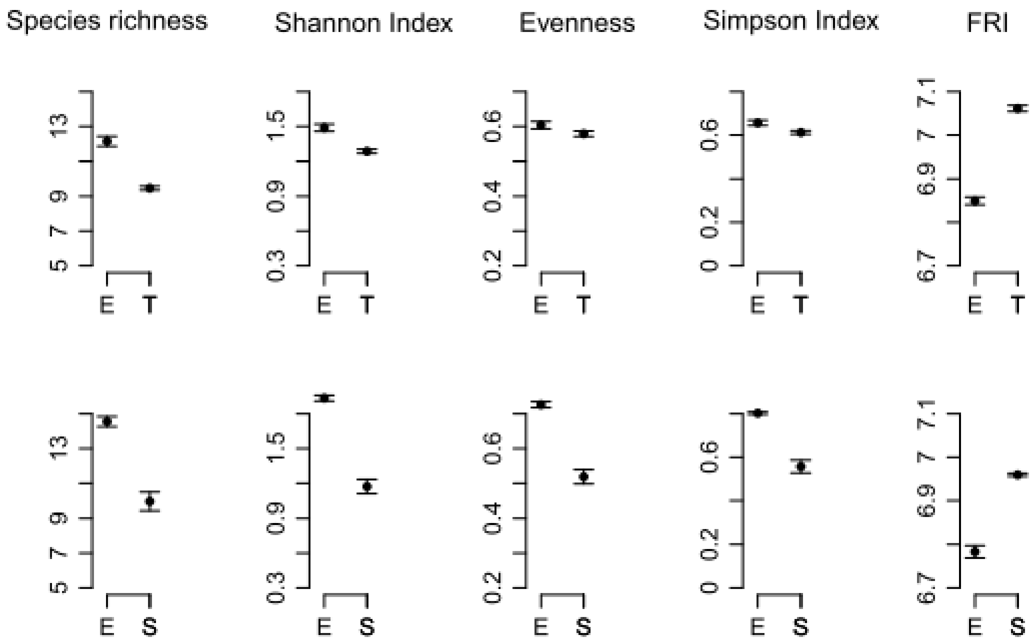

Figure 4. Biodiversity indices as estimated in the standardized gear comparisons of electrofishing (E) vs. trawling (T) [samples: E = 162; T = 284] and E vs. seining (S) [E = 56; S = 22]. “FRI” = Fish Region Index. All differences are significant. Mean +/- standard errors (Tables S9, S11) are shown

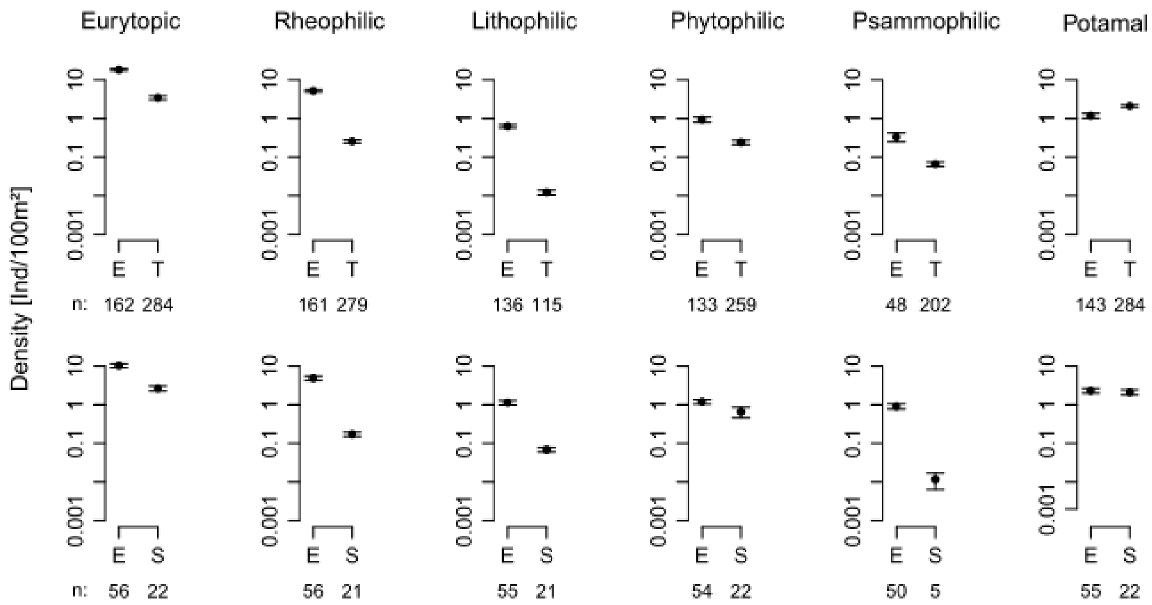

Figure 5. Densities of selected guilds as estimated in the standardized gear comparisons of electrofishing (E) vs. trawling (T) [samples : E = 162; T = 284] and E vs. seining (S) [E = 56; S = 22]. All differences are significant except the density of the potamal guild within the E vs. S comparison. Sample sizes (n) differ between guilds and same gears due to non-catches of fish belonging to the respective guild in some samplings. Y-axis is log-scaled, mean and +/- standard errors (Tables S9, S11) are shown

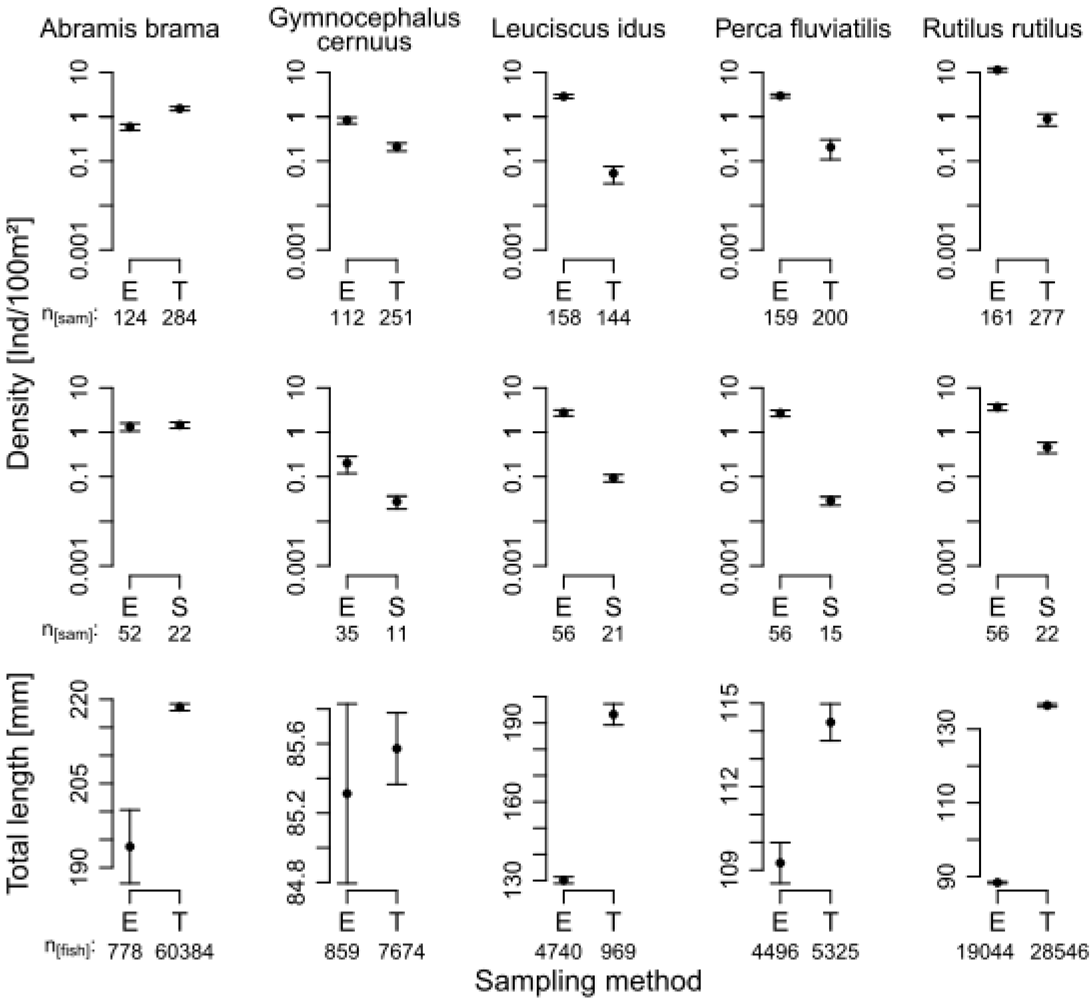

Figure 6. Densities and total lengths of common species as estimated in the standardized gear comparisons of electrofishing (E) vs. trawling (T) [samples: E = 162; T = 284] and densities of common species as estimated in the comparison of E vs. seining (S) [E = 56; S = 22]. Sample sizes ($n_{[sam]}$ = number of samplings) differ between species and gears due to non-catches of species in some samplings; $n_{[fish]}$ = number of measured fish. All differences are significant despite total lengths of *Gymnocephalus cernuus*. Y-axis is log-scaled concerning density-plots. Mean and +/- standard errors (Tables S14, S16, S18) are shown in all plots