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Characterization of European lampreys and fishes by their longitudinal and lateral distribution traits

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ABSTRACT

This study aims to complement existing fish-based assessment approaches by classifying European lampreys and fish species according to their probability of occurrence in six different longitudinal river regions and five types of floodplain water bodies under unimpaired conditions. The main objective was to provide for the first time harmonized occurrence traits for European lampreys and fishes in both longitudinal and lateral dimensions of floodplain river systems in a Fish Region Index (FRI) and Floodplain Fish Index (FFI), respectively.

Altogether 163 lamprey and fish species established in European rivers have been scored according to their longitudinal and lateral occurrence probabilities. The species-specific Fish Region and Floodplain Fish indices and their variances inform about species' occurrence probabilities, dispersal traits and potential species inventories of different river regions and floodplain waters. The final scores allow identifying characteristic fish assemblages, i.e. a set of type-specific species for the different longitudinal river regions and lateral floodplain water bodies.

The species-specific index values and variances serve to calculate summary metrics for the total fish assemblage (FRI_{total} and FFI_{total}) as macro-scale indicators for the deviation of the total fish assemblage from a reference state. The resulting index values indicate degradation as well as rehabilitation success at the level of fish assemblages, i.e. at an ecologically relevant macro-scale. Both species-specific and total assemblage indices are directly comparable among all biogeographic regions of Europe independent of the local species pool. As such, the indices serve as assemblage indicators for the fish-based assessment of the ecological status of water body types and river regions in floodplain river systems, which are required in particular for the assessment of large floodplain rivers.

1. Introduction

Fishes are rather long-living, mobile organisms that depend on a variety of resources and habitats during their ontogeny, e.g. for spawning, nursing, feeding, and shelter (Schiemer et al., 2001; Schwartz and Herricks, 2008; Wolter et al., 2016). Therefore, fishes provide highly suitable biological indicators that integrate information over wide temporal and spatial scales as well as environmental conditions (Karr, 1981; Fausch et al., 1990). However, this particular indicator strength of fishes is commonly under-utilized when applying them at the scale of micro- and mesohabitats (Wolter et al., 2016), where the results are substantially subjected to sampling effects (e.g., Angermeier and Smogor, 1995). Although numerous fish-based assessment systems are applied (Birk et al., 2012), assessing the ecological quality of large

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floodplain river systems remains challenging (De Leeuw et al., 2007; Dolédec et al., 2015; Erős et al., 2017) and quantitative indicators at the macroscale are still lacking. Therefore, this study aims to improve the utilisation of fish as macroscale indicator.

River systems provide dendritic networks of hierarchically nested spatial units, with habitats at lower levels embedded in and controlled by spatial structures at larger levels and hydromorphological processes connecting the habitats at different spatio-temporal scales (Frissell et al., 1986). Characteristic patterns of habitat structures and fluvial dynamics form functional process zones with distinct ecological communities and functions (Thorp et al., 2006), which usually align along a river course (Vannote et al., 1980). Accordingly, river systems provide a hierarchical, longitudinal array of functional process zones supporting different styles and dynamics of river channels with species assemblages equally differentiated from up or downstream communities based on local processes (Poole, 2002; Thorp et al., 2006; Wolter et al., 2016). The empirical knowledge about distinct fish communities from the headwaters to the lowland river sections resulted in the formulation of characteristic fish regions already more than hundred years ago (Frič, 1872; von dem Borne, 1882).

In addition to the longitudinal zonation of river reaches, the flood pulse of the lotic system also induces natural processes in a lateral dimension, e.g. floodplain inundation and connectivity (Junk et al., 1989; Junk, 2005). Natural floodplains form complex mosaics of dynamic habitat patches ranging from lotic and lentic aquatic, to semi-aquatic and terrestrial habitats (Gregory et al., 1991; Pander et al., 2018). These ranges and spatial varieties of successional patterns have frequently been considered to determine biodiversity (e.g., Welcomme, 1979; Ward et al., 1999; Strayer and Findlay, 2010), fish recruitment (Bischoff and Wolter, 2001; Górski et al., 2011) and productivity (Welcomme, 1979; 2008;; Junk et al., 1989) of floodplains. The environmental heterogeneity is further subjected to water level fluctuations providing spatio-temporal variability in habitat quality and connectivity at scales ranging from diurnal fluctuations to centennial flooding with substantial habitat rejuvenation (Geerling et al., 2006; Strayer and Findlay, 2010). Corresponding to the longitudinal river zonation, distinct groups of fishes were identified preferring more distant or longer isolated floodplain water bodies (Navodaru et al., 2002; Górski et al., 2010; 2013;; Schomaker and Wolter, 2011; Scharbert and Borcherding, 2013).

Pronounced preferences of species for environmental conditions found in specific river sections and floodplain waters can be considered as reproducible traits and be assigned to indicator values. This has been utilized already in fish region indices developed for example, as part of the National fish-based assessment systems in Austria (Schmutz et al., 2000) and Germany (Dußling et al., 2004). These indices classify all fish species, not only the eponymous reference species, according to their preference for and occurrence in different fish regions of the National river systems, embedding in the index the difference between river types. Such metric identifies river and water body type-specific fish assemblages that comprise all species including accompanying and rare species according to their probability of occurrence.

A comparable biological indicator system was developed for the integrity of the lateral hydrologic connectivity of floodplain habitat types, the Floodplain Index (Chovanec et al., 2005; Waringer et al., 2005). This multi-taxon index uses only a limited number of fish species, but also amphibians, molluscs, dragon- and caddisfly species. Further developments of the Floodplain Index included a broader variety of benthic invertebrate taxa to assess the ecological status and connectivity of floodplain water bodies (Šporka et al., 2016; Funk et al., 2017). However, there remains substantial need for developing informative diagnostic tools for the environmental assessment of large floodplain rivers (Erős et al., 2019). For example, evaluation systems considering both the longitudinal and lateral distribution of characteristic biotic assemblages or taxa are still missing, despite their utility in environmental assessment. Such evaluation system would allow for comparative assessment of reference assemblages with the actual species composition to identify the degree of environmental alteration, but also to evaluate rehabilitation success. It might even serve for benchmarking environmental targets in rehabilitation planning.

This study aimed to enhance the existing assessment approaches by classifying European lampreys and fish species according to their probability of occurrence in six different longitudinal river regions and five types of floodplain water bodies under least disturbed conditions. The main objective was to provide harmonized occurrence traits for European lampreys and fishes in both longitudinal and lateral dimensions of floodplain river systems in form of a Fish Region Index (FRI) and Floodplain Fish Index (FFI), respectively. Together FRI and FFI characterize the two-dimensional macro-habitat space preferably occupied by each species, i.e. the species-specific occurrence traits.

2. Material and methods

In total 163 lamprey and fish species occurring in European freshwaters and with sufficiently detailed spatial distribution data available, were classified by regional experts. Experts from all over Europe have contributed to the classification by scoring their local species' probability of occurrence to the same six river regions and five floodplain water body types using historic and recent species distribution data. However, climatic conditions, river hydrology, hydro-morphologic status and baseline human-induced degradation of rivers and floodplains widely vary between regions resulting in variations of scoring of the same species in different regions. Therefore, the Delphi technique (Crance, 1987; Yousuf, 2007) was applied and controlled feedback provided to the experts regarding ranges of classification for species assessed. During several iterations, the most consensus final score has been derived for all species. At the end, these most consensus scores level out variations between experts. This might lead to some variation or unexpected results when applying the indices for community assessments at the local level.

2.1. Calculation of the Fish Region Index (FRI)

Six river regions from the Epirhithral to the Hypopotamal usually sustain fish communities (Table 1, Illies, 1961; Dußling et al., 2004; Thorp et al., 2006; Erős, 2017). For each fish species, the probability of occurrence within these six river regions was scored with expectation values from 0 to 12 summing up to 12 in total. The probability of occurrence values for each river region and the region number (Table 1) were used to calculate the species-specific Fish Region Index (FRI) as weighted averages and its variance (S^2 FRI) as weighted variance according to Sachs (1997):

$$\mathrm{FRI} = \frac{3*\mathrm{p3}+4*\mathrm{p4}+5*\mathrm{p5}+6*\mathrm{p6}+7*\mathrm{p7}+8*\mathrm{p8}}{12}$$

$$S^2\ \mathrm{FRI} = \frac{\mathrm{p3}(3\text{-FRI})^2 + \mathrm{p4}(4\text{-FRI})^2 + \mathrm{p5}(5\text{-FRI})^2 + \mathrm{p6}(6\text{-FRI})^2 + \mathrm{p7}(7\text{-FRI})^2 + \mathrm{p8}(8\text{-FRI})^2}{11}$$

Table 1
River and fish regions according to Illies (1961) and von dem Borne (1882) considered to calculate the FRI.

	3 Epirhithral Upper trout region	4 Metarhithral Lower trout region	5 Hyporhithral Grayling region	6 Epipotamal Barbel region	7 Metapotamal Common bream region	8 Hypopotamal Ruffe-flounder region
Species	Sum of expectation values = 12					

Table 2
Floodplain water body types according to Ward and Stanford (1995) considered to calculate the FFI (*= once every 1–3 years, **= 15 + years disconnected).

	1 Eupotamon Main channel	2 Eupotamon Both sides connected backwater	3 Parapotamon One side connected backwater	4 Plesiopotamon Isolated, frequently connected* water body	5 Palaeopotamon Long-term isolated** water body
Species	Sum of expectation values = 10				

p3 – p8 = probabilities of occurrence from 3 = Epirithral to 8 = Hypopotamal from 0 to 12, in sum 12. FRI values range from 3.00 (p3 = 12), occurring only in the upper trout region, to 8.00 (p8 = 12), restricted to the ruffe-flounder region.

While the FRI indicates the preference of a given fish species for a specific river region, its variance indicates the spread of a given species' occurrence over several river regions. Species restricted to a single river region show low S^2 FRI values, those typically occurring in a range of fish regions have high S^2 FRI values.

The species-specific FRI represents an indicator value of this species for its probable occurrence in a specific river region, i.e. in a functional process zone *sensu* Thorp et al. (2006) with characteristic patterns of typical habitat structures and fluvial dynamics. All species occurring in similar habitat structures and river regions express corresponding FRI scores. Accordingly, the typical fish assemblage of a specific river region is represented by its community FRI (FRI_{total}). This FRI_{total} is calculated as average of the FRI characteristics of all species in the fish assemblage considering unequal variances and random samples according to Sachs (1997):

$$FRI_{total} = \frac{\sum_{i=1}^{s}\left(FRIi\ \frac{ni}{S^2FRIi}\right)}{\sum_{i=1}^{s}\frac{ni}{S^2FRIi}}$$

FRI_i, S^2FRI_i and n_i are the FRI, variance of the FRI, and number of specimens of species i in the sample, respectively.

The index value FRI_{total} for the entire sample yields the coenotic classification of the fish assemblage surveyed according to the longitudinal functional process zones of a river.

2.2. Calculation of the Floodplain Fish Index (FFI)

Five major floodplain water body types have been identified sustaining fish communities (Table 2, Amoros and Roux, 1988; Ward and Stanford, 1995; Amoros and Bornette, 2002). Corresponding to the longitudinal zonation, for each fish species the probability of occurrence within these five floodplain water body types was scored with expectation values from 0 to 10 summing up to 10 in total. The probability of occurrence values and the number of each floodplain water body type (Table 2) were used to calculate the species-specific Floodplain Fish Index (FFI) as weighted averages and its variance (S^2 FFI) as weighted variance according to Sachs (1997):

$$FFI = \frac{1*p1 + 2*p2 + 3*p3 + 4*p4 + 5*p5}{10}$$

$$S^2\ FFI = \frac{p1(1\text{-}FFI)^2\ +\ p2(2\text{-}FFI)^2\ +\ p3(3\text{-}FFI)^2\ +\ p4(4\text{-}FFI)^2\ +\ p5(5\text{-}FFI)^2}{9}$$

p1 – p5 = probabilities of occurrence from 1 = main channel to 5 = Palaeopotamon, from 0 to 10, in sum 10. FFI values range from 1.00 (p1 = 10), i.e. occurring only in the main channel, to 5.00 (p5 = 10), occurring only in long-term isolated floodplain water bodies.

Corresponding to FRI and S^2FRI, the FFI and its variance S^2FFI indicate the preferred occurrence of a species in a certain type of floodplain water bodies and the variation in using different types.

Similar to the longitudinal zonation, the species-specific FFI represents an indicator value of this species for its probable occurrence in a specific floodplain water body type with characteristic habitat structures and connectivity patterns. All species occurring in similar habitats and floodplain water bodies express corresponding FFI scores and thus, the typical fish assemblage of a specific floodplain water body can be represented by its community FFI (FFI_{total}). The FFI_{total} is calculated as average of the FFI characteristics of all species in the fish assemblage considering unequal variances and random samples according to Sachs (1997):

$$FFI_{total} = \frac{\sum_{i=1}^{s}\left(FFIi\ \frac{ni}{S^2FFIi}\right)}{\sum_{i=1}^{s}\frac{ni}{S^2FFIi}}$$

FFI_i, S^2FFI_i and n_i are the FFI, variance of the FFI, and number of specimens of species i in the sample, respectively.

The index value FFI_{total} for the entire sample represents the coenotic classification of the fish assemblage surveyed according to the lateral zonation of floodplain rivers.

3. Results

Altogether 163 lamprey and fish species established in European rivers have been scored according to their longitudinal and lateral occurrence probabilities in floodplain river systems (Supplement Table S1). The final scores allow identifying characteristic fish assemblages, i.e. a set of type-specific species for the different longitudinal river regions and lateral floodplain water bodies.

Between one (upper trout region) and 71 species (common bream region) represent the single longitudinal fish regions. However, the

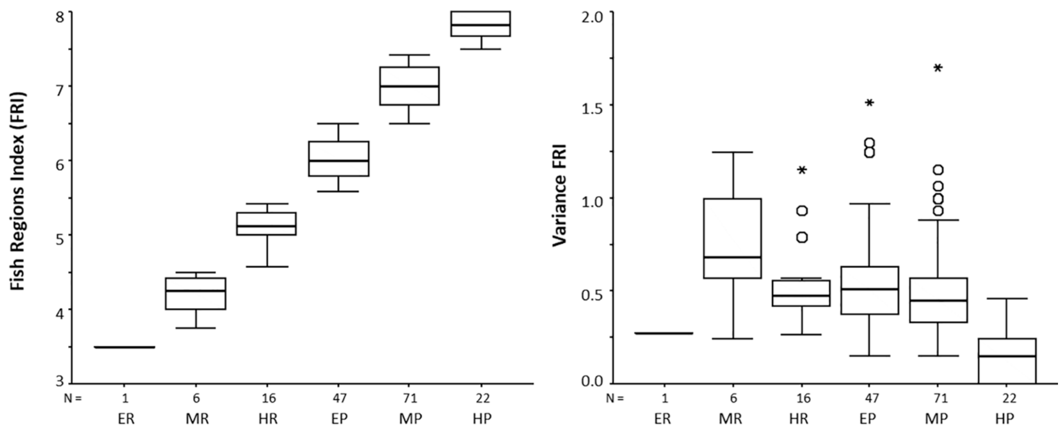

Fig. 1. Boxplots of individual Fish Region Indices (left) and variances (right) per river region from Epirhitral (ER) to Hypopotamal (HP); N = number of species; boxes represent 50% of values, whiskers 90%, the bold line indicates the median.

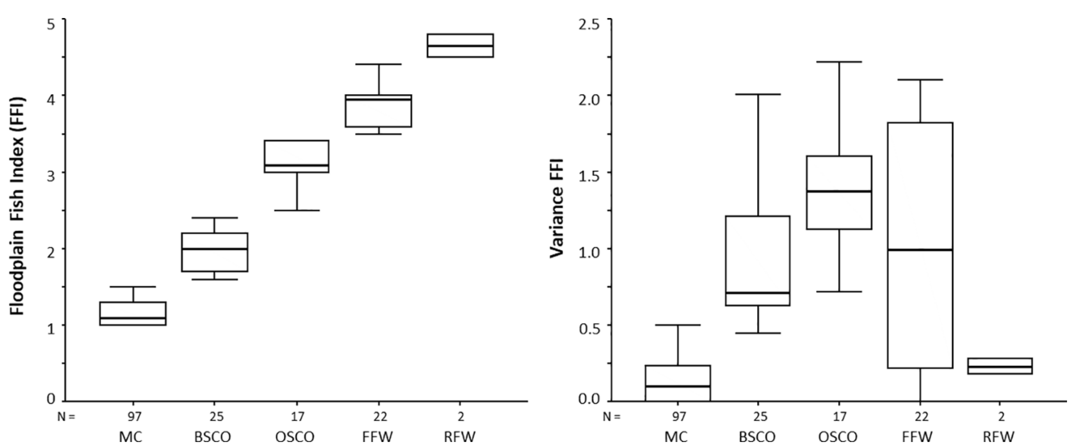

Fig. 2. Boxplots of individual Floodplain Fish Indices (left) and variances (right) per floodplain water body, MC = main channel, BSCO/OSCO = both/one side/s connected oxbow, FFW/RFW = frequently/rarely flooded isolated water bodies; N = number of species; boxes represent 50% of values, whiskers 90%, the bold line indicates the median.

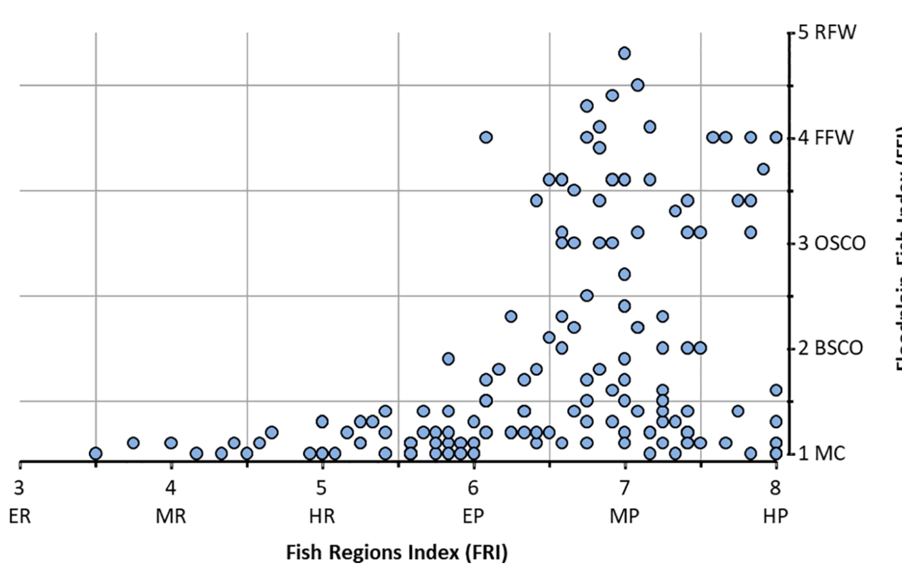

Fig. 3. Scatterplot of individual Fish Region and Floodplain Fish Indices from the headwaters (ER) to the mouth (HP) of rivers. The lateral dimension is indicated by the floodplain water bodies (MC = main channel, BSCO/OSCO = both/one side/s connected oxbow, FFW/RFW = frequently/rarely flooded isolated waters).

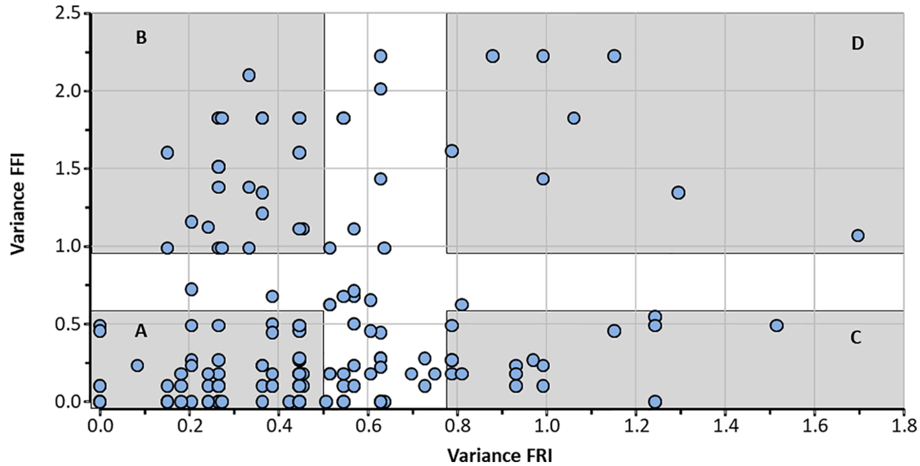

Fig. 4. Variances in longitudinal (Variance FRI) and lateral (Variance FFI) occupancy of river regions and floodplain water bodies differentiate groups of species according to their dispersal potential: A = restricted to single water body types and river regions, B = lateral dispersal only, C = longitudinal dispersal only, and D = dispersing in both dimensions. Species in between are rather unspecific in terms of dispersal potential.

variances indicate that substantial numbers of species usually occur in more than one fish region (Fig. 1). Only the species characteristic for the most upstream and downstream fish regions spread less into neighbouring river regions (Fig. 1).

The individual floodplain water body types and the main channel are characterized by between two (rarely flooded water bodies), 25 (both sides connected backwater) and 97 species (main channel), respectively (Fig. 2). The variances are rather low for typical main channel species indicating their limited utilization of water bodies in the floodplain as well as for floodplain specialist species in the long-term isolated water bodies (Fig. 2). Species typical for the other floodplain water body types, especially those preferring one side connected water bodies, frequently use the whole floodplain depending on connectivity as indicated by high variances of the FFI (Fig. 2).

The two-dimensional occupancy space of European lampreys and fishes clearly indicates the significance of the lateral dimension for type-specific fish communities especially in the downstream river regions, i.e. in the large lowland floodplain rivers. In particular, species of the Metapotamal or common bream region substantially utilize the floodplain water bodies (Fig. 3).

Based on the variances of FRI and FFI the two dimensional occupancy niches of the species can be further narrowed and species can additionally be classified according to their spatial distribution potential (Fig. 4). Species with very low variances are rather restricted in their distribution to a single water body type within a single river region. Examples are the Bermejuela (*Achondrostoma arcasii*) and the European mudminnow (*Umbra krameri*), which prefer the main channel in the Epipotamal and long-term isolated floodplain water bodies in the Metapotamal of large floodplain rivers, respectively (Supplement Table S1). A second group is characterized by limited longitudinal and high lateral dispersal. Examples for this group are the bitterling (*Rhodeus amarus*) and the Caucasian dwarf goby (*Knipowitschia caucasica*). Species of the third group show the opposite patterns, a limited lateral range, i.e. usually preferring the main channel and substantial longitudinal

Barbel	99
Bleak	11
Brook lamprey	1
Chub	73
Common carp	1
Dace	58
Grayling	77
Gudgeon	6
Minnow	1
Nase	1
Perch	50
Pike	9
Roach	79
Rudd	1
Spirlin	27
Stone loach	1
Streber	4
Sunbleak	2
FRI_{total}	**5.88**

Bleak	61
Chub	3
Common bream	21
Common carp	4
Dace	1
Gudgeon	42
Nase	2
Pike	5
Roach	93
Rudd	2
Spirlin	1
Stone loach	1
Sunbleak	23
Tench	4
FRI_{total}	**6.66**

Barbel	11
Bleak	2
Brown trout	20
Chub	10
Dace	13
Grayling	91
Gudgeon	9
Nase	2
Perch	6
Pike	1
Roach	1
Spirlin	2
Stone loach	22
Tench	1
FRI_{total}	**5.10**

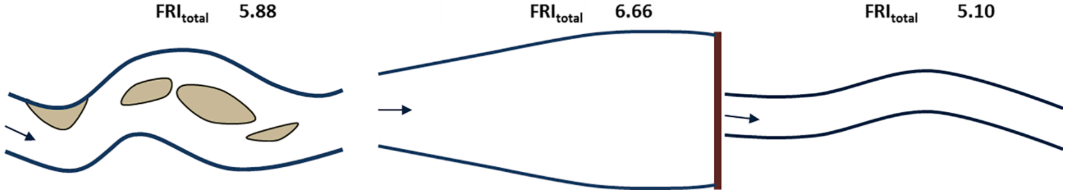

Fig. 5. Indicator value of the FRI_{total} illustrated at the epipotamal River Danube in Germany, in a near natural stretch (left), an impounded section subjected to potamalization (middle), and a residual flow stretch subjected to rhithralization (right). Data from Dußling et al. (2005).

distribution over several river regions, such as e.g. chub (*Squalius cephalus*), sculpin (*Cottus gobio*) and most of the anadromous species. A rather small forth group contains species that substantially disperse in both dimensions. These species are able to colonize and can thus be expected in nearly the whole floodplain river system, as e.g. the European eel (*Anguilla anguilla*) and the three-spined stickleback (*Gasterosteus aculeatus*). In addition, a number of species exhibit an unspecific distribution potential (Fig. 4).

3.1. Application

The species-specific FRI and FFI scores can be used to calculate community indices for single fish samples up to whole fish assemblages. Both, FRI_{total} and FFI_{total} provide metrics to assess how far a sample or community deviates from the type-specific trait composition of a specific river region or floodplain type. Both indices have the main advantage that they are able to indicate effects of opposing pressures. For example the FRI_{total} can indicate potamalization as well as rhithralization impacts at the same time as they are commonly observed at barriers (Dußling et al., 2004) and diversion hydropower plants (Merciai et al., 2018). The reduced flow velocities in impoundments upstream of barriers provide habitats that would naturally occur further downstream in the same river and that support a respective fish assemblage. This so-called potamalization effect is indicated by an increased FRI_{total} value (Dußling et al., 2004). In contrast, increased flow velocities in channelized stretches and downstream of weirs result in a so-called rhithralization impact, i.e. support species assemblages of naturally more upstream fish regions indicated by a lower FRI_{total} value (Dußling et al., 2004). An example for a 25 km long epipotamal stretch of the River Danube in Germany is provided in Fig. 5. Samples from the most natural river stretch show a FRI_{total} value of 5.88 corresponding to the barbel region. In the impoundment upstream of the Weir Rechtenstein the fish assemblage was subjected to a potamalization effect indicated by the increase of the FRI_{total} value to 6.66, which comes closer to the common bream region. In contrast, in the residual flow stretch downstream of Weir Rottenacker, the FRI_{total} value dropped to 5.1 closer to the respective value for the grayling region indicating a rhithralization effect (Fig. 5, data from Dußling et al., 2005).

Correspondingly, in an analysis of multiple pressure effects at 142 fish sampling sites in German rivers, the FRI_{total} appeared as fish metric, which was best related to the anthropogenic pressures (Kail and Wolter, 2013). Beside deficits in rheophilic fish abundance the FRI_{total} was the only metric performing in all river types studied by Kail and Wolter (2013).

The FFI_{total} is sensitive in particular to failures in long-term connectivity. Its value will increase if floodplain water bodies become overly isolated and cut-off from the active floodplain and decrease if the variety of typical floodplain water body types becomes reduced to some connected oxbows. In lowland rivers the indication of the FFI_{total} might even outperform the FRI_{total}, because extensive impoundments in high order lowland river regions will result in rather low increase of the FRI_{total} value, but in a significant shift towards a "backwater fish assemblage" (Kruk and Penczak, 2003; Penczak and Kruk, 2005).

For example, in the lowland River Havel, Germany, the isolation of a one side connected backwater by a levee resulted in a rather immediate increase of the FFI_{total} value from 2.65 to 3.32 (Fig. 6) and is expected to increase further with isolation time. In contrast, the reconnection of a former isolated backwater, which is a common floodplain rehabilitation measure, resulted in an immediate decrease of the FFI_{total} value indicating a shift of the fish assemblage towards flowing, permanently connected conditions (Fig. 6)

To be able to distinguish between opposing effects, capture data for calculating FRI_{total} and FFI_{total} fish community indices should not be pooled beyond distinct river regions and floodplain water body types. Otherwise, type-specific indications might become merged and opposing assessment results neutralised.

In addition, for assessing whole, complex river systems, community indices should be separately calculated for river region and water body types respectively for degraded and rehabilitated sites.

4. Discussion

This is the first harmonized comprehensive classification of lamprey and fish species commonly occurring in European floodplain river systems according to their spatial distribution preferences in lateral and longitudinal dimension. It goes well beyond previous assignments of

Asp	32
Bitterling	17
Bleak	1672
Chub	2
Common bream	975
Crucian carp	2
Gudgeon	5
Ide	20
Perch	875
Pike	105
Roach	4442
Rudd	113
Ruffe	228
Silver bream	2035
Spined loach	8
Tench	28
Zander	9
FFI_{total}	2.65

Bitterling	1093
Bleak	45
Common bream	15
Common carp	1
Crucian carp	46
Gudgeon	166
Perch	810
Pike	124
Prussian carp	107
Roach	1215
Rudd	469
Ruffe	1
Silver bream	149
Spined loach	11
10sp stickleback	3
3sp stickleback	570
Sunbleak	440
Tench	393
Weatherfish	16
FFI_{total}	3.32

Bitterling	215
Bleak	475
Burbot	5
Common bream	48
Gudgeon	25
Ide	3
Perch	402
Pike	27
Roach	2365
Rudd	581
Ruffe	7
Silver bream	455
Spined loach	28
Tench	32
FFI_{total}	2.93

Asp	17
Bitterling	63
Bleak	589
Burbot	33
Chub	27
Common bream	126
Dace	9
Gudgeon	66
Ide	41
Perch	549
Pike	102
Roach	1474
Rudd	122
Ruffe	36
Silver bream	604
Spined loach	71
Tench	8
Wels	6
Zander	9
FFI_{total}	2.55

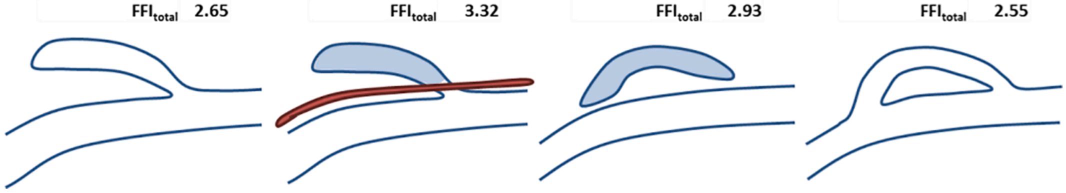

Fig. 6. Two examples for the response of the FFI_{total} to modifications of floodplain water bodies and connectivity: the cut-off of a formerly one side connected backwater (left) and the reconnection of an isolated floodplain water body to the main channel (right). Data from extensive fish samplings in the lower River Havel, Germany, 2002–2010.

species to fish regions from Austria (Schmutz et al., 2000) and Germany (Dußling et al., 2004) by covering species throughout Europe and by scoring for the first time both the longitudinal and lateral occurrence probabilities of species. However, both indices reflect the weighted probability of occurrence of a species in a certain river region and floodplain water body but do not allow any conclusions about the species' abundance or dominance therein.

It must also be noted that there are actually 614 species of freshwater and diadromous lampreys and fishes recognized in Europe (Fricke et al., 2020). Thus, there is ample opportunity to expand the database and to add new species if trait and distribution data become available. The scoring system presented is easily applicable to new species.

The resulting index values, species-specific as well as total assemblage indices, are directly comparable among all biogeographic regions of Europe independent of the local species pool. Accordingly, FRI_{total} and FFI_{total} can serve for comparing the ecological status of floodplain river water bodies across Europe. This constitutes a major advantage for common implementation strategies, e.g. for the Water Framework Directive (WFD, 2000/60/EC), the Habitats Directive (HD, 92/43/EEC), but also the Floods Directive (FD, 2007/60/EC) and the Environmental Impact Assessment Directive (EIA, 2011/92/EU). In addition, FRI_{total} and FFI_{total} might also guide assigning and assessing environmental flows based on typical fish communities.

Among European ecoregions, the rivers and their floodplains are exposed to very different climatic and hydrologic pressures as well as to very different degrees of human intervention and degradation (Tockner and Stanford, 2002; Cooper et al., 2013; Verhoeven, 2014; Grizzetti et al., 2017; Erős et al., 2019). This environmental variety results in significant variations of the ecological status and functional integrity of water bodies (Schindler et al., 2016; Grizzetti et al., 2017; EEA, 2018). Accordingly, the scoring of species occurrence covers the whole range from highly suitable to suboptimal or even sink habitats, which have the potential to introduce uncertainty and variability to the species classification. Despite this potential uncertainty, this scoring system for the first time provides species-specific occurrence traits as indicators for preferred river section and floodplain utilization that are functionally similar and applicable throughout all biogeographic realms of Europe.

5. Conclusion

This study provides for the first time longitudinal and lateral occurrence traits of the most commonly observed 163 lampreys and fish species in European floodplain river systems. The species-specific Fish Region and Floodplain Fish indices and their variances inform about species occurrences, dispersal traits and potential species inventories of different river regions and floodplain waters. As such, the indices serve as assemblage indicators for the fish-based assessment of the ecological status of water body types and river regions in floodplain river systems, which are in particular demanded for the assessment of large floodplain rivers (Erős et al., 2019). This constitutes a major advantage for common implementation strategies, e.g. for the Water Framework Directive (WFD, 2000/60/EC), the Habitats Directive (HD, 92/43/EEC), but also the Floods Directive (FD, 2007/60/EC) and the Environmental Impact Assessment Directive (EIA, 2011/92/EU).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107350.

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