Large rivers' fish assemblages under multiple pressures

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Preview

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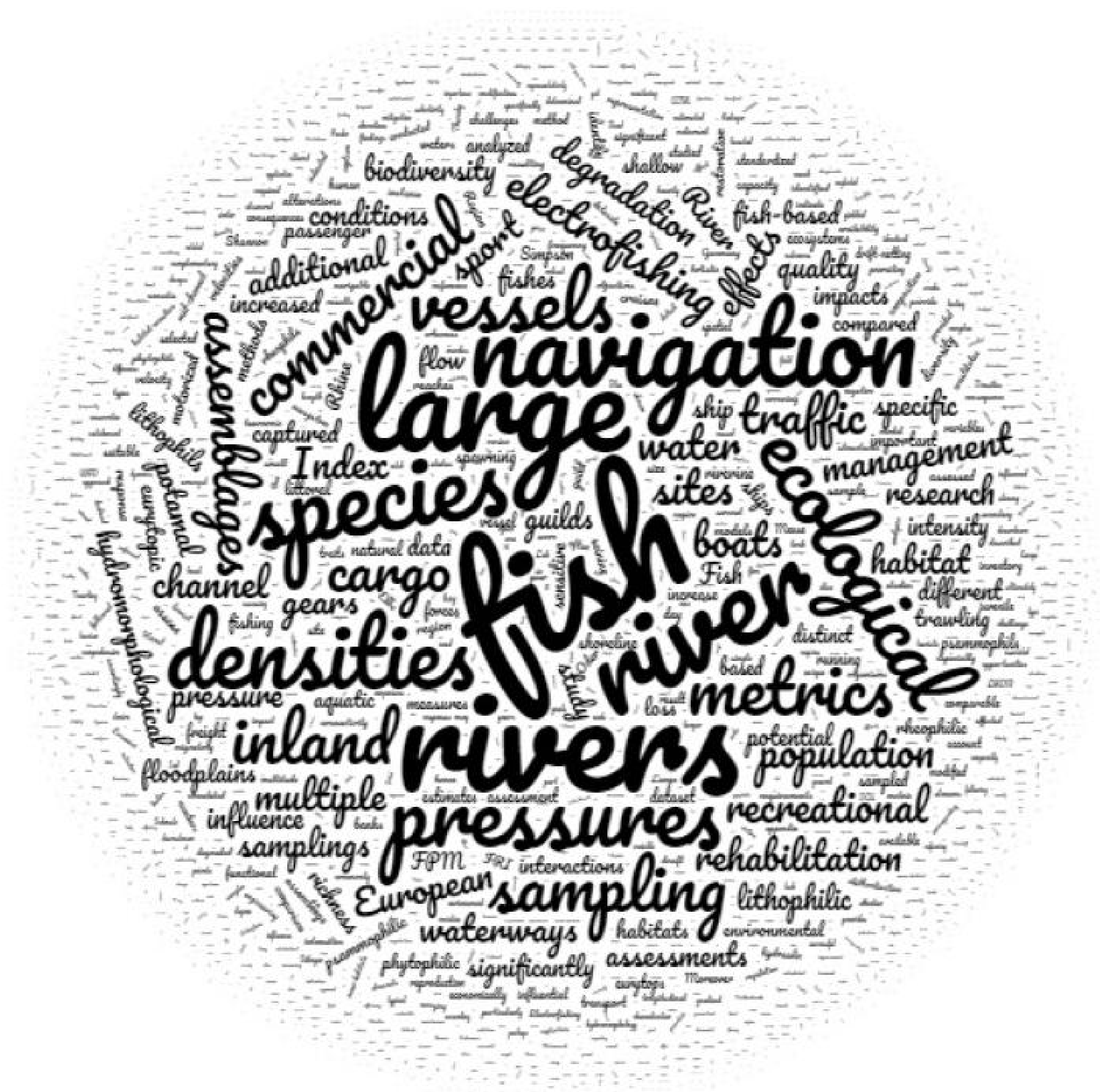

Word cloud representing the most relevant words within this thesis

Petr Zajicek
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Thesis outline

This thesis was conducted between 13.06.2015 and 12.06.2018 as part of the EU FP7 Project MARS (Managing Aquatic ecosystems and water Resources under multiple Stress, Contract No. 603378) under supervision of Dr. Christian Wolter at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries in Berlin. This thesis is a cumulative dissertation consisting of three separate studies (chapters), i.e., three research articles that are published in peer-reviewed journals (chapters one, two and three). Each of the published manuscripts follows distinct research objectives and therefore consists of its own introduction, methods, results, discussion and reference parts. Therefore, each chapter can be read separately. The overall context of this thesis is provided in a general introduction and key findings are coherently summarized and discussed in a general discussion. A reference section at the end of this thesis refers to (up to date) references provided within the general introduction and discussion. Resulting from this thesis' structure, general introduction and discussion overlap to some degree with the content of the main three chapters. All manuscripts were published by the publisher Elsevier, who generally permits the use of the manuscripts within the framework of a doctoral thesis. Therefore, the three main chapters consisting of published articles are provided in their original formatting styles as provided by the publisher.

Summary

Large rivers are important freshwater ecosystems and provide a great variety of differently structured habitats for aquatic organisms. However, European large rivers have historically become subject to tremendous anthropogenic alterations (e.g., river straightening, cut-off of meanders, water pollution), strongly delimiting the extent of habitat variability and suitability for aquatic animals such as fish. Shallow littoral areas were affected in particular. Today, large rivers are subject to multiple pressures such as flow alterations, loss of longitudinal connectivity to upstream and downstream river segments and loss of lateral connectivity to adjacent floodplains. Moreover, large rivers represent economically important, maintained and engineered (e.g., shore stabilization and channel dredging) waterways for inland navigation. Regular ship traffic, both commercial and recreational imposes strong and distinct hydraulic forces on shallow shore areas. Today, large rivers often resemble monotonous water channels that have lost the great variety of structural complexity that many fishes require to reproduce, to grow and to live. As a consequence of human exploitation, large rivers are amongst the most threatened ecosystems on earth.

Large rivers are strongly underrepresented in science and research. Accordingly, many open questions pertain regarding the fish-based assessment of large rivers. For instance, to assess the ecological status of large rivers, representative samples of the fish assemblages are required. Although electrofishing constitutes the most applied fishing method, its suitability, advantages and disadvantages compared to other gears such as trawling have never been extensively assessed in European large rivers. However, representative fish samples are indispensable for representative fish-based ecological assessments. Although a vast variety of different, “multiple” pressures has been identified in running waters, ecological consequences of large rivers’ human exploitation remain largely understudied. Which of the many pressures are most detrimental for the fish assemblages of large rivers? How can influential pressures be identified and which parts of the fish assemblages react to which pressures and are most useful within fish-based ecological assessments? Moreover, large rivers resemble highways for the transportation of goods but the role of inland navigation has not been quantified yet as a potential additional

pressure amongst all the other persisting pressures in large rivers. However, such knowledge is essential to derive appropriate recommendations for fish-based ecological assessments, river management and successful river rehabilitation. While commercial cargo traffic is rather stagnant or even declining, recreational ship traffic with motorized sport boats and commercial river cruises constitute strongly growing modes of inland navigation. However, potentially distinct ecological consequences of distinct modes of inland navigation such as commercial and recreational ship traffic have not been extensively evaluated under field conditions. Knowledge on the potential impacts of recreational navigation is important, especially for the successful rehabilitation of large rivers with low freight transportation and also for smaller waterways. This doctoral thesis addresses the above outlined research bottlenecks in three separate studies (chapters). A unique dataset, the Large River Fish Database (LRDB), containing 2693 fish samplings and sampling site characteristics (pressures) and navigation frequencies across several European large rivers was explored. Within each study, representative subsamples of the 2693 fish samplings were selected from the LRDB and several fish population metrics derived and studied in regard to the research objectives of each study. This large amount of data allowed to uniquely identifying some gradients in fish-based metrics, pressure expressions and navigation intensities, so that "large rivers' fish assemblages under multiple pressures" could be studied and recommendations for fish-based assessments, river management and river rehabilitation derived.

The first study assesses the suitability of commonly applied fishing gears for the fish based ecological assessment of large rivers. It demonstrates that electrofishing well represents the overall fish assemblages of large rivers (e.g., overall highest fish densities and biodiversity) despite its limited applicability to shorelines only. Additional fishing gears applied in the mid-channel such as trawling have important benefits for fish diversity assessments. For instance, trawling captures additional, potamal, rare and migrating species as well as larger fish compared to electrofishing. The availability of two distinct macro-habitats in large rivers, the shallow shore areas along the banks and the open water zone within the mid-channel is outlined and resulting consequences for the performance of the fishing gears applied therein are discussed. Fish based assessments need to apply appropriate sampling methods to derive representative fish population metrics for the fish assemblages of large rivers. The selection of an appropriate sampling method strongly depends on the research objectives. Electrofishing well represents the fish assemblages of large rivers in general and is particularly well suited to assess the outcomes of hydromorphological rehabilitation along the river banks. Complementary additional gears such as trawling are needed to capture the whole species inventory and all size-classes of fishes. Therefore, additional gears are most beneficial for assessments of biodiversity. Chapter one provides a highly relevant and solid baseline for the further studies of this thesis in particular and for fish-based ecological assessments of large rivers in general.

The second study disentangles the influence and effects of ten distinct pressure variables on fish assemblages of large rivers, also assessing the role of inland navigation intensity (frequency of cargo vessels) as an additional pressure (11 pressures in total). Responses of several fish population metrics (derived according to the standards defined in study one) to the most influential of the eleven pressures are analyzed and discussed. This study reveals a major influence of inland navigation besides increased flow velocity and the loss of floodplains. It shows that inland navigation acts on top of the prevailing hydromorphological degradation of the river channel. The fish assemblages show a general trend towards strongly reduced densities of fish, especially in habitat-sensitive reproduction guilds, as a response to multiple pressures and in particular to inland navigation intensity. Thereby, already eight cargo vessels per day trigger a decline of densities of fish with particularly strong declines for habitat-sensitive spawners. Diagnostic fish population metrics that are indicative for specific pressures were derived: Functional life-history traits of fish such as the density of obligate lithophilic spawners are particularly beneficial to identify ecological consequences of hydromorphological degradation and inland navigation. Taxonomic traits such as the Simpson or Fish Region Index are indicative for rhithralisation of the potamal river region. River rehabilitation and conservation needs to provide and conserve both natural river flows and floodplains while simultaneously protecting shallow areas from hydraulic forces caused by passing vessels. As a starting point to successfully mitigate multiple pressures in large rivers, diverse flow velocity patterns and access to floodplains need to be maintained, while shallow areas require protection from hydraulic disturbances caused by passing vessels. Chapter two provides highly relevant advice for river management, in particular for the rehabilitation of large rivers.

The third study investigates the ecological consequences of recreational and commercial ship traffic on selected fish population metrics that proofed most useful in the previous studies. It reveals that motorized recreational sport boats as well as commercial river cruises impoverish fish assemblages of large rivers besides and distinctly to the negative effects of commercial cargo vessels. Thereby, habitat sensitive fish, in particular lithophils, suffer most from any mode of inland navigation. This study confirms previous results in showing that any kind of motorized ship traffic degrades ecological quality in addition to river maintenance and river regulation. Even more importantly, ecological consequences of passing sport boats and river cruises can be as detrimental as of cargo vessels, particularly when frequency of cargo vessels is low and frequency of motorized recreational sport boats or river cruises is high. Therefore, ship traffic of sport boats and river cruises require each an equally strong attention in river management as commercial cargo vessels. Any mode of motorized navigation has the potential to counteract mitigation, rehabilitation and conservation measures that aim to improve and preserve ecological quality. Particularly, study three reveals a dramatic potential of recreational motorized sport boats that foredooms rehabilitation of economically less important waterways to failure in increasing ecological quality, as long as water based tourism such as pleasure boating is supported at the same time. Consequently, study three identifies particular challenges for river management as well as opportunities for future research that arise from the hitherto neglected impacts of motorized recreational navigation on fish assemblages in any type of navigated waters.

Selecting the proper sampling gear(s), representatively analyzing large-scale datasets, mitigating multiple pressures adequately while accounting for commercial navigation traffic as well as recreational sport boat traffic also in secondary waterways result in major implications for the management and rehabilitation of regulated large rivers and other engineered waterways. Management implications, arising challenges and recommendations for river management are coherently discussed in a general discussion at the end of this thesis.

Zusammenfassung

Große Flüsse sind wichtige Süßwasser-Ökosysteme. Sie bieten eine Vielfalt an Habitaten für aquatische Lebewesen. In Europa wurden diese großen Flussökosysteme jedoch über Jahrhunderte entscheidend durch menschliche Eingriffe verändert (z. B. Flussbegradigungen, Durchstich von Mäandern, Wasserverschmutzung) und viele Lebensräume für aquatische Lebewesen wie Fische gingen verloren. Strukturierte Flachwasserbereiche entlang der Ufer sind mit am Stärksten betroffen. Heute sind große Flüsse multiplen Stressoren ausgesetzt, beispielsweise der Änderung der Strömung, dem Verlust der longitudinalen Durchgängigkeit zu stromab und stromauf gelegenen Flusssegmenten oder dem Verlust der lateralen Konnektivität zu benachbarten Überschwemmungsflächen. Zusätzlich stellen große Flüsse ökonomisch wichtige und bewirtschaftete (z. B. Uferstabilisierung und Ausbaggerung der Flussrinne) Verkehrswege für die Schifffahrt dar. Regelmäßiger Schiffsverkehr, sowohl kommerzieller als auch freizeitlicher, erzeugt starke hydraulische Kräfte, welche auf flache Uferbereiche einwirken. Dabei unterscheiden sich Art und Intensität des Wellenschlages zwischen beispielsweise Güterschiffen, Passagierschiffen und Sportbooten. Hierdurch wird der Lebensraum für Fische in allen Wasserstraßen zusätzlich eingeschränkt. Heute sind große Flüsse oftmals monotone Wasserwege: Sie haben die ehemals vorhandene Vielzahl an Lebensräumen verloren, die viele Fische zur Fortpflanzung, zum Wachstum und zum Überleben benötigen.

In Wissenschaft und Forschung sind große Flüsse stark unterrepräsentiert, so dass die fisch-basierte ökologische Bewertung in großen Flüssen viele offene Fragen birgt. Alleine die Erfassung der Fischgemeinschaften der großen Flüsse stellt bislang eine ungeklärte Herausforderung dar: Welche der bekannten Befischungsmethoden repräsentiert am ehesten die gesamte Fischgemeinschaft der großen Flüsse? Auch wenn die Elektrofischerei die am meisten angewandte Methode in großen Flüssen ist, wurde bislang nicht untersucht, ob die Elektrofischerei auch das gesamte Fischspektrum der großen Flüsse repräsentativ wiedergeben kann. Dies ist vor allem deswegen wichtig, weil die Anwendung der Elektrofischerei in großen Flüssen technisch auf flache Uferbereiche begrenzt ist. Können andere Fangmethoden, die in der tieferen Flussrinne angewendet werden, wie die Schleppnetzfischerei, Vorteile gegenüber

der Elektrofischerei haben? Diese Fragen zu klären ist unabdingbar für die fisch-basierte ökologische Bewertung von großen Flüssen. Erst dann können ökologische Konsequenzen menschlicher Eingriffe mittels fisch-basierten Indikatoren verlässlich untersucht werden.

Ökologische Konsequenzen menschlicher Eingriffe auf die Fischgemeinschaften sind in großen Flüssen ebenfalls weitestgehend unerforscht. Welche der vielen Veränderungen des gesamten Flussökosystems wirken sich wie und auf welche „Teile“ der Fischgemeinschaften aus? Sind Habitat-sensitive Arten besonders betroffen? Wie reagieren welche fisch-basierten Bioindikatoren auf welche Veränderungen? Welche der bekannten Stressoren haben in einem von multiplen Stressoren geprägten Umfeld die größten Auswirkungen auf die Fischgemeinschaften und müssen daher prioritär im Gewässermanagement betrachtet werden? Viele dieser Fragen sind bis heute teilweise oder gänzlich unbeantwortet. Obwohl große Flüsse „Wasser-Autobahnen“ für Frachtschiffe darstellen, ist darüberhinaus vollkommen unbekannt, welche Rolle die Frachtschifffahrt zwischen der Vielzahl der in großen Flüssen vorherrschenden multiplen Stressoren einnimmt. Sind Frachtschiffe selbst ein Stressor für Fischgemeinschaften und wie relevant ist der Stressor „Schifffahrt“ zwischen all den anderen vorherrschenden Stressoren in großen Flüssen? Wirkt sich die Schifffahrt zusätzlich zur hydromorphologischen Degradierung negativ auf die Fischgemeinschaften großer Flüsse aus? Muss die Schifffahrt daher gesondert (zusätzlich zur Hydromorphologie) im Gewässermanagement betrachtet werden?

Während der kommerzielle Gütertransport (Frachtschiffe) über die Jahre hinweg eher konstant oder sogar rückläufig ist, gewinnen der kommerzielle Personentransport (Flusskreuzfahrten) sowie die Freizeitschifffahrt (private Sportmotorboote) zunehmend an Bedeutung. Insbesondere in solchen Wasserstraßen, in denen der Gütertransport vernachlässigbar ist, könnten zunehmende Kreuzfahrten und Freizeitschifffahrt ökologische Konsequenzen nach sich ziehen. Daher ist eine differenzierte Betrachtung der verschiedenen Schiffskategorien erforderlich: Können spezifische ökologische Konsequenzen anhand fisch-basierter Bioindikatoren für spezifische, freizeitliche und kommerzielle Schiffskategorien in großen Flüssen, in welchen alle Schiffskategorien vorherrschen, differenziert aufgezeigt werden? Haben Sportboote und Flusskreuzfahrtschiffe einen Einfluss auf Fischgemeinschaften und somit auf die ökologische Qualität in schiffbaren Gewässern? Welche

Konsequenzen ergeben sich aus Freizeitschifffahrt für die Renaturierung von sekundären Wasserstraßen, wie beispielsweise der Initiative „Das Blaue Band“, in welchen der Freizeittourismus zeitgleich zur Renaturierung gefördert wird?

In dieser Doktorarbeit werden die genannten Herausforderungen und Forschungslücken in großen Flüssen in drei einzelnen Studien adressiert. Ermöglicht wurden diese Studien durch einen einzigartigen Datensatz zu europäischen großen Flüssen, die „Large River Fish Database“ (LRDB), die in einem Vorgängerprojekt am Leibnitz-Institut für Gewässerökologie und Binnenfischerei in Berlin zusammengestellt und im Rahmen dieser Doktorarbeit ergänzt wurde. Die LRDB umfasst 2693 Befischungen in 16 großen Europäischen Flüssen, verteilt auf 358 Probestellen. Befischungen wurden mit unterschiedlichen Fangmethoden durchgeführt. Alle Probestellen sind durch zahlreiche (multiple) Stressoren charakterisiert und in der Datenbank entsprechend beschrieben. In dieser Doktorarbeit wurde die LRDB durch Daten zur Schifffahrt ergänzt, wie beispielsweise der Frequenz von Frachtschiffen, Kreuzfahrtschiffen und Sportbooten zum Zeitpunkt der Befischungen an den befischten Probestellen. Die LRDB ist daher der zum jetzigen Zeitpunkt umfassendste Datensatz weltweit, mit welchem Fangmethoden in großen Flüssen repräsentativ verglichen (Studie eins), ökologische Konsequenzen multipler Stressoren unter Berücksichtigung der Frachtschifffahrt als potentiellen Stressor identifiziert (Studie zwei) und ökologische Konsequenzen verschiedener Schiffskategorien differenziert werden können (Studie drei).

Studie eins

In der ersten Studie (Kapitel eins) wurden sowohl die Vorteile als auch die Nachteile von vier in großen Flüssen anwendbaren Befischungsmethoden wie beispielsweise der Elektrofischerei und der Schleppnetzfischerei im Detail analysiert. Die Eignung der Elektrofischerei für die fisch-basierte ökologische Bewertung von großen Flüssen wurde überprüft und die Vorteile zusätzlicher Fangmethoden wurden identifiziert. Hierfür wurden zunächst aus allen 2693 in der LRDB vorhandenen Befischungen nur diejenigen ausgewählt, welche die Kriterien für eine repräsentative Bestandsaufnahme (u. a. befischte Länge, Anzahl gefangener Fische) für alle angewandten Befischungsmethoden erfüllen. Basierend darauf wurden fisch-basierte Bioindikatoren (z. B. die Dichte von Fischen in Habitat-sensitiven Gilden, Biodiversität [z. B. Artenreichtum], Länge der am häufigsten gefangenen Fischarten) ermittelt und für vier Fangmethoden

(Elektrofischerei, Schleppnetzfischerei, Zugnetzfischerei, Treibnetzfischerei) verglichen. Da die Fangmethoden in unterschiedlichen Makro-Habitaten (im flacheren Uferbereich und in der tieferen Flussmitte) angewendet werden, wurde dieser Aspekt in der Beurteilung der Ergebnisse besonders hervorgehoben.

Obwohl die Elektrofischerei auf die flachen Bereiche entlang der Flussufer beschränkt ist, wurden mit der Elektrofischerei mit einer Ausnahme (potamale Fische) in allen Gilden (Eurytope, Rheophile, Lithophile, Phytophyle, Psammophile) die höchsten Fischdichten bestimmt. Die Dichte der potamalen Fische war mit der Schleppnetzfischerei am Höchsten. Auch die Biodiversität (Artenanzahl, Shannon Index, Evenness, Simpson Index) war mit der Elektrofischerei am höchsten und der Fish-Regions-Index am niedrigsten. Die meisten (sechs) zusätzlichen Arten, die mit der Elektrofischerei nicht gefangen wurden, wurden mit der Schleppnetzfischerei gefangen und waren alle rheophil-lithophil. Auch mit dem Zugnetz (Lachs *Salmo salar*) und dem Treibnetz (Zope *Abramis ballerus*) wurde jeweils eine zusätzliche Art nachgewiesen. Mit dem Schleppnetz wurden größere Fische als mit der Elektrofischerei gefangen.

In der ersten Studie wurde aufgezeigt, dass die Elektrofischerei eine geeignete Befischungsmethode darstellt, um große Flüsse fisch-ökologisch zu bewerten. Durch ihre Anwendung in flachen Uferbereichen ist sie zudem besonders geeignet, um hydromorphologische Degradierungen oder Renaturierungen entlang der Flussufer fisch-ökologisch zu bewerten. Zusätzliche Fangmethoden wie die Schleppnetzfischerei sind erforderlich, um das komplette Arteninventar (insbesondere seltene und wandernde Arten), potamale Fische und die Größenverteilung (bzw. Altersverteilung) von Fischen zu erfassen. In der ersten Studie wird daher eine wichtige und solide Basis nicht nur für die weiteren Studien dieser Arbeit, sondern vielmehr für die fisch-basierte ökologische Bewertung von großen Flüssen gelegt.

Studie zwei

In der zweiten Studie (Kapitel zwei) wurden die einflussreichsten Stressoren identifiziert, im Besonderen auch die Rolle der Frachtschifffahrt, sowie ihr Einfluss auf die Fischgemeinschaften großer Flüsse (anhand zehn fisch-basierter Bioindikatoren zu Fischdichten und Biodiversität, wie sie bereits in Studie eins abgeleitet wurden). Darüberhinaus wurden Bioindikatoren identifiziert, die auf bestimmte Stressoren besonders sensitiv reagieren. Hierfür wurden aus den 2693 in der LRDB erfassten Befischungen nur repräsentative Elektrobefischungen ausgewählt. Weiterhin wurden nur Probestellen ausgewählt, die alle durch elf verschiedene Stressoren (inklusive Intensität von Frachtschifffahrt) charakterisiert waren.

Die Frachtschifffahrt war einer der drei einflussreichsten Stressoren auf die Fischgemeinschaften großer Flüsse. Am einflussreichsten waren neben der Frachtschifffahrt eine erhöhte Strömung und der Verlust von Überschwemmungsflächen. Diese drei Stressoren bildeten auch die häufigsten paarweisen Interaktionen untereinander aus. Weitere Stressoren mit einem hohen Einfluss auf einzelne Bioindikatoren waren Sedimentation, Flussbegradigung („Kanalisierung"), organische Verschlickung, künstliche Uferbefestigung und Querbauwerke (Auf- / Abstiegsbarrieren). Multiple Stressoren und im Besonderen der Schiffsverkehr führten zu stark verminderten Fischdichten, vor allem in Habitat-sensitiven Reproduktionsgilden (Phytophile, Lithophile, Psammophile). Fischdichten nahmen bereits ab einer Frequenz von durchschnittlich acht Frachtschiffen pro Tag ab. Ein negativer Einfluss der Schifffahrt auf Biodiversität war ebenfalls vorhanden, aber weniger stark ausgeprägt. Die Biodiversität (v. a. Shannon und Simpson Index) wurde am Stärksten von erhöhter Strömung beeinflusst und deutete auch anhand des Fisch-Regions-Index' eine Rhithralisierung der potamalen Flussregion an. Der Verlust von Überschwemmungsflächen hatte den höchsten negativen Einfluss auf Dichten eurytoper, rheophiler und phytophiler Fische.

In der zweiten Studie wurde aufgezeigt, dass sich die Frachtschifffahrt zusätzlich zur hydromorphologischen Degradierung des Flussbettes auswirkt und einen zusätzlichen, bislang vernachlässigten und entscheidenden Stressor in großen Flüssen darstellt. Die ökologische Sanierung von großen Flüssen sollte sowohl flusstypische Fließgeschwindigkeits-Dynamiken als auch Überschwemmungsflächen wieder herstellen und erhalten sowie zusätzlich und zeitgleich Flachwasserbereiche vor schiffsbedingtem Wellenschlag schützen. Daher muss die Frachtschifffahrt gesondert im Gewässermanagement großer Flüsse betrachtet werden. Funktionelle Merkmale der Fischgemeinschaft wie die Fischdichte obligater Kieslaicher sind besonders geeignet, um ökologische Auswirkungen von hydromorphologischer Degradierung und der Schifffahrt zu erkennen. Taxonomische Merkmale wie der Simpson- oder der Fisch-Region-Index zeigen Rhithralisierung der potamalen Flussregion an. In der zweiten

Studie wurden daher die bedeutendsten Stressoren und fisch-basierte Bioindikatoren für diese Stressoren identifiziert, welche eine hohe Relevanz für die Flussbewirtschaftung und die fisch-basierte Bewertung großer Flüsse haben.

Studie drei

In der dritten Studie (Kapitel drei) wurde der freizeitliche und kommerzielle Schiffsverkehr differenziert betrachtet und der Einfluss von Frachtschiffen, Passagierschiffen und Sportbooten auf die Fischgemeinschaften in großen Flüssen analysiert. Hierfür wurden aus den 2693 in der LRDB erfassten Befischungen nur repräsentative Elektrobefischungen ausgewählt. Weiterhin wurden nur solche Probestellen ausgewählt, für welche jährliche Daten zu Frachtschiffen, Passagierschiffen oder Sportbooten vorlagen.

Sowohl motorisierte Sportboote als auch Passagierschiffe führten zu geringeren Dichten lithophiler und eurytoper Fische. Passagierboote führten außerdem zu niedrigeren Dichten rheophiler Fische. Zusätzlich zu diesen Effekten führten Frachtschiffe zu niedrigeren Dichten rheophiler und lithophiler Fische. Die Auslastung von Frachtschiffen wirkte sich zudem negativ auf den Artenreichtum aus. Es wurde weiterhin aufgezeigt, dass sich der Schiffsverkehr zusätzlich zum Ausbau der Wasserstraßen negativ auf die Fischgemeinschaft auswirkt. Dichten lithophiler Fische wurden vom Schiffsverkehr am stärksten beeinträchtigt. Phytophile und psammophile Fische waren so selten, dass diese statistisch nicht analysiert werden konnten.

In der dritten Studie wurde eine spezifische Wirkung von Freizeitschifffahrt und kommerzieller Schifffahrt auf die Fischgemeinschaften in europäischen großen Flüssen nachgewiesen, welche als Wasserstraßen für Frachtschiffe, Passagierschiffe und Sportboote dienen. Nicht nur kommerzieller Güterverkehr sondern auch kommerzielle Flusskreuzfahrten (Passagierschiffe) sowie freizeitliche motorisierte Sportboote haben einen differenzierbaren Einfluss auf die Fischgemeinschaft. Von all diesen drei Schiffskategorien sind Habitat-sensitive Fische, allem voran lithophile Fische am Stärksten betroffen. Ein ebenso hoher Einfluss auf Phytophile und Psammophile ist sehr wahrscheinlich. Die dritte Studie bestätigt und vertieft Ergebnisse der zweiten Studie, indem sie aufzeigt, dass jegliche Art der motorisierten Schifffahrt die ökologische Güte zusätzlich zur Bewirtschaftung und Instandsetzung der Flüsse herabsetzt. Noch wichtiger ist die Erkenntnis, dass ökologische Konsequenzen durch vorbeifahrende Sportboote und Passagierschiffe ebenso verheerend sind wie diejenigen von Frachtschiffen, insbesondere dann, wenn die Anzahl von Frachtschiffen gering und der Verkehr von Sportbooten oder Passagierschiffen hoch ist. Ausschlaggebend für die ökologischen Folgen sind die unterschiedlichen hydraulischen Kräfte (z. B. Wellenschlag), die von allen drei Schiffskategorien ausgehen und wichtige Fischhabitate entlang der Ufer beeinträchtigen. Diese Erkenntnis ist für die Bewirtschaftung und Renaturierung von kleineren Wasserstraßen ohne Güterverkehr von höchster Bedeutung: Der private Freizeitschiffsverkehr mit motorisierten Sportbooten, ebenso wie kommerzielle Flusskreuzfahrten, werden der Renaturierung von kleineren Wasserstraßen entgegenwirken. Deswegen muss die Freizeit- und Tourismusschifffahrt mit motorisierten Sportbooten und Kreuzfahrtschiffen (zusätzlich zum Güterverkehr) eine gesonderte Stellung und Beachtung im Gewässermanagement einnehmen.

Allgemeine Schlussfolgerungen

Im Rahmen dieser Doktorarbeit wurde aufgezeigt, dass die Elektrofischerei eine geeignete Befischungsmethode darstellt, um große Flüsse fisch-ökologisch zu bewerten. Die Elektrofischerei stellt daher auch eine geeignete Fangmethode für Bestanderhebungen dar, wie sie beispielsweise im Rahmen der europäischen Wasserrahmenrichtline durchgeführt werden. Zusätzliche Fangmethoden zur Elektrofischerei wie die Schleppnetzfischerei sind vor allem für die Erfassung des gesamten Arteninventars seltener, wandernder und potamaler Fische wichtig. Die Elektrofischerei ist in Kombination mit der Fischerei mit Schleppnetzen an erster Stelle oder auch mit Zugnetzen oder Kiemennetzen, je nach möglichem Einsatz, für Erhebungen der Fischbiodiversität empfehlenswert. Die Frachtschifffahrt stellt neben veränderten Strömungsmustern und dem Verlust von Überschwemmungsflächen einen der bedeutendsten Stressoren in großen Flüssen dar und wirkt sich zusätzlich zur hydromorphologischen Degradierung auf die Fischgemeinschaften großer Flüsse aus. Maßnahmen, welche in großen Flüssen die ökologische Qualität anheben sollen, müssen daher auch zusätzliche Maßnahmen ergreifen, mittels welchen (bestehende oder neu geschaffene) Flachwasserhabitate vor schiffsbedingtem Wellenschlag geschützt werden. In großen Flüssen sollten Rehabilitierungsmaßnahmen an erster Stelle flusstypische Strömungsmuster wiederherstellen, Zugang zu Überschwemmungsflächen schaffen und zeitgleich Flachwasserhabitate vor schiffsbedingtem Wellenschlag schützen. Auch die Freizeitschifffahrt mit motorisierten Sportbooten sowie die kommerzielle

Passagierschifffahrt mit Flusskreuzfahrtschiffen führen zu ökologischen Konsequenzen, welche ebenso gravierend sind wie diejenigen des Güterverkehrs mit Frachtschiffen. Initiativen wie das Blaue Band, welche den Wassertourismus und die Gewässerrenaturierung zeitgleich fördern, kann die Freizeitschifffahrt zum Scheitern hinsichtlich der Steigerung der ökologischen Qualität verurteilen. Sowohl in großen Flüssen als auch in jeglichen kleineren aber schiffbaren Gewässern wie beispielsweise sekundären Wasserstraßen senken motorisierte Sportboote und Passagierschiffe die ökologische Qualität. Habitat-sensitive Fische reagieren am stärksten mit einem Rückgang von Fischdichten auf hydromorphologische Degradierung und auf schiffbedingten Wellenschlag. Nach erfolgter Flussrenaturierung, welche auch die Schifffahrt mit berücksichtigt, sollte ein Anstieg der ökologischen Qualität erfolgen, der durch einen Anstieg von Fischdichten Habitat-sensitiver Arten messbar ist. Lithophile Fische sind besonders sensitiv auf motorisierte Schifffahrt und am ehesten als Bioindikator für erfolgreiche Revitalisierungsmaßnahmen in Fließgewässern geeignet. Maßnahmen zum Schutz vor schiffsbedingten hydraulischen Kräften sind in allen schiffbaren Gewässern wichtig und sollten gefördert werden. Dies kann beispielsweise durch Geschwindigkeitsbegrenzungen oder durch Schutzwälle erfolgen. Eine weitere Alternative bildet der Anschluss von Seitenarmen, Altarmen und Nebengewässern, um zusätzliche Brut- und Aufwuchshabitate für Fische zu erschließen.

General introduction

Large rivers are heavily modified waters (Jungwirth et al., 2003) that resemble the most severely impacted ecosystems on earth (Malmqvist and Rundle, 2002). Nearly all large rivers are flow regulated and fragmented (Dynesius and Nilsson, 1994) since they have been extensively engineered over centuries (Gurnell and Petts, 2002; Haidvogl, 2018) to serve multiple human demands (Nõges et al., 2015). Today, 90% of European lowland rivers are impacted by a combination of different pressures relating to altered hydrology, morphology, connectivity and to water pollution (Schinegger et al., 2012). Various kinds of river alterations, i.e., multiple pressures, interactively affect organisms, populations and communities (Crain et al., 2008). Hence, large rivers are globally amongst the most threatened ecosystems with the highest losses of biodiversity (Pimm et al., 2014; Reid et al., in press; Sala et al., 2000; Vörösmarty et al., 2010). For example, in Europe 37% of all freshwater fish species are threatened (Freyhof and Brooks, 2011). However, large rivers just started to receive priority attention in freshwater research (Darwall et al., 2018).

Extensive alterations of the riverine landscape have taken place for centuries (e.g., Buck et al., 1993; Diaz-Redondo et al., 2017; Gurnell and Petts, 2002), with some initial forms of river course modifications such as channelization backdating for millennia (Gregory, 2006; Haidvogl, 2018). To safeguard flood protection and to access highly fertile floodplains for agricultural cultivation or even for urban settlements during the 19^{th} century (Haidvogl, 2018), river courses were narrowed to a single channel in between artificially stabilized and diked river banks. Floodplains were decoupled from periodical inundations and natural hydromorphology was profoundly altered (e.g., Strayer and Findlay, 2010). For instance, sedimentary deposits indicated altered fluvial morphodynamics and channel shifts and thus the onset of anthropogenic channel correction works in the Upper Rhine River between the years 1828 - 1838 (Eschbach et al., 2018). Urbanization and industrialization strongly increased water pollution (Meybeck and Helmer, 1989) and rivers have been intensely fragmented and river flows regulated by weirs and dams (Nilsson et al., 2005; Poff et al., 1997; Schmutz and Moog, 2018) for hydropower generation (Piria et al., 2019; e.g., Schmutz et al., 2015), water abstraction (e.g., Benejam et al., 2010), fairway depth and flow regulation (e.g., Buck et al., 1993).

The economical importance of European large rivers as waterways to transport all sorts of goods increased in parallel to the overarching population growth and technical advances during the last century (Athammer, 1969; Förster, 1964). Intense inland navigation led to regular maintenance and engineering works within the river channel such as technical channel profiles with steep shores, regular sediment dredging to maintain a minimum navigable depth in the fairway or embanked and strengthened river banks with large boulders to prevent bank erosion (e.g, Bączyk et al., 2018; Buck et al., 1993; Décamps et al., 1988; Raška et al., 2017). Hence, floodplains became entirely decoupled from the more and more straightened, narrowed, channelized, stabilized, embanked, reinforced and ultimately monotonously engineered river channels (e.g., Strayer and Findlay, 2010). In addition to the navigation-related engineering impacts, vessels, ships and boats displace water during vessel passages, thereby inducing significant hydraulic forces on the river shorelines and shallow areas (BAW, 2016; Söhngen et al., 2008). The resulting dynamics from waves and drawdown degrade shoreline morphology (e.g., Zaggia et al., 2017) and strongly negatively affect aquatic biota through e.g., displacement, air exposure and habitat degradation (Arlinghaus et al., 2002; Gabel et al., 2017; Wolter et al., 2004a). Moreover, while large rivers resemble highways for cargo transport for decades, commercial passenger transport for recreational purposes as well as private recreational sport boats constitute a strongly growing mode of inland navigation in Europe nowadays (CCNR, 2016; Pauli, 2010). Consequently, today, large rivers represent ecosystems under even growing multiple pressures that have been broadly subsumed as alterations of hydrology, morphology, connectivity and water quality (Schinegger et al., 2012), although inland navigation has been rather disregarded. Millennia, centuries and decades of anthropocentric channel optimization and river engineering, with heavily increasing intensity from the onset of the industrial time to the present, have profoundly changed the original riverscapes (e.g., Gurnell and Petts, 2002; Hohensinner et al., 2018) and the inherent ecosystems with their life forms ("ecological change", Poff and Zimmerman, 2010). Hence, large rivers persistently lack pristine environmental and ecological conditions today.

Worldwide, fish-based assessments are regularly conducted to assess ecological quality in running waters based on fish assemblages (e.g., De Leeuw et al., 2007; Dußling et al., 2004; Erős et al., 2017; Goffaux et al., 2005; Karr, 1981; Lima et al., 2017; Schmutz et al., 2000). Large rivers take up a specific role within running waters because of the pure size of their water body resulting from a catchment area larger than 10.000 km² (Berg et al., 2004). Large rivers encompass distinct macro-habitats such as the deep open water and the shallow river banks (e.g., Ball et al., 2018; Flotemersch et al., 2011). Large rivers also provide distinct localized habitat structures such as sand banks, gravel bars and aquatic vegetation (e.g., Erős et al., 2008; Lapointe, 2014; Lechner et al., 2014). Sampling methods, i.e. fishing gears, take up a decisive role in fish-based ecological assessments of large rivers due to their restricted applicability either to the shallow river banks (e.g. electrofishing) or to the deep open water zone (e.g. trawling). Any gear selectively samples fish (e.g., Lyon et al., 2014; Mueller et al., 2017; Paukert, 2004; Porreca et al., 2013; Ravn et al., in press) and this gear-based selectivity is inevitably amplified by the extent and availability of macro-habitats in large rivers. Performance of electrofishing has been extensively tested and validated as a suitable gear for fish-based ecological assessments in small streams (e.g., Bohlin et al., 1989; Vincent, 1971). However, while firmly established as a standard fishing gear in fish-based ecological assessments of large rivers, the suitability of electrofishing to representatively depict large rivers' fish assemblages has never been profoundly validated. Moreover, additional sampling gears also covering the open water might be required for fish-based ecological assessments in large rivers to provide a full species inventory also capturing fishes with a strong preference for the open water area in large rivers. Accordingly, representatively assessing fish assemblages of large rivers is a yet unresolved challenge for both science and river management (e.g., Bonar et al., 2017) but an indispensable prerequisite for representative fish-based ecological assessments.

Assessing single or multiple pressures constitutes another particular challenge in large rivers due to the prevalence of a multitude of pressures and their potential interactions (e.g., Hein et al., in press; Jackson et al., 2016). Indeed, the lack of natural settings, i.e. undisturbed reference conditions, prevents a direct comparison of modified versus non-modified environments in ecological assessments of large rivers (e.g., Birk et al., 2012b; Melcher et al., 2007; Ramos-Merchante and Prenda, 2018). Moreover, environmental degradations inevitably overlap in the monotonously engineered channels of large rivers and particularly challenge the identification of the most influential pressures within the existing pressures pool. However, highly influential pressures are likely the ones with the greatest potential to lower ecological quality and thus require primary attention in river management and rehabilitation. Moreover, environmental degradations inevitably overlap in the monotonously engineered channels of large rivers and particularly challenge the identification of the most influential pressures (within the existing pressures pool) that most tremendously alter ecological quality. Therefore, multiple river reaches across multiple large rivers need to be evaluated (i.e., sampled) to cover as many environmental and ecological conditions as possible and to allow for an identification of both a pressure gradient amongst the prevalent pressures and a gradient in ecological quality across the sampled river reaches and finally, to establish a relationship between the influence of multiple pressures and a response in ecological quality. However, large rivers were significantly underrepresented in freshwater research and hence remain largely understudied (Erős et al., 2019; Hering et al., 2015b; Schinegger et al., 2013). The lack of research on large rivers can clearly be attributed to the challenges inherent in acquiring sufficient amounts of field data across large, transboundary spatial (e.g., European) scales (e.g., Wetzel et al., 2018) and to the lack of standardized sampling procedures (Birk et al., 2012a). Moreover, inland navigation has not been considered yet as a potential additional pressure in studies accounting for the prevailing multitude of pressures at the same time, although the water-based transportation of goods has changed many large rivers into navigation highways. Therefore, the potential influence and impacts of inland navigation as a hitherto neglected but relevant pressure on fish assemblages has not been considered amongst other prevailing pressures yet. Accordingly, disentangling multiple pressures – while explicitly accounting for inland navigation – and their implications for fish assemblages and ultimately ecological quality in large rivers are unresolved challenges for both science and river management.

Ship traffic is omnipresent in large rivers and any such waterway is shared by commercial cargo vessels, commercial touristic river cruises and recreational motorized sport boats (CCNR, 2016; PINE, 2004). Comparable challenges as described above regarding the lack of undisturbed reference conditions and the challenges to assemble data across large spatial extents are associated when it comes to study the particular effects of different modes of navigation traffic – recreational and commercial. Near natural reference conditions including references without ship traffic or with and without the one or the other modes of navigation are not existent for European large rivers. Practically all large rivers serving as waterways are shared by sport boats, river cruises and cargo vessels. Further, distinct ship traffic discerning different modes of navigation intensities covering multiple river reaches and rivers has not been considered yet in ecological research. Previous studies addressing ecological consequences of passing vessels, ships and boats on juvenile fishes relied on the comparison of mostly single river reaches within one river (e.g., Kucera-Hirzinger et al., 2008; Schludermann et al., 2013) or even on an experimental design (Holland and Sylvester, 1983). Nevertheless, detrimental effects on juvenile fishes and fish larvae were clearly indicated for both recreational and commercial navigation (Holland and Sylvester, 1983; Kucera-Hirzinger et al., 2008; Schludermann et al., 2013). Addressing different recreational (motorized sport boats in particular) and commercial navigation (commercial cargo vessels and river cruises) is therefore required across large spatial scales to identify gradients in ship traffic in each of the modes of motorized navigation. Discerning distinct effects of recreational and commercial navigation and their implications for fish assemblages and ultimately ecological quality under field conditions in large rivers is an unresolved challenge for both science and river management. In particular, recreational sport boats might require as much attention in river management as commercial cargo vessels due to their prevalence in commercially less important waterways.

An extensive database (the Large River Fish Database, LRDB, described in detail in the next sub-chapter) consisting of fish samplings and sampling site characteristics in several of the largest rivers in Europe was available at the Leibniz-Institute of Freshwater Ecology and Inland Fisheries in Berlin. The LRDB provided the unique opportunity to address major research gaps in European large rivers in the framework of this doctoral thesis. Major research gaps related to

(i) fish-based assessments,

(ii) multiple pressures and

(iii) inland navigation.

More particularly, research questions of this thesis addressed

(i) benefits and drawbacks of commonly applied fishing gears in the different macro-habitats of large rivers to derive recommendations for the fish-based assessment of large rivers,

(ii) the influence and effects of the most relevant pressures to derive indicative fish population metrics for specific types of degradation while specifically assessing the role of inland navigation amongst the prevailing pressures in large rivers,

(iii) the particular effects of different modes of ship traffic on fish assemblages to assess whether wave actions of passing cargo vessels, river cruises and sport boats are all detrimental to fish assemblages, in particular to habitat-sensitive fishes.

The Large River Fish Database

The Large River Fish Database (LRDB) was originally compiled within the EU project “Improvement and Spatial Extension of the European Fish Index” (EFI+, EC 044096). The LRDB is structurally comparable to the Fish Database of European Streams as described by Beier et al. (2007). In contrast to the latter, it contains

(i) only samples collected in the largest rivers of Europe,

(ii) multiple samplings of the same sites and

(iii) repeated samplings of the same reaches using different fishing gears.

The LRDB constitutes a unique collection of fish samples from large rivers, allowing to derive robust estimates of European large rivers’ fish assemblages. After review and extension of the LRDB within this thesis, the LRDB consisted of 2693 fish samplings at 358 sampling sites located across 16 European large rivers in total. For each study, data (subsets) were retrieved from the LRDB to fulfill requirements on representative and standardized samples according to the respective research objectives. The applied standardization procedures are described in each main chapter separately.

Fish samplings were conducted using different fishing methods. Beside standard electric fishing, active (trawling, seining, drift netting) and passive (gillnets, fyke nets) fishing methods have been applied. This variety of fishing gears applied allowed analyzing and discussing the benefits and drawbacks of specific fishing gears, the need for complementary gears in large rivers, as well as of different fish population metrics derived from the fish samplings for the fish-based ecological assessment of large rivers (chapter one).

For each fish sampling site, site descriptors were available indicating the ranked degree of human alteration at each site. Pressure ranks were assigned by local water authorities in accordance with national survey standards that follow the requirements of the European Water Framework Directive (2000/60/EC, WFD). This unique availability of information on multiple pressures across a substantial number of sites that were representatively sampled for fish, covering several large rivers, allowed to identifying gradients in both pressure intensities and ecological responses, ultimately allowing to disentangling multiple pressures on fish assemblages in European large rivers (chapter two).

The LRDB was further extended within this thesis by assigning navigation intensities of cargo vessels, river cruises and motorized sport boats – as officially documented at ship locks – to the fish sampling sites located in proximity of the ship locks on a yearly basis. Data on navigation intensities were provided by the Water and Navigation Authority (wsv.de) in Germany and by the Ministry of Infrastructure and the Environment (rijkswaterstaat.nl) in The Netherlands. The resulting availability of data on yearly navigation intensities – including statistics on sport boats, river cruises and cargo vessels – across a substantial number of sites across several large rivers that were sampled for fish is unique. It allowed to determine several navigation metrics and to assess the effects of recreational and commercial navigation on fish assemblages in European large rivers (chapter three).

The fish-based ecological assessment

Fish population metrics

Fish are excellent indicators for the ecological integrity of water bodies (Karr, 1981). However, many fishes have species-, life-stage -and season-specific requirements on their living environment (e.g., Balon, 1975; Bunn and Arthington, 2002; Winemiller, 1989): Even in the same habitat fish densities and abundance of species will vary, e.g., during ontogeny (Blondel, 2003; Britton and Pegg, 2011), between seasons (Baer et al., 2018; Dettmers et al., 2001; Wolter and Bischoff, 2001) and even between day and night (Benitez et al., 2018; Erős et al., 2008; Muška et al., 2018; Wolter and Freyhof, 2004). Moreover, fish populations consist of stationary and mobile specimens, i.e., rather resident and rather explorative fish (Radinger and Wolter, 2014; Winemiller, 1989). Therefore, fish densities were assembled into "*groups of species that exploit the same class of environmental resources in a similar way*" (Root, 1967). Such groups equal ecological guilds with distinct requirements on e.g., environmental conditions for spawning (Balon, 1981, 1975). The guild concept found broad application to assess the response of fish assemblages to specific hydrological, morphological and functional river changes (e.g., Noble et al., 2007; Welcomme et al., 2006). The guild concept thereby describes the species' response to ecosystem patterns and processes and is often more stable in time than the abundance of single species or the relative species composition (e.g., Aarts and Nienhuis, 2003). In addition, biodiversity metrics such as the Shannon Index (Shannon, 1948; Shannon and Weaver, 1949; see also Spellerberg, 2008 for a concise description) or the Simpson Index (Simpson, 1949; see also Somerfield et al., 2008 for a concise description) are commonly used in fish-based ecological assessments (e.g., Dußling et al., 2004). Functional and taxonomic fish population metrics referring to life-history traits and biodiversity constitute suitable ecological indicators for fish-based assessments (e.g., Colin et al., 2018; Lima et al., 2017; Sagouis et al., 2017). Consequently, several fish population metrics reflecting both functional and taxonomic traits of the sampled fish assemblages were determined within this thesis and their utility for fish-based assessments of large rivers analyzed within the separate studies.

Fish-based ecological assessments of large rivers

Fish-based ecological assessments of large rivers constitute a crucial challenge for researchers and river managers due to the difficulty to representatively sample fishes in these water bodies (De Leeuw et al., 2007; Poikane et al., 2014). In large rivers, key challenges arise from

(i) the sheer size of the water body (Flotemersch et al., 2011)

(ii) the existence of two distinct macro-habitats referring to the shoreline and the open-water zone, which both offer distinct habitat structures and hence support distinct parts of the overall fish assemblages (Muška et al., 2018; Wolter et al., 2004b),

(iii) specific habitat requirements of fishes that can further change during ontogeny (Noble et al., 2007),

(iv) the selectivity of fishing gears (e.g., Dembkowski et al., 2012) as well as their restricted applicability to specific habitats yielding method-specific fractions of the total fish assemblage (Loisl et al., 2013), and

(v) the substantial spatial extents large rivers cover, which enforces ecological assessments of various river reaches to be often conducted by different research institutions. Sampling methodologies lack standardization across different research institutions and agencies, imposing a major challenge and even a restriction in comparability of the fish samples and the derived fish population metrics (e.g., Birk et al., 2012a).

Despite its restriction to shallow littoral zones, electrofishing constitutes the most often applied fish sampling method in all running waters (Aparicio et al., 2011; Beier et al., 2007; Dußling, 2009). Based on the gear specific limitations, electrofishing potentially underestimates fishes that are rather channel-dwelling in the potamal macro-habitat (Wolter and Bischoff, 2001) and overestimates the ones inhabiting the shallow littoral macro-habitat (e.g., Randall et al., 1996) in large rivers. Hence, additional sampling methods also covering the potamal open water zone such as trawling could have additional benefits for fish-based assessments of large rivers. The suitability of electrofishing for ecologically assessing small streams has been scientifically well validated (e.g., Bohlin et al., 1989; Vincent, 1971), which is not yet the case regarding large rivers. Hence, assessing suitability of electrofishing for the fish-based assessment of large rivers and outlining its benefits and drawbacks compared to additional gears also covering the open water zone constitutes an important requirement for research and river management. Therefore, key goals of this thesis addressed in study one were to

(i) test the widely held assumption of the suitability of electrofishing for the fish-based assessment of large rivers and to

(ii) elucidate the benefits of additional fishing gears to electrofishing.

Large rivers and multiple pressures

Natural rivers are conceptualized in the River Continuum Concept (Vannote et al., 1980) as a longitudinal gradient of ecological and environmental conditions from source to mouth with distinct compositions of the local fish assemblages forming the overall fish community. Correspondingly, the biocoenotic concept of river regions (Illies, 1961) relates regional hydromorphological river properties to regional properties of the fish assemblages and accordingly classifies distinct biocoenotic regions within a river from source (e.g., rhithron, trout zone) to mouth (potamon, bream zone). In large rivers, the lateral gradient likewise describes a succession within the fish assemblage that is comparable with the longitudinal gradient (Aarts et al., 2004). Hence, "*modern river ecology concepts perceive running waters as a unity of river channel, riparian area and interrelating floodplains*" (sensu Schmutz et al., 2000; Fig. 1, left frame: Year 1743), which serve as nexus for regional biodiversity (Hauer et al., 2016; Hjältén et al., 2016). Naturally, large rivers offer a great variety of dynamic hydromorphological conditions (Eschbach et al., 2018) and should have comparable ratios of differently specialized fishes, i.e., a balance of ecological guilds of fish with specific habitat requirements (e.g., Schletterer et al., 2018, in press).

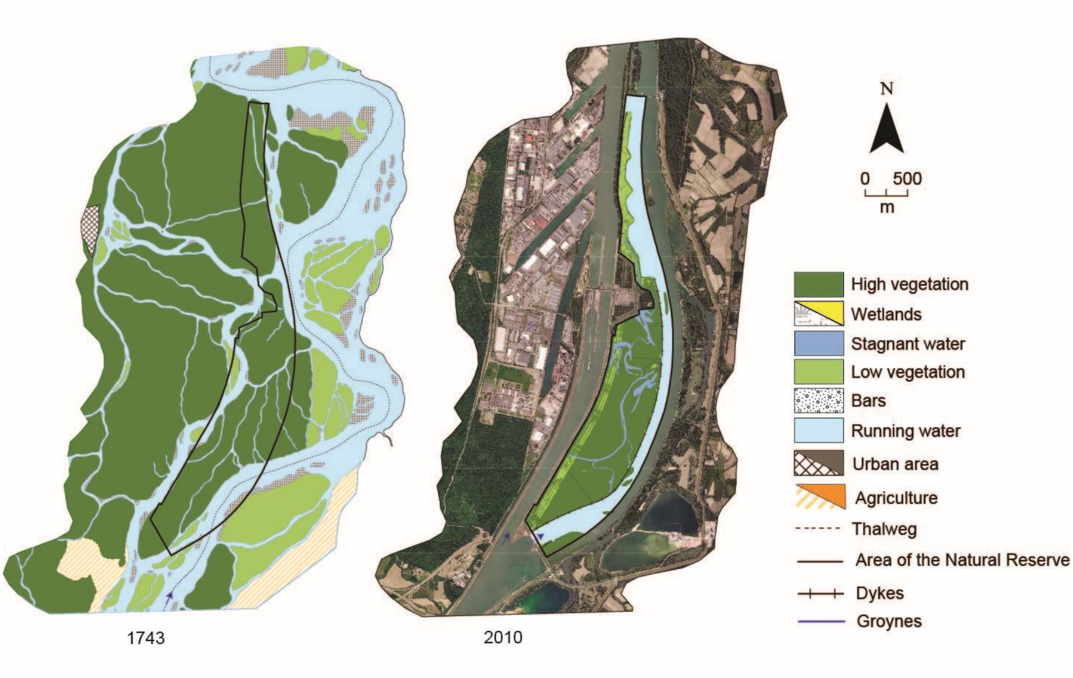

Fig. 1. The River Rhine nearby the city of Strasbourg in its more natural state in the year 1743 (left) and in its current modified state (year 2010, right). In its natural state, the river course was characterized by a meandering main river channel and an intact large floodplain including riparian areas, side-arms, oxbows and gravel bars. Centuries of river alterations resulted in a highly modified river channel in 2010: The river consists of a highly engineered riverbed evidenced by its narrow channelized course that is decoupled from any physical structure. Rural areas (year 2010, left of the river channel) and agricultural cultivation (year 2010, right of the river channel) have developed at the expense of the former floodplains indicated in 1743. This figure is adapted from Eschbach et al. 2018 and was kindly provided by David Eschbach and Laurent Schmitt.

In sharp contrast, nearly all of Europe's large rivers are so profoundly modified (e.g., Petts et al., 1989) that they resemble monotonous water channels (e.g., Diaz-Redondo et al., 2017) that are decoupled from their oxbows, side-channels and even from the entire floodplain (e.g., Strayer and Findlay, 2010; Fig. 1, right frame: Year 2010). 15 different modes of human alterations (i.e., pressures) on European running waters (mainly small streams and intermediate rivers) have been identified and assigned to four major pressure groups: Hydrology, morphology, water quality, connectivity (Schinegger et al., 2012). To give an example, stream hydraulics strongly impact fish community structure (Jager and Houser, 2016; Lamouroux et al., 1999; Poff and Zimmerman, 2010). Hence, juvenile fishes are more prevalent in shallow water with low flow velocities (Love et al., 2017). However, habitat degradation and subsequent loss of reproduction areas was the most frequently identified pressure in 44 French river restoration projects (Morandi et al., 2014), consequently delimiting living space for juvenile fishes. Water pollution was considered a major driver of ecological alterations (Meybeck and Helmer, 1989) before the role of hydromorphological degradation has been recognized (e.g., Friberg et al., 2016) and the term of biological integrity [“*a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region*”] of aquatic biota has been introduced (Karr and Dudley, 1981). Loss of longitudinal connectivity can hinder migrating species from reaching their spawning and nursery grounds (e.g., Branco et al., 2017; Musil et al., 2012; Puijenbroek et al., 2019; Verhelst et al., 2018), alter the hydrologic regime (Radinger et al., 2018a) and induce shifts in the fish community (Dußling et al., 2004; Radinger et al., 2018b). Likewise, loss of lateral connectivity impairs access to complex habitat structures such as submerged macrophytes or woody debris required by specialized fishes (e.g., Boys and Thoms, 2006; Sindilariu et al., 2006). Loss of natural floods and periodical inundation can alter ecosystem functioning and delimit functional diversity (Baumgartner et al., 2018; Davis et al., 2018). Accordingly, habitat generalists are overabundant in highly modified large rivers masking (Aarts and Nienhuis, 2003) the original longitudinal fish zonations (Illies, 1961; Vannote et al., 1980), while specialized fishes are highly underrepresented (e.g., Vriese et al., 1994). Therefore, further goals addressed throughout this thesis were to

(i) compile functional and taxonomic fish population metrics such as densities of habitat-sensitive fish and biodiversity across a multitude of heavily modified large rivers,

(ii) elucidate how the compiled fish population metrics react to the most prevalent pressures in large rivers and

(iii) derive fish population metrics that constitute suitable tools for the fish-based ecological assessment of large rivers.

Because of the multitude of pressures impacting freshwater ecosystems, awareness for the importance of multiple pressures and their interactions on the aquatic environment has steadily increased in recent research (e.g., Nõges et al., 2015; Ormerod et al., 2010; Radinger et al., 2016; Segner et al., 2014). However, research on multiple pressures strongly focused on alpine streams (e.g., Schinegger et al., 2018), headwaters (e.g., Bierschenk et al., 2019) and small rivers (e.g., Schinegger et al., 2016, 2012; Trautwein et al., 2013) while large rivers were rather underrepresented (Hering et al., 2015b; Schinegger et al., 2013). Large rivers are complex hydrological, ecological, economical, political and social systems (Campbell, 2016) and accordingly receive multiple impacts both from the upstream catchment and the local river reaches (Wolter et al., 2016). Therefore, large rivers clearly differ from smaller rivers, alpine streams and headwaters. Further, most research in the aquatic environment has focused on pairwise interactions of two preselected pressures (reviewed in Crain et al., 2008; Darling and Côté, 2008; Jackson et al., 2016). Considering only a few preselected pressures does not resemble field conditions and can neglect effects of other prevalent pressures or interactions (e.g., Vaughan et al., 2009). Hence, it remains unknown which specific pressures of the many ones have the greatest influence on riverine fishes and which interactions prevail in a natural setting (Craig et al., 2017) in large rivers, even if broad pressure groups referring to alterations of hydrology, morphology, connectivity and water pollution have been identified for smaller sized rivers and streams (Schinegger et al., 2012). Therefore, other goals addressed in study two were to identify

(i) the most influential pressures and

(ii) the most frequent interactions

among the under field conditions persistent multiple pressures in large rivers.

In addition to the hitherto described prevailing pressures in large rivers, large rivers such as the River Rhine form economically important waterways for commercial cargo transport (BVB, 2017; CCNR, 2016; PINE, 2004). Surprisingly, so far inland navigation has not been considered as a potential pressure in any of the studies on the impacts of multiple pressures in running waters (e.g., Schinegger et al., 2018, 2016, 2013, 2012; Trautwein et al., 2013), except in the study of Leclere et al. (2012). However, inland navigation has tremendous effects on the aquatic environment (reviewed in Gabel et al., 2017) through hydrodynamic forces along the shorelines introduced by vessel passages (BAW, 2016; Söhngen et al., 2008). Waves, drawdown and water currents affect shallow areas which constitute the only spawning and nursery habitats for fish (e.g., Blabolil et al., 2018) in the navigable river channel. Hence, hydraulic forces result in a habitat bottleneck for fish regarding successful reproduction (Navigation-induced habitat-bottleneck hypothesis, Wolter et al., 2004a). Accordingly, Leclere et al. (2012) showed that inland navigation and anthropogenic disturbances negatively influenced the occurrence of juvenile fish species in three tributaries of the Seine River in France. Consequently, inland navigation traffic could interact with other prevailing pressures and even add on top of the hydromorphological degradation of the river channel, further impoverishing fish assemblages and ultimately ecological quality. Hence, vessel operation could counteract the success of mitigation measures that, for instance, aim to rehabilitate river hydromorphology to improve ecological quality in large rivers that serve as waterways. Therefore, another of the key goals of this thesis was to

(i) assess the role of commercial inland navigation as an additional pressure among the most prevailing pressures in large rivers.

Inland navigation

Besides commercial cargo navigation, commercial river cruises and recreational motorized sport boats are omnipresent in large rivers nowadays. However, consequences of water-based recreational activities such as recreational boating on freshwater ecosystems have been underestimated in the past (Venohr et al., 2018). Specifically, recreational boating constitutes a strongly growing mode of inland navigation in Europe (CCNR, 2016; Pauli, 2010). Vessel type, hull shape, weight and speed determine the kinetic energy of the flow field and wake wash induced by passing vessels (e.g., Liedermann et al., 2014; Pearson and Skalski, 2011). Consequently, distinct hydraulic forces are caused by private sport boats, commercial touristic river cruises and commercial cargo transport (e.g., Kucera-Hirzinger et al., 2008) that erode the river channels' shallow shore areas (e.g., Zaggia et al., 2017) and restrict the living conditions for aquatic organisms (Gabel et al., 2017; Söhngen et al., 2008; Wolter et al., 2004a). In Germany, the Federal initiative "The Blue Band" (http://www.blaues-band.bund.de, 2018) aims at enhancing the ecological status of waterways while improving water-bound recreation and water tourism at the same time, with a major focus on minor, economically less important waterways with low volume of cargo traffic. Hence, the influence of recreational navigation such as motorized sport boats might require specific attention in river management (in particular in minor waterways) and further, potential ecological consequences of all motorized modes of inland navigation traffic need to be evaluated. Therefore, one of the key goals of this thesis addressed in study three was to

(i) assess distinct fish-based ecological consequences of recreational (sport boats) and commercial (river cruises and cargo vessels) ship traffic.

Research aims

The guiding aims of this doctoral thesis were to

(i) comprehensively study fish assemblages in European large rivers under field conditions,

(ii) assess the pros and cons of commonly applied fishing gears for fish-based assessments of European large rivers and thereby

(iii) derive robust estimates of fish population metrics representing the fish assemblages,

(iv) identify the most influential human modifications of the riverine environment (i.e., pressures) based on fish population metrics,

(v) assess the role of inland navigation as a specific pressure amongst all the other prevailing pressures,

(vi) identify how these pressures affect fish assemblages,

(vii) elucidate which fish population metrics prove responsive to which pressures,

(viii) study the impacts of inland navigation, both recreational and commercial, on the fish assemblages in greater detail, and overall,

(ix) derive complementary management recommendations for the fish-based-assessment and rehabilitation of large rivers.

Research objectives

Key objectives arising from the overall research aims were defined and addressed in each separate chapter:

Chapter 1: Comparatively evaluate common sampling methodologies applied in fish-based assessment to identify strengths and weaknesses of the fishing gears for fish-based ecological assessments of large rivers;

Chapter 2: Explore prevailing pressures in large rivers to identify the most influential pressures and their interactions on the fish assemblages of large rivers, while explicitly clarifying the role of commercial inland navigation as an additional pressure amongst the other pressures

Chapter 3: Determine frequencies of all motorized vessels, ships and boats to assess distinct effects of common recreational and commercial modes of inland navigation on the fish assemblages of large rivers.

Research hypotheses

Finally, specific hypotheses were derived in accordance to the research objectives and tested in each chapter:

Chapter 1: Electrofishing is generally a representative sampling method for the fish-based assessment of large rivers, well reflecting the composition of fish assemblages, while additional fishing gears have additional gains, in particular for estimates relating to biodiversity and channel-dwelling fishes. Hence, the most appropriate fish sampling procedure depends on each study's research objectives.

Chapter 2: Inland navigation is a highly influential pressure in large rivers and appears as such amongst the most prevailing human alterations of the riverine environment. Hence, inland navigation forms an additional, yet neglected, challenge for river rehabilitation.

Chapter 3: Any mode of inland navigation, be it commercial cargo vessels, commercial touristic river cruises or private recreational sport boats alters the composition of fish assemblages, in particular the densities of typical riverine, habitat-sensitive fish. Hence, the propagation of water tourism such as recreational boating counteracts the propagation of river rehabilitation in economically less important waterways.

Chapter one

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

This chapter consists of the following publication:

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Authors' contributions:

PZ and CW developed the concept; PZ did the literature research; PZ developed the methods; PZ analyzed the data; PZ wrote the manuscript; PZ and CW revised the manuscript.

The supplementary information mentioned in this publication is provided in the appendix of this thesis.

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Full length article

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 2693 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.

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 km^2 (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

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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 2693 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 2693 sampling occasions from 358 sampling sites located in 16 European large rivers, i.e., rivers with a catchment size > 10,000 km^2 (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 2221 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 m^2;
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

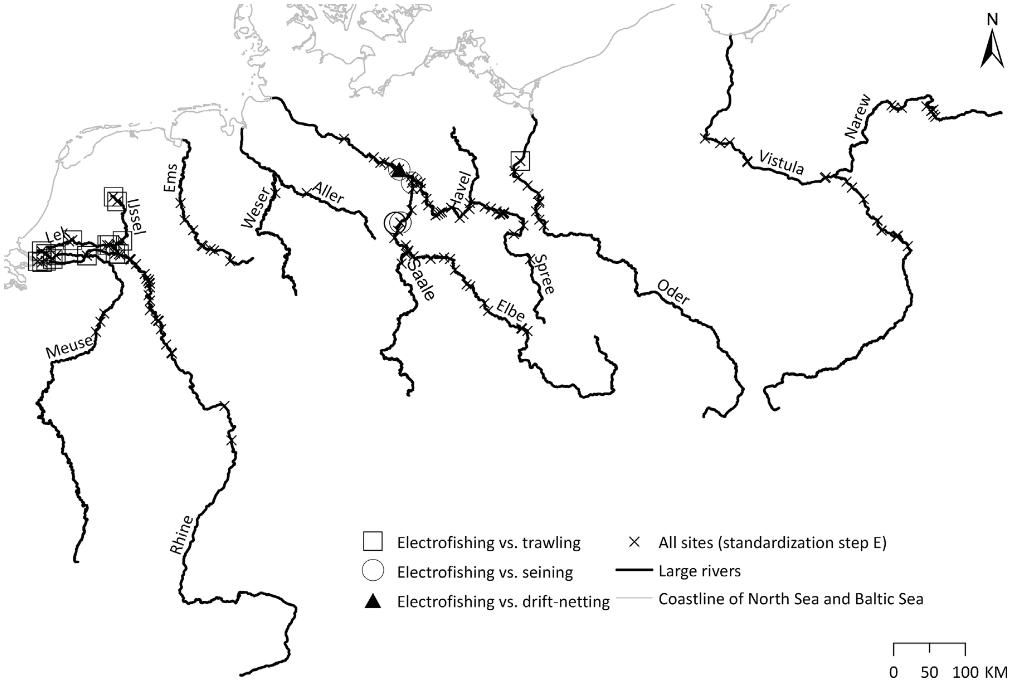

Fig. 1. Location of sampling sites.

(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 m^2 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, 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 $FRI_{(total)}$

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

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 (five models, Table S15) and ES (five 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 4192 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).

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.

Gear	Sam	Sp	Excl	Fi	EURY		RH		LITH		PHYT		PSAM		POT		MIG		HD	
					[n]	[PROP]	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]	[n]	[PROP]
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

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 lifecycle. 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

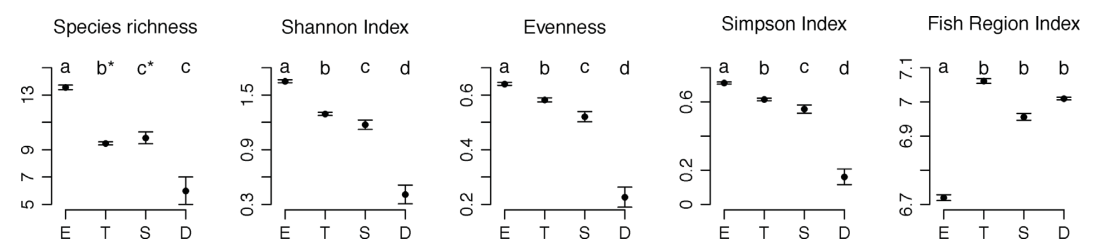

Fig. 2. Biodiversity as estimated across 849 samples in European large rivers (E = electrofishing [512 samples]; T = trawling [297], S = seining [38], D = drift-netting [2]). Different lower case letters indicate significant differences; *note that species richness estimated by T is significantly higher 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.

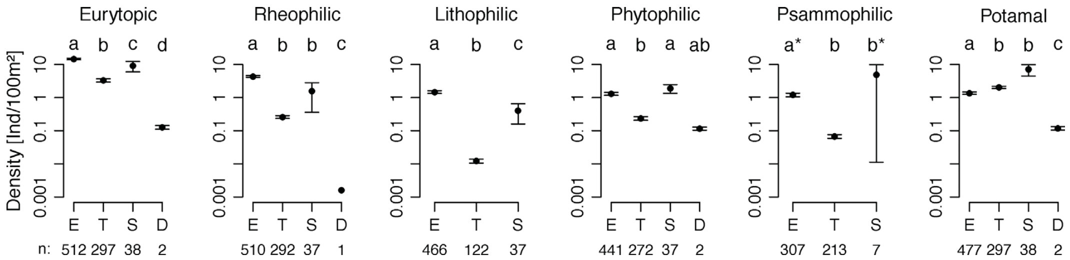

Fig. 3. Densities of selected guilds as estimated across 849 samples in European large rivers (E = electrofishing [512 samples]; T = trawling [297], S = seining [38], D = drift-netting [2]; sample sizes (n) differ between guilds and same gears due to non-catches of fish in some samplings). Different 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.

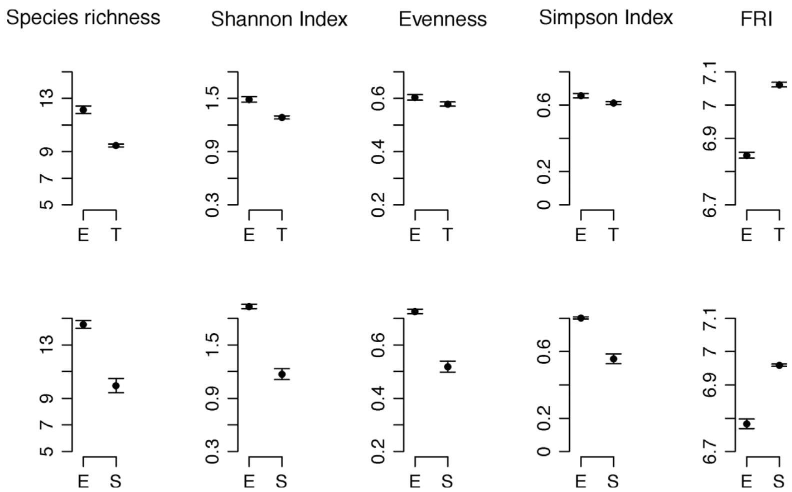

Fig. 4. Biodiversity indices as estimated in the standardized gear comparisons of electrofishing (E) vs. trawling (T) [samples: E = 162; T = 284] and E vs. seining (S) [E = 56; S = 22]. 'FRI' = Fish Region Index. All differences are significant. Mean and +/− standard errors (Tables S9, S11) are shown.

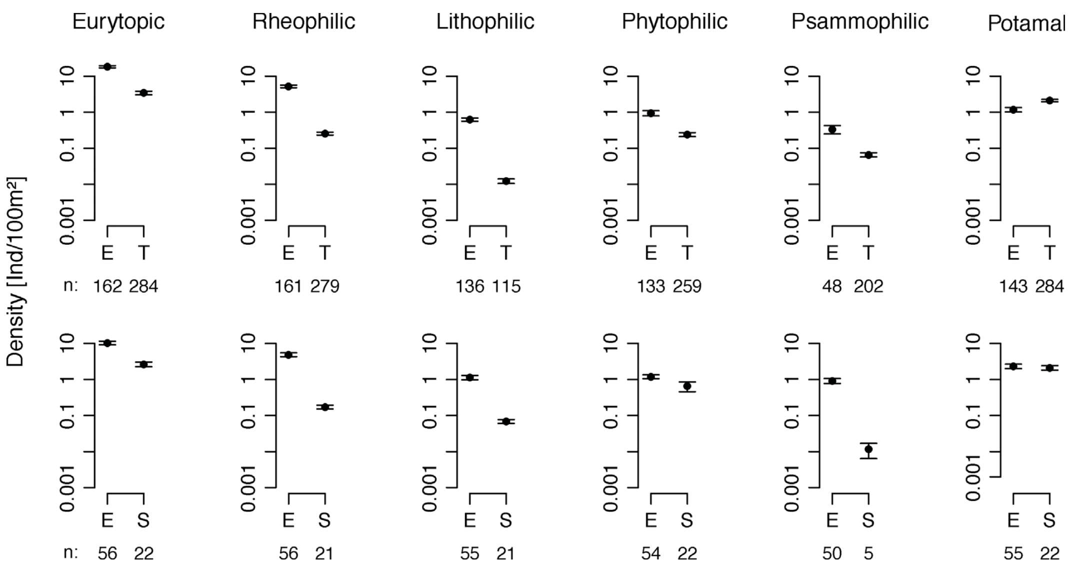

Fig. 5. Densities of selected guilds as estimated in the standardized gear comparisons of electrofishing (E) vs. trawling (T) [samples: E = 162; T = 284] and E vs. seining (S) [E = 56; S = 22]. All differences are significant except the density of the potamal guild within the E vs. S comparison. Sample 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.

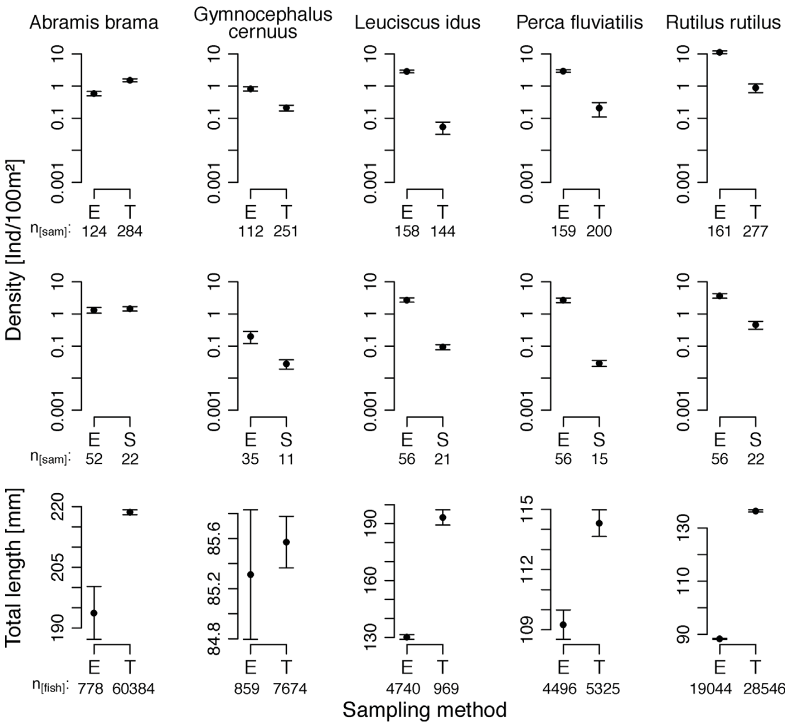

Fig. 6. Densities and total lengths of common species as estimated in the standardized gear comparisons of electrofishing (E) vs. trawling (T) [samples: E = 162; T = 284] and densities of common species as estimated in the comparison of E vs. seining (S) [E = 56; S = 22]. Sample sizes ($n_{[sam]}$ = 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.

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 m^2). 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.

4.1. 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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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.fishres.2017.09.018.

References

Akaike, H., 1981. Likelihood of a model and information criteria. J. Econom. 16, 3–14. http://dx.doi.org/10.1016/0304-4076(81)90071-3.

Aparicio, E., Carmona-Catot, G., Moyle, P.B., García-Berthou, E., 2011. Development and evaluation of a fish-based index to assess biological integrity of Mediterranean streams. Aquat. Conserv.: Mar. Freshw. Ecosyst. 21, 324–337. http://dx.doi.org/10.1002/aqc.1197.

Barton, K., 2016. MuMIn: Multi-Model Inference [WWW Document] R Package Version 1.15.6. URL https://CRAN.R-project.org/package=MuMIn (Accessed 25 June 16).

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67. http://dx.doi.org/10.18637/jss.v067.i01.

Beier, U., Degerman, E., Melcher, A., Rogers, C., Wirlöf, H., 2007. Processes of collating a European fisheries database to meet the objectives of the European Union Water Framework Directive. Fish. Manag. Ecol. 14, 407–416. http://dx.doi.org/10.1111/j.1365-2400.2007.00579.x.

Benitez, J.-P., Matondo, B.N., Dierckx, A., Ovidio, M., 2015. An overview of potamodromous fish upstream movements in medium-sized rivers, by means of fish passes monitoring. Aquat. Ecol. 49, 481–497. http://dx.doi.org/10.1007/s10452-015-9541-4.

Berg, R., Gaumert, T., Kämmereit, M., Klinger, H., Lemcke, R., Leuner, E., Wolter, C., Dußling, U., 2004. The German river typology with respect to fish-faunistic reference conditions. In: Steinberg, C., Calmano, W., Klapper, H., Wilken, R.-D. (Eds.), Handbuch Angewandte Limnologie. Ecomed-Verlag, Landsberg, pp. 12–17.

Blondel, J., 2003. Guilds or functional groups: does it matter? Oikos 100, 223–231. http://dx.doi.org/10.1034/j.1600-0706.2003.12152.x.

Bohlin, T., Hamrin, S., Heggberget, T., Rasmussen, G., Saltveit, S., 1989. Electrofishing — theory and practice with special emphasis on salmonids. Hydrobiologia 173, 9–43. http://dx.doi.org/10.1007/BF00008596.

Casselman, J., Lewis, C., 1996. Habitat requirements of Northern pike (Esox lucius). Can. J. Fish. Aquat. Sci. 53, 161–174. http://dx.doi.org/10.1139/f96-019.

Clark, S.J., Jackson, J.R., Lochmann, S.E., 2007. A comparison of shoreline seines with fyke nets for sampling littoral fish communities in floodplain lakes. North Am. J. Fish. Manag. 27, 676–680. http://dx.doi.org/10.1577/M06-197.1.

Council Directive 92/43/EEC,, 1994. Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Off. J. Eur. Communities L 206, 7–50.

De Leeuw, J.J., Buijse, A.D., Haidvogl, G., Lapinska, M., Noble, R., Repecka, R., Virbickas, T., Wiśniewolski, W., Wolter, C., 2007. Challenges in developing fish-based ecological assessment methods for large floodplain rivers. Fish. Manag. Ecol. 14, 483—494. http://dx.doi.org/10.1111/j.1365-2400.2007.00576.x.

Dembkowski, D.J., Wuellner, M.R., Willis, D.W., 2012. Sampling glacial lake littoral fish assemblages with four gears. North Am. J. Fish. Manag. 32, 1160–1166. http://dx.doi.org/10.1080/02755947.2012.728176.

Dettmers, J.M., Gutreuter, S., Wahl, D.H., Soluk, D.A., 2001a. Patterns in abundance of fishes in main channels of the upper Mississippi River system. Can. J. Fish. Aquat. Sci. 58, 933–942. http://dx.doi.org/10.1139/f01-046.

Dettmers, J.M., Wahl, D.H., Soluk, D.A., Gutreuter, S., 2001b. Life in the fast lane: fish

and foodweb structure in the main channel of large rivers. J. North Am. Benthol. Soc. 20, 255–265. http://dx.doi.org/10.2307/1468320.
Dußling, U., Bischoff, A., Haberbosch, R., Hoffmann, A., Klinger, H., Wolter, C., Wysujack, K., Berg, R., 2004a. The fish-based assessment system — description of the German approach. In: Steinberg, C., Calmano, W., Klapper, H., Wilken, R.-D. (Eds.), Handbuch Angewandte Limnologie. Ecomed-Verlag, Landsberg, pp. 27–38.
Dußling, U., Bischoff, A., Haberbosch, R., Hoffmann, A., Klinger, H., Wolter, C., Wysujack, K., Berg, R., 2004b. Ecological characters of river fish species occurring in Germany. In: Steinberg, C., Calmano, W., Klapper, H., Wilken, R.-D. (Eds.), Handbuch Angewandte Limnologie. Ecomed-Verlag, Landsberg, pp. 4–12.
Dußling, U., 2009. Handbuch zu fiBS, Schriftenreihe des Verbandes Deutscher Fischereiverwaltungsbeamter und Fischereiwissenschaftler. Verband Deutscher Fischereiverwaltungsbeamter und Fischereiwissenschaftler, Offenbach am Main.
EFI+ Consortium, 2009. Manual for the application of the new European Fish Index −EFI+. A fish-based method to assess the ecological status of European running waters in support of the Water Framework Directive.
Eggleton, M.A., Jackson, J.R., Lubinski, B.J., 2010. Comparison of gears for sampling littoral-zone fishes in floodplain lakes of the lower White River, Arkansas. North Am. J. Fish. Manag. 30, 928–939. http://dx.doi.org/10.1577/M09-127.1.
Erős, T., Tóth, B., Sevcsik, A., Schmera, D., 2008. Comparison of fish assemblage diversity in natural and artificial rip-rap habitats in the littoral zone of a large river (River Danube, Hungary). Int. Rev. Hydrobiol. 93, 88–105. http://dx.doi.org/10.1002/iroh.200710976.
Fladung, E., 2002. Untersuchungen zum adulten Fischbestand im Hauptstrom (Fahrrinne) der Mittelelbe. Zeitschrift für Fischkunde Supplement 1, 121–131.
Flotemersch, J.E., Stribling, J.B., Hughes, R.M., Reynolds, L., Paul, M.J., Wolter, C., 2011. Site length for biological assessment of boatable rivers. River Res. Appl. 27, 520–535. http://dx.doi.org/10.1002/rra.1367.
Fullerton, A.H., Burnett, K.M., Steel, E.A., Flitcroft, R.L., Pess, G.R., Feist, B.E., Torgersen, C.E., Miller, D.J., Sanderson l, B., 2010. Hydrological connectivity for riverine fish: measurement challenges and research opportunities. Freshw. Biol. 55, 2215–2237. http://dx.doi.org/10.1111/j.1365-2427.2010.02448.x.
Galat, D.L., Zweimüller, I., 2001. Conserving large-river fishes: is the highway analogy an appropriate paradigm? J. North Am. Benthol. Soc. 20, 266–279. http://dx.doi.org/10.2307/1468321.
Goffaux, D., Grenouillet, G., Kestemont, P., 2005. Electrofishing versus gillnet sampling for the assessment of fish assemblages in large rivers. Archiv für Hydrobiologie 162, 73–90. http://dx.doi.org/10.1127/0003-9136/2005/0162-0073.
Gonzales, R., Griffin, D., 2004. Measuring individuals in a social environment: conceptualizing dyadic and group interaction. In: Sansone, C., Morf, C.C., Panter, A.T. (Eds.), The Sage Handbook of Methods in Social Psychology. Sage Publications, Inc., California, London, New Delhi, pp. 313–334.
Gutreuter, S., Burkhardt, R., Lubinski, K., 1995. Long Term Resource Monitoring Program Procedures: Fish Monitoring (No. LTRMP 95-P002-1). National Biological Service, Environmental Management Technical Center, Onalaska, Wisconsin.
Heino, J., Schmera, D., Erős, T., 2013. A macroecological perspective of trait patterns in stream communities. Freshw. Biol. 58, 1539–1555. http://dx.doi.org/10.1111/fwb.12164.
Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., Scheibe, S., 2016. Multcomp: Simultaneous Inference in General Parametric Models [WWW Document]. R Package Version 1.4-5. URL https://cran.r-project.org/web/packages/multcomp/index.html (Accessed 23 June 16).
Illies, J., 1961. Versuch einer allgemeinen biozönotischen Gliederung der Fließgewässer. Int. Revue ges. Hydrobiol. Hydrogr. 46, 205–213. http://dx.doi.org/10.1002/iroh.19610460205.
Jacobsen, L., Perrow, M.R., 1998. Predation risk from piscivorous fish influencing the diel use of macrophytes by planktivorous fish in experimental ponds. Ecol. Freshw. Fish. 7, 78–86. http://dx.doi.org/10.1111/j.1600-0633.1998. tb00174.x.
Kail, J., Wolter, C., 2011. Analysis and evaluation of large-scale river restoration planning in Germany to better link river research and management. River Res. Appl. 27, 985–999. http://dx.doi.org/10.1002/rra.1382.
Kemp, P.S., O'hanley, J.R., 2010. Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. Fish. Manag. Ecol. 17, 297–322. http://dx.doi.org/10.1111/j.1365-2400.2010.00751.x.
Kennedy, G., Strange, C., 1981. Efficiency of electric fishing for salmonids in relation to river width. Fish. Manag. 12, 55–60. http://dx.doi.org/10.1111/j.1365-2109.1981.tb00010.x.
Kucera-Hirzinger, V., Schludermann, E., Zornig, H., Weissenbacher, A., Schabuss, M., Schiemer, F., 2008. Potential effects of navigation-induced wave wash on the early life history stages of riverine fish. Aquat. Sci. 71, 94–102. http://dx.doi.org/10.1007/s00027-008-8110-5.
Kuznetsova, A., Brockhoff, B., Christensen, H.B., 2016. LmerTest: Tests in Linear Mixed Effects Models [WWW Document]. R Package Version 2.0-32. URL https://CRAN.R-project.org/package=lmerTest (Accessed 23 June 16).
Lechner, A., Keckeis, H., Schludermann, E., Loisl, F., Humphries, P., Glas, M., Tritthart, M., Habersack, H., 2014. Shoreline configurations affect dispersal patterns of fish larvae in a large river. ICES J. Mar. Sci. 71, 930–942. http://dx.doi.org/10.1093/icesjms/fst139.
Lechner, A., Keckeis, H., Humphries, P., 2016. Patterns and processes in the drift of early developmental stages of fish in rivers: a review. Rev. Fish. Biol. Fish. 26, 471–489. http://dx.doi.org/10.1007/s11160-016-9437-y.
Lewin, W.-C., Mehner, T., Ritterbusch, D., Brämick, U., 2014. The influence of anthropogenic shoreline changes on the littoral abundance of fish species in German lowland lakes varying in depth as determined by boosted regression trees. Hydrobiologia 724, 293–306. http://dx.doi.org/10.1007/s10750-013-1746-8.
Lintermans, M., 2016. Finding the needle in the haystack: comparing sampling methods for detecting an endangered freshwater fish. Mar. Freshw. Res. 67, 1740–1749. http://dx.doi.org/10.1071/MF14346.
Loisl, F., Singer, G., Keckeis, H., 2013. Method-integrated fish assemblage structure at two spatial scales along a free-flowing stretch of the Austrian Danube. Hydrobiologia 729, 77–94. http://dx.doi.org/10.1007/s10750-013-1588-4.
Lynch, W.E.J., Johnson, D.L., 1989. Influences of interstice size, shade, and predators on the use of artificial structures by bluegills. North Am. J. Fish. Manag. 9, 219–225. http://dx.doi.org/10.1577/1548-8675(1989)009<0219:IOISSA>2.3.CO;2.
Lyon, J.P., Bird, T., Nicol, S., Kearns, J., O'Mahony, J., Todd, C.R., Cowx, I.G., Bradshaw, C.J.A., 2014. Efficiency of electrofishing in turbid lowland rivers: implications for measuring temporal change in fish populations. Can. J. Fish. Aquat. Sci. 71, 878–886. http://dx.doi.org/10.1139/cjfas-2013-0287.
Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422, 714–716. http://dx.doi.org/10.1038/nature01547.
Morales, M., R Development Core Team, Murdoch, D., 2012. Sciplot: Scientific Graphing Functions for Factorial Designs [WWW Document]. R Package Version 1.1-0. URL https://CRAN.R-project.org/package=sciplot (Accessed 15 October 15).
Morandi, B., Piégay, H., Lamouroux, N., Vaudor, L., 2014. How is success or failure in river restoration projects evaluated? Feedback from French restoration projects. J. Environ. Manag. 137, 178–188. http://dx.doi.org/10.1016/j.jenvman.2014.02.010.
Morris, E.K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S.A., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S., Rillig, M.C., 2014. Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. Ecol. Evol. 4, 3514–3524. http://dx.doi.org/10.1002/ece3.1155.
Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. http://dx.doi.org/10.1111/j.2041-210x.2012.00261.x.
Neebling, T.E., Quist, M.C., 2011. Comparison of boat electrofishing, trawling, and seining for sampling fish assemblages in iowa's nonwadeable rivers. North Am. J. Fish. Manag. 31, 390–402. http://dx.doi.org/10.1080/02755947.2011.576198.
Noble, R. a. A., Cowx, I.G., Goffaux, D., Kestemont, P., 2007. Assessing the health of European rivers using functional ecological guilds of fish communities: standardising species classification and approaches to metric selection. Fish. Manag. Ecol. 14, 381–392. http://dx.doi.org/10.1111/j. 1365–2400.2007.00575.x.
Penczak, T., Jakubowski, H., 1990. Drawbacks of electric fishing in rivers. In: Cowx, I.G. (Ed.), Developments in Electric Fishing. Blackwell, Oxford, pp. 115–122.
Piper, A.T., Manes, C., Siniscalchi, F., Marion, A., Wright, R.M., Kemp, P.S., 2015. Response of seaward-migrating European eel (Anguilla anguilla) to manipulated flow fields. Proc. R. Soc. B 282, 20151098. http://dx.doi.org/10.1098/rspb.2015.1098.
Poesch, M.S., 2014. Developing standardized methods for sampling freshwater fishes with multiple gears: effects of sampling order versus sampling method. Trans. Am. Fish. Soc. 143, 353–362. http://dx.doi.org/10.1080/00028487.2013.860047.
Poikane, S., Zampoukas, N., Borja, A., Davies, S.P., van de Bund, W., Birk, S., 2014. Intercalibration of aquatic ecological assessment methods in the European Union: lessons learned and way forward. Environ. Sci. Policy 44, 237–246. http://dx.doi.org/10.1016/j.envsci.2014.08.006.
Poos, M.S., Mandrak, N.E., McLaughlin, R.L., 2007. The effectiveness of two common sampling methods for assessing imperilled freshwater fishes. J. Fish Biol. 70, 691–708. http://dx.doi.org/10.1111/j. 1095–8649.2007.01349.x.
Porreca, A.P., Pederson, C.L., Laursen, J.R., Colombo, R.E., 2013. A comparison of electrofishing methods and fyke netting to produce reliable abundance and size metrics. J. Freshw. Ecol. 28, 585–590. http://dx.doi.org/10.1080/02705060.2013.810555.
R Development Core Team, 2016. R: A Language and Environment for Statistical Computing [WWW Document]. R Foundation For Statistical Computing, Vienna, Austria URL https://www.r-project.org/ (Accessed 21 June 16).
Radinger, J., Wolter, C., 2014. Patterns and predictors of fish dispersal in rivers. Fish 15, 456–473. http://dx.doi.org/10.1111/faf.12028.
Randall, R.G., Minns, C.K., Cairns, V.W., Moore, J.E., 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. Can. J. Fish. Aquat. Sci. 53, 35–44. http://dx.doi.org/10.1139/f95-271.
Scharf, J., Brämick, U., Fredrich, F., Rothe, U., Schuhr, H., Tautenhahn, M., Wolter, C., Zahn, S., 2011. Fische in Brandenburg − Aktuelle Kartierung und Beschreibung der märkischen Fischfauna.
Somerfield, P.J., Clarke, K.R., Warwick, R.M., 2008. Simpson index. In: Fath, B.D. (Ed.), Encyclopedia of Ecology. Academic Press, Oxford, pp. 3252–3255.
Spellerberg, I.F., Fedor, P.J., 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. Global Ecol. Biogeogr. 12, 177–179. http://dx.doi.org/10.1046/j.1466-822X.2003.00015.x.
Spellerberg, I.F., 2008. Shannon–Wiener index. In: Fath, B.D. (Ed.), Encyclopedia of Ecology. Academic Press, Oxford, pp. 3249–3252.
Strayer, D.L., Findlay, S.E.G., 2010. Ecology of freshwater shore zones. Aquat. Sci. 72, 127–163. http://dx.doi.org/10.1007/s00027-010-0128-9.
Szalóky, Z., György, Á.I., Tóth, B., Sevcsik, A., Specziár, A., Csányi, B., Szekeres, J., Erős, T., 2014. Application of an electrified benthic frame trawl for sampling fish in a very large European river (the Danube River)—Is offshore monitoring necessary? Fish. Res. 151, 12–19. http://dx.doi.org/10.1016/j.fishres.2013.12.004.
Tokeshi, M., 1993. Species abundance patterns and community structure. Adv. Ecol. Res. 24, 111–186. http://dx.doi.org/10.1016/S0065-2504(08)60042-2.
Tukey, J.W., 1949. Comparing individual means in the analysis of variance. Biometrics 5, 99–114, https://doi.org/10.2307/3001913.
Ward, J.V., Tockner, K., Arscott, D.B., Claret, C., 2002. Riverine landscape diversity. Freshw. Biol. 47, 517–539. http://dx.doi.org/10.1046/j.1365-2427.2002.00893.x.

Weaver, M.J., Magnuson, J.J., Clayton, M.K., 1997. Distribution of littoral fishes in structurally complex macrophytes. Can. J. Fish. Aquat. Sci. 54, 2277–2289. http://dx.doi.org/10.1139/cjfas-54-10-2277.
Welcomme, R.L., Winemiller, K.O., Cowx, I.G., 2006. Fish environmental guilds as a tool for assessment of ecological condition of rivers. River Res. Appl. 22, 377–396. http://dx.doi.org/10.1002/rra.914.
Wiley, M.L., Tsai, C.-F., 1983. The relative efficiencies of electrofishing vs seines in piedmont streams of maryland. North Am. J. Fish. Manag. 3, 243–253. http://dx.doi.org/10.1577/1548-8659(1983)3 < 243:TREOEV > 2.0. CO;2.
Wolter, C., Bischoff, A., 2001. Seasonal changes of fish diversity in the main channel of the large lowland River Oder. Regul. Rivers: Res. Manag. 17, 595–608. http://dx.doi.org/10.1002/rrr.645.
Wolter, C., Freyhof, J., 2004. Diel distribution patterns of fishes in a temperate large lowland river. J. Fish Biol. 64, 632–642. http://dx.doi.org/10.1111/j.1095-8649.2004.00327.x.
Wolter, C., Bischoff, A., Faller, M., Schomaker, C., Wysujack, K., 2004. Sampling design and site selection in large rivers. In: Steinberg, C., Calmano, W., Klapper, H., Wilken, R.-D. (Eds.), Handbuch Angewandte Limnologie. Ecomed-Verlag, Landsberg, pp. 38–57.
Wolter C., Lorenz S., Scheunig S., Lehmann N., Schomaker C., Nastase A., García de Jalón D., Marzin A., Lorenz A.W., Krakova M., Brabec K., Noble R., 2013. Review on ecological response to hydromorphological degradation and restoration (Project Report REFORM No. D1.3) URL http://www.reformrivers.eu/deliverables/d1-3 (Accessed 10 October 16).
Zitek, A., Schmutz, S., Unfer, G., Ploner, A., 2004. Fish drift in a Danube sidearm-system: i. Site-, inter- and intraspecific patterns. J. Fish Biol. 65, 1319–1338. http://dx.doi.org/10.1111/j.0022-1112.2004.00533.x.
Zuur, A.F., Ieno, E.N., 2016. A protocol for conducting and presenting results of regression-type analyses. Methods Ecol. Evol. 7, 636–645. http://dx.doi.org/10.1111/2041-210X.12577.
Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, NY.

Chapter two

Disentangling multiple pressures on fish assemblages in large rivers

This chapter consists of the following publication:

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Authors’ contributions:

PZ and CW developed the concept; PZ did the literature research; PZ developed the methods; PZ and JR analyzed the data; PZ wrote the manuscript; PZ, CW and JR revised the manuscript.

The appendix mentioned in this publication is provided in the appendix of this thesis.

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Disentangling multiple pressures on fish assemblages in large rivers

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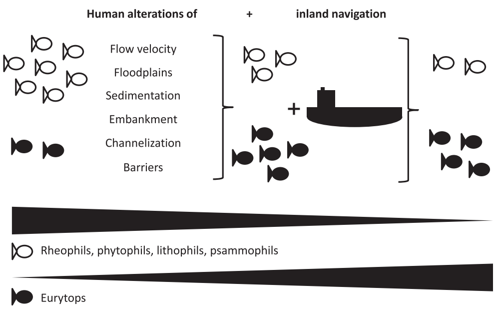
HIGHLIGHTS

- Large rivers serve as waterways with highly degraded hydromorphology.
- Multiple pressures reduce densities of habitat-sensitive fish.
- Inland navigation adds on top of the prevailing hydromorphological degradation.
- Increased velocity, navigation intensity and loss of floodplains matter most.
- Diagnostic fish population metrics were derived for specific pressures.

GRAPHICAL ABSTRACT



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ABSTRACT

European large rivers are exposed to multiple human pressures and maintained as waterways for inland navigation. However, little is known on the dominance and interactions of multiple pressures in large rivers and in particular inland navigation has been ignored in multi-pressure analyzes so far. We determined the response of ten fish population metrics (FPM, related to densities of diagnostic guilds and biodiversity) to 11 prevailing pressures including navigation intensity at 76 sites in eight European large rivers. Thereby, we aimed to derive indicative FPM for the most influential pressures that can serve for fish-based assessments. Pressures' influences, impacts and interactions were determined for each FPM using bootstrapped regression tree models. Increased flow velocity, navigation intensity and the loss of floodplains had the highest influences on guild densities and biodiversity. Interactions between navigation intensity and loss of floodplains and between navigation intensity and increased flow velocity were most frequent, each affecting 80% of the FPM. Further, increased sedimentation, channelization, organic siltation, the presence of artificial embankments and the presence of barriers had strong influences on at least one FPM. Thereby, each FPM was influenced by up to five pressures. However, some diagnostic FPM could be derived: Species richness, Shannon and Simpson Indices, the Fish Region Index and lithophilic and psammophilic guilds specifically indicate rhithralisation of the potamal region of large rivers. Lithophilic, phytophilic and psammophilic guilds indicate disturbance of shoreline habitats through both (i) wave action induced by passing vessels and (ii) hydromorphological degradation of the river channel that comes along with inland navigation. In European large rivers, inland navigation constitutes a highly influential pressure that adds on top of the prevailing hydromorphological degradation. Therefore, river management has to consider river hydromorphology and inland navigation to efficiently rehabilitate the potamal region of large rives.

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1. Introduction

Large rivers are the most severely impacted ecosystems on earth due their manifold exploitations and modifications to serve multiple human demands (Malmqvist and Rundle, 2002; Nõges et al., 2015). Up to the late 1980s, river assessments focused primarily on water quality, in particular eutrophication and pollution by chemicals and heavy metals (reviewed by Meybeck and Helmer, 1989). Meanwhile, the focus has shifted to ecological quality as alterations of hydrology, morphology, habitat availability and connectivity have been recognized as key pressures on surface water bodies (EEA, 2012; Melcher et al., 2007).

More recently, the importance of impacts by multiple pressures and their interactions became increasingly acknowledged and addressed by research (Hering et al., 2015; Jackson et al., 2016; Milošević et al., 2018; Radinger et al., 2016; Segner et al., 2014), as single pressures could barely account for the vast amount of observed ecosystem changes (Vaughan et al., 2009). For example, 90% of lowland rivers in 14 European countries are affected by a combination of four pressure groups referring to alterations of water quality, hydrology, morphology and connectivity (Schinegger et al., 2012). Disentangling the effects of these pressure groups and their interactions on fish assemblages were broadly explored since then (Schinegger et al., 2016, 2013; Trautwein et al., 2013). However, pressure groups subsume common types of degradation which might neglect intensity and direction of the underlying single pressures (Schinegger et al., 2012). Further, local-scale pressure variables can have a high influence on fish communities (Sagouis et al., 2017). Therefore, knowledge on the effects of single pressures is required to provide management advice and enhance restoration success (e.g., Friberg et al., 2016). Moreover, previous studies primarily focused on small and medium sized rivers, while large rivers were rather underrepresented (Schinegger et al., 2013). Since large rivers constitute complex hydrological, ecological, economic, political and social systems (Campbell, 2016), they receive multiple impacts both from the upstream catchment and at the reach scale (Wolter et al., 2016). Therefore, in large rivers, the lack of knowledge on dominance, interactions and impacts of human pressures constitutes a particular research gap.

Assessing the impact of multiple pressures across large rivers is challenging, because sampling methods are extremely resource-demanding and not standardized and data availability is limited (Milošević et al., 2018; Nõges et al., 2015; Oliver and Morecroft, 2014). Not surprisingly, large rivers are significantly under-researched. Hence, extraordinarily little is known about impacts and interactions of multiple pressures in large rivers (Hering et al., 2015).

A common approach to assess effects of pressures is the comparison of impacted sites with reference sites resembling unimpaired conditions (e.g., Pont et al., 2006). This approach works well in small rivers and streams, where less disturbed or near natural reference reaches still exist. In contrast, almost all large rivers are so heavily degraded (e.g., Malmqvist and Rundle, 2002) that near natural reference channel reaches do not exist anymore (Birk et al., 2012). For instance, in Europe nearly all large rivers are rectified, channelized and regulated, and hence substantially modified in hydromorphology (e.g., Petts et al., 1989). Channelization invokes artificial embankment and steepening of shorelines, thus a loss of important shallow nursery areas for fish. Further, channelization concomitantly increases flow velocity as a result of the straightened and deepened river channel. Together with meander cut-offs and levee constructions these changes result in the wide-spread loss of periodically inundated floodplains (e.g., Strayer and Findlay, 2010). As a consequence of the high overall degradation of large rivers, a comparative assessment approach was chosen along a gradient of more or lesser disturbed river reaches to identify single pressure impacts on fish assemblages (e.g., Clapcott et al., 2012).

Large rivers are commonly maintained as waterways for commercial navigation. Navigation-induced physical forces are well-known to impact on various riverine taxa mainly in shallow areas along the banks (Gabel et al., 2017; Söhngen et al., 2008) that often represent suitable habitats for reproduction (Wolter et al., 2004). Impacts of navigation-induced forces have in particular been shown for aquatic plants (Ali et al., 1999; Asplund and Cook, 1997; Murphy and Eaton, 1983), benthic invertebrates (e.g., Gabel et al., 2012), and juvenile fish (e.g., Arlinghaus et al., 2002; Huckstorf et al., 2011; Wolter and Arlinghaus, 2003). Hydraulic forces causing drawdown (Liedermann et al., 2014), shear stress

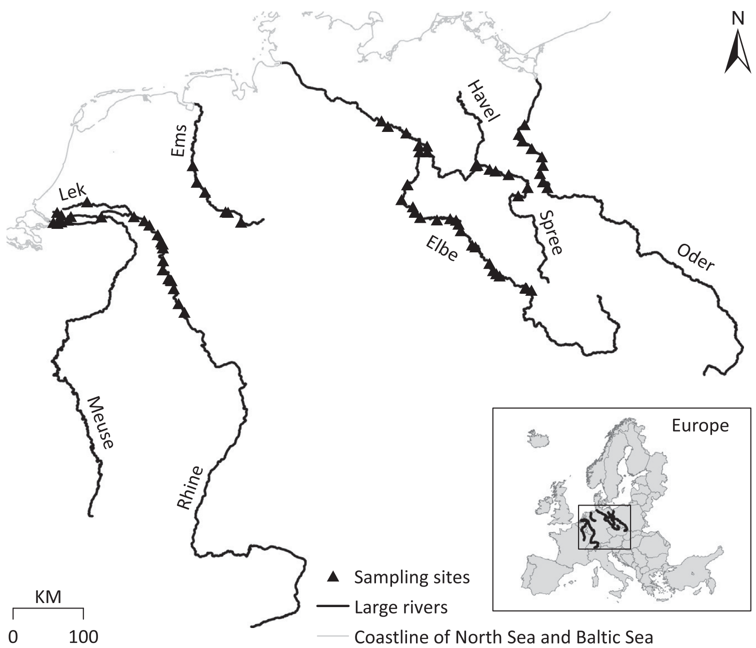


Fig. 1. Location of sampling sites.

and dewatering (Wolter and Arlinghaus, 2003) affect important shallow nursery areas of fish larvae and juveniles along the banks (Huckstorf et al., 2011). Vessel-induced return currents commonly exceed the critical swimming speed of young fish resulting in dislocation (Wolter and Arlinghaus, 2003), stranding (reviewed by Nagrodski et al., 2012) and direct mortality (Adams et al., 1999; Pearson and Skalski, 2011). Accordingly, inland navigation constitutes a key limiting factor for littoral fish recruitment in waterways (Wolter and Arlinghaus, 2003). Therefore, navigation intensity provides a significant pressure on fish assemblages of large rivers, which moreover interacts with the hydromorphological degradation of the river channel. Surprisingly, inland navigation has not been considered in analyzes of multiple pressures so far, except the study by Leclere et al. (2012). The authors modeled occurrence of fish species based on environmental parameters. They reported that inland navigation and physico-chemical disturbances both negatively influence the occurrence of juveniles of selected fish species (Leclere et al., 2012).

Most studies on the impacts of “multiple” pressures considered pairwise interactions of two pressures based on predefined hypotheses (reviewed in Crain et al., 2008; Darling and Côté, 2008; Jackson et al., 2016). Further, such studies often aimed to untangle the direction of the expected interaction (e.g., antagonistic, synergistic, additive; reviewed in Piggott et al., 2015). In contrast, this study aimed to identify dominant pressures and their potential interactions in large rivers, rather than addressing specific interactions and their directions. To our knowledge this is the first study, which explicitly considered potential additional effects of inland navigation on fish assemblages in relation to the other prevailing pressures on European large rivers.

We analyzed the effects of 11 ranked pressure variables on ten fish population metrics (FPM) referring to biodiversity (e.g., species richness, Simpson Index), river type specific species composition (Fish Region Index, FRI), and densities of sensitive life history traits (e.g., rheophils, lithophils). Thereby, we expected to identify indicative FPM for specific types of degradation, serving as valuable ecological tools for the fish-based assessment of large rivers. Both pressure variables and FPM (fish samplings were conducted 250 times in total) were available for 76 sites in eight European large rivers. It was hypothesized: i) that inland navigation intensity appears as a significant pressure on fish assemblages in large rivers and ii) that impacts of vessel operation positively correlate with hydromorphological degradation of the river channel. The expected impacts of inland navigation comprise decreasing densities of habitat-sensitive guilds that require shoreline areas for reproduction. Hence, it was expected that Inland navigation appears as a very specific pressure, which accordingly offers potential for targeted rehabilitation of large rivers and the recovery of the inherent fish communities.

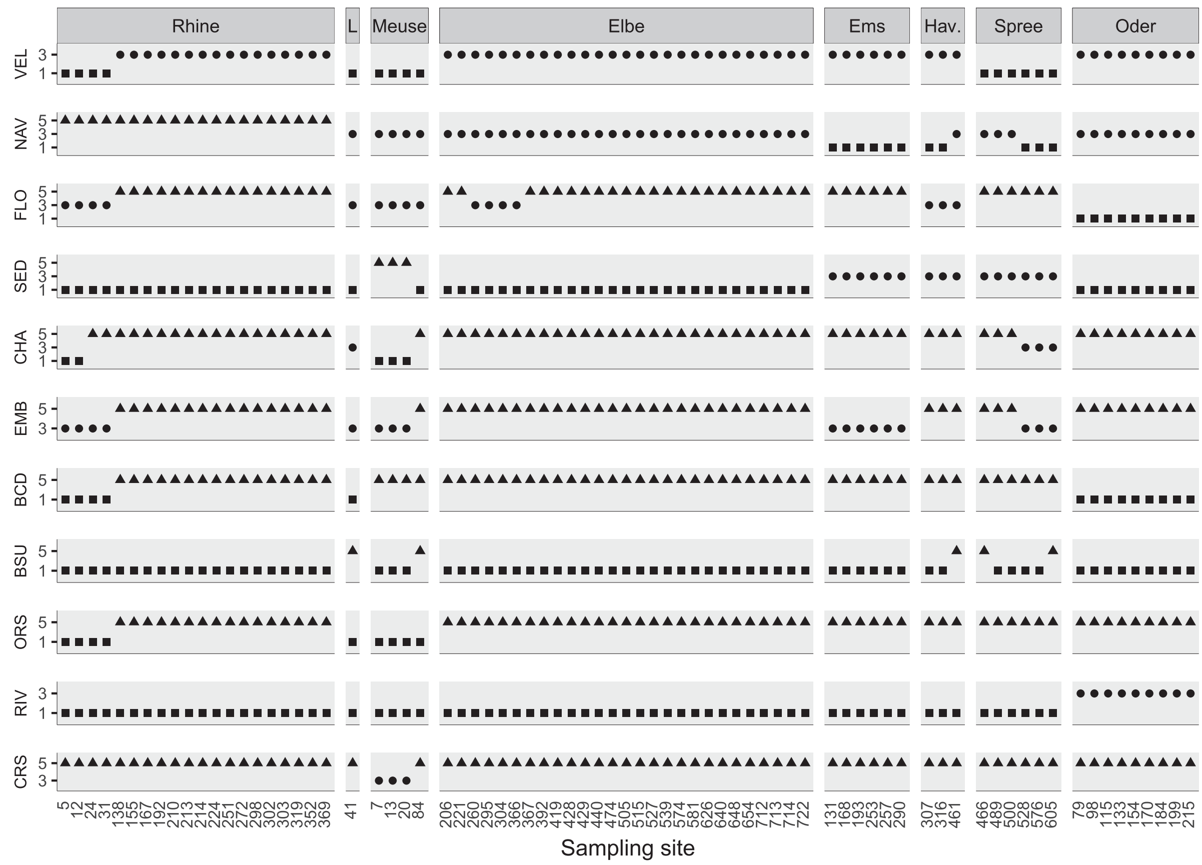


Fig. 2. River-specific classification of sampling sites by pressures. L = Lek; Hav. = Havel. VEL = increase of flow velocity; NAV = navigation intensity; FLO = loss of floodplains; SED = increase of sedimentation; CHA = channelization; EMB = artificial embankment; BCD = barriers catchment down; BSU = barriers segment up; ORS = organic siltation; RIV = cover of riparian vegetation; CRS = cross-section. Alteration of the natural state increases from one to five different symbols are used for better visualization: 1 = square: low or no alteration; 3 = circle: intermediate alteration; 5 = triangle: high alteration, compare Table 1. The x-axis labels show the distance of each sampling site to the Ocean in kilometers.

Table 1
Pressure variables: classification and description.

Pressure	Abbreviation	Classes	Labels	Sites [%]	Description
Barriers catchment down	BCD	1/3/5	No/Partial/Yes	18/82/0	Barriers within the catchment downstream
Barriers segment up	BSU	1/3/5	No/Partial/Yes	93/0/7	Barriers within 5 km upstream
Channelization	CHA	1/3/5	No/Intermediate/Straightened	7/5/88	Alteration, straightening of natural river plan form
Cross section	CRS	1/3/5	No/Intermediate/U-profile	0/5/95	Alteration, enlargement of cross-section
Embankment	EMB	1/3/5	No or local/Permeable/Impermeable	0/22/78	Artificial embankment
Loss of Floodplains	FLO	1/3/5	Little/Severe/Extinct	12/21/67	Floodplain degradation
Inland navigation	NAV	1/3/5	Low/Intermediate/High	14/59/26	1: 0–3000; 3: 3.001–33.000; 5: 33.001–133.000 cargo vessels/year
Organic siltation	ORS	1/3/–	No/Yes/–	12/88/–	Presence of organic siltation
Riparian vegetation	RIV	1/3/5	High/Intermediate/Rare	88/12/0	Cover of riparian vegetation
Sedimentation	SED	1/3/5	No/Weak + Medium/High	76/20/4	Increased sedimentation
Velocity increase	VEL	1/3/–	No/Yes/–	20/80/–	Artificially increased velocity, Rhithralisation

2. Methods

2.1. The large river database

The large river database (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 compiles 2693 fish samplings conducted at 358 sampling sites in 16 European large rivers, i.e., rivers with a catchment size >10,000 km^2 (Berg et al., 2004). Samplings were carried out using different sampling methods, in different seasons and during both day and night. From this vast and unique dataset of fish samplings across European large rivers, a representative subset of comparable sites and samplings was extracted as follows: We selected fish samplings that (i) were obtained by boat electrofishing along the banks during daytime, which was found well representing the fish assemblages of large rivers (Zajicek and Wolter, 2018), (ii) originated from large rivers draining into the North Sea and Baltic Sea to ensure generally comparable fish species inventories (e.g., Sommerwerk et al., 2017), (iii) conducted under low flow conditions in autumn to avoid seasonal bias (Schmutz et al., 2007), (iv) had covered a minimum fished length of 100 m and (v) captured at least 100 fish (Flotemersch et al., 2011). The resulting dataset used for analyzes consisted of 250 fish samplings assembled at 76 sites in eight large rivers between 1996 and 2008 (Fig. 1). The average length fished per site was 1659 ± 100 m (mean ± standard error). The area fished varied according to the size of the anode used and was on average 5287 ± 456 m^2 per site. Therefore, all samplings have been standardized as fish densities per 100 m^2 prior analyses. Fifty percent of the sites were sampled only once, 93% <10 times, and 7% between 10 and 26 times. The vast majority (96%) of the sampling sites was at least 1 km apart of each other and the distance between sampling sites by far exceed 1 km in most cases (compare x-axis in Fig. 2). All sites were situated in comparable river reaches allowing for representative fish based-assessments (Wolter et al., 2016).

Each sampling site was characterized by a set of 26 pressure variables ranked on a scale from 1 to 5 associated with little (class 1), intermediate (class 3) and severe (class 5) alteration of the natural state, respectively. Pressure ranks were assigned by the local water authorities in accordance with national survey standards and the requirements of the European Water Framework Directive (2000/60/EC, WFD) and provided with the fish data. Pressure variables with insufficient gradient among sites, i.e., with >95% of the observations in the same class, have been excluded prior analyses. Ten pressure variables remained (Table 1 and Fig. 2). In addition, for each site the intensity of inland navigation was determined based on counts of annually passing cargo vessels at the nearest ship lock. Vessel counts at ship locks were provided by the Water and Navigation Authority (wsv.de) in Germany and by the Ministry of Infrastructure and the Environment (rijkswaterstaat.nl) in The Netherlands. Navigation intensity has been classified in accordance to the other pressures as 1 = 0–3000 passing vessels per year, 3 = 3.001–33.000 and 5 = 33.001–133.000.

2.2. Data analyzes

For each sampling, we determined ten diagnostic fish population metrics (FPM) for the ecological status of river systems (Noble et al., 2007; Welcomme et al., 2006; Wolter et al., 2013): Densities of eurytopic (EURY), rheophilic (RH), lithophilic (LITH), phytophilic (PHYT) and psammophilic (PSAM) fish as well as species richness (SPR), Shannon Index (SHA), Evenness (EVE), Simpson Index (SIM), and the Fish Region Index (FRI). All FPM were calculated based on standardized fish densities (fish per 100 m^2 sampled area, referred to as Ind./100 m^2). The assignment of fish species to guilds and to the species-specific Fish Region Index followed the classification provided by Scharf et al. (2011). For species not listed there we used Dußling et al. (2004) and EFI+ Consortium (2009) (compare appendix, Table A.1).

Five FPM refer to habitat preferences for flow velocities (rheophilic and eurytopic fish) and for spawning substrates (lithophilic, phytophilic

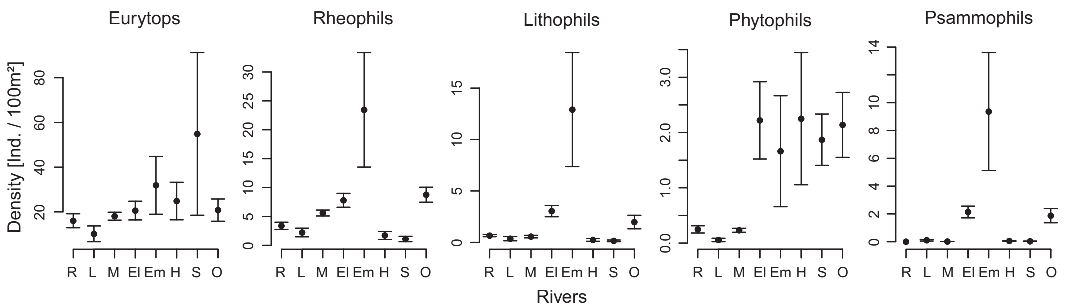


Fig. 3. River-specific estimates of guild densities. R: Rhine (number of samplings: 41); L: Lek (5); M: Meuse (62); El: Elbe (100); Em: Ems (7); H: Havel (4); S: Spree (8); O: Oder (23). Means ± standard errors are shown. Note: Fig. A.1 in the appendix provides a site-specific overview.

and psammophilic fish). Rheophilic fish prefer flowing river reaches and are thus considered sensitive to the impairment of fluvial dynamics and habitats. In contrast, eurytopic fish show no flow preferences and are further tolerant to low oxygen saturation. Therefore, high densities of eurytopic fish are commonly considered as indicators for the degradation of natural river dynamics (Dußling et al., 2004; Wolter and Vilcinskas, 1997). However, in large rivers, low densities of eurytopic fish could as well indicate degradation through rhithralisation of typically slow flowing potamal river reaches. Lithophilic fish are gravel spawners with benthic larvae. They are considered most sensitive to the impairment of hydromorphological processes, especially of sediment sorting and the provision of coarse gravel (Wolter et al., 2016). Psammophilic (sand spawning) and phytophilic (plant spawning) fish also form guilds with obligatory spawning substrate requirements. Both guilds are sensitive to habitat degradation, especially to losses of shallow littoral areas with low flow conditions and submerged and emerged macrophytes. Plant spawners further suffer from the loss of periodically inundated floodplain habitats. Guild densities were calculated for each sample as the number of fish with the respective flow or habitat preferences per 100 m^2.

The other five FPM refer to measures of alpha diversity, dominance structure and river type specific species composition: Species richness, the Shannon Index and the Evenness according to Spellerberg (2008), the Simpson Index (Somerfield et al., 2008) and the whole-sample Fish Region Index (Dußling et al., 2004). The FRI is a species-specific metric, which characterizes the preferred longitudinal distribution of a species within a river course, from the trout region in the headwaters to the ruffe-flounder region close to the estuary. It serves to characterize river reach specific fish communities (e.g., Schmutz et al., 2000). Species-specific FRI values have been derived from empirical occurrence data for all common European fish species (Dußling et al., 2004; Wolter et al., 2013, appendix Table A.1). The whole-sample or total FRI was calculated according to Dußling et al. (2004) based on the species-specific FRI and abundance of each species captured at a sampling site. It describes the correspondence of the entire fish assemblage of a sampling site to the respective river region. The total FRI is a generic index, which can be applied in different biogeographic regions. In large rivers, the total FRI (referred to as FRI in our study) is especially valuable for fish-based assessments as it indicates both rhithralisation and potamalisation, i.e., bi-directional hydromorphological changes (Schmutz et al., 2000; Wolter et al., 2013).

The metrics were calculated for each sample as follows:

Species richness $(SPR) = number\ of\ species$

$$\text{Shannon Index } (SHA) = -\sum\left(\frac{n_i}{N}\right)\log\left(\frac{n_i}{N}\right)$$

$$\text{Evenness } (EVE) = \frac{SHA}{\log SPR}$$

$$\text{Simpson diversity Index } (SIM) = 1-\sum\left(\frac{n_i}{N}\right)^2$$

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

where n_i = n individuals of species i; N = all individuals per sample; FRI_i = FRI of species i; S^2FRI = variance of the FRI of species i (Wolter et al., 2013).

2.3. Statistics

Boosted regression tree (BRT) models were applied to identify most influential pressures and their interactions on the fish population metrics (FPM). BRTs determine the relative influence of explanatory variables on a response variable as the contribution of each explanatory variable in reducing the overall model deviance (Lewin et al., 2014). Major advantages of BRTs are their ability to handle collinearity, nonlinearity, outliers and to automatically identify interactions between explanatory variables (Elith et al., 2008). BRTs therefore constitute a powerful tool to investigate relationships between the environment and ecological responses (Dahm and Hering, 2016; Pilière et al., 2014; Segurado et al., 2016) and hence to identify the impact of multiple pressures in aquatic environments (Feld et al., 2016; Lewin et al., 2014). To model the continuous response variables (the FPM), a BRT model with a Gaussian distribution was selected as loss function for minimizing squared errors. To improve homogeneities of variances, all guild densities were $\log(x + 1)$ transformed, EVE was arcsine-, SHA was exponential-, and SIM was arcsine-exponential-transformed. To obtain robust estimates, we followed recommendations of Feld et al. (2016) and Elith et al. (2008) and set bag-fraction to 0.7, tree complexity to 5 and learning rate to 0.001 so that at least 1000 trees contributed to the final model. All BRTs were modeled with the default 10-fold cross-validation. The 11 pressure variables (Fig. 2) were included as ordered factors. The relative importance (%) of each pressure variable in each BRT was quantified based on the number of times each of the variables was used for splitting, weighted by the squared improvement at each split and averaged over all trees (Elith et al., 2008). We calculated 500 parametric bootstrap simulations of each BRT model to obtain confidence intervals (95%-CI, percentile method, Carpenter and Bithell, 2000) of the relative importance of each explanatory variable and its effects on the response variable. Model quality (Mac Nally et al., 2017) of each BRT model was determined as goodness-of-fit (R^2_{COR}) based on the linear correlation between fitted and observed values (Cameron and Windmeijer, 1996).

Data were analyzed in R 3.3.1 (R Development Core Team, 2016) using the R packages 'gbm' (version 2.1.1; Ridgeway, 2016) and

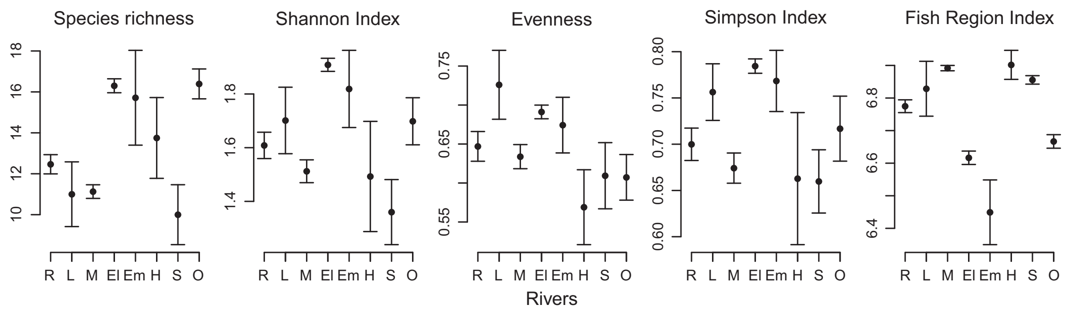


Fig. 4. River-specific estimates of biodiversity metrics. R: Rhine (number of samplings: 41); L: Lek (5); M: Meuse (62); El: Elbe (100); Em: Ems (7); H: Havel (4); S: Spree (8); O: Oder (23). Note: Fig. A.1 in the appendix provides a site-specific overview.

Table 2
Relative influence [%] of each pressure on fish population metrics. Each column represents one boosted regression tree (BRT) model with the fish metric as response variable (EURY = eurytopic fish, RH = rheophilic, LITH = lithophilic, PHYT = phytophilic, SPR = species richness, SHA = Shannon Index, EVE = Evenness, SIM = Simpson Index, FRI = Fish Region Index). The last row provides goodness-of-fit measures (R^2_{COR}) for each BRT model. Values in parenthesis provide the upper and lower limit of the 95% confidence interval of each parameter based on 500 bootstrap simulations of the respective BRT model. Bold font highlights pressures with the strongest relative influence (>10%) on the fish population metrics.

Pressures	EURY	RH	LITH	PHYT	PSAM	SPR	SHA	EVE	SIM	FRI
Barriers catchment down	4.0 (3.6–4.6)	**15.1 (14.3–18.4)**	2.8 (2.0–3.2)	4.1 (3.8–4.4)	2.1 (1.3–2.2)	3.6 (3.6–4.1)	4.1 (4.2–4.8)	**16.7 (15.8–18.5)**	6.6 (5.7–6.6)	3.6 (3.5–3.7)
Barriers segment up	1.3 (0.8–1.6)	**11.1 (10.6–14.3)**	1.8 (1.6–1.8)	0.6 (0.5–0.8)	0.3 (0.2–0.3)	2.7 (2.4–2.9)	0.7 (0.7–1.3)	2.2 (1.4–2.5)	1.0 (0.9–1.6)	0.4 (0.2–0.5)
Channelization	9.4 (9.1–9.8)	**12.5 (9.7–13.0)**	6.1 (2.8–6.6)	3.8 (3.7–4.3)	3.7 (0.7–4.1)	8.8 (8.9–10.2)	2.3 (2.3–3.0)	**16.4 (15.6–16.7)**	5.0 (4.7–5.5)	0.5 (0.3–0.6)
Cross-section	0.2 (0.2–0.3)	0.9 (0.5–1.0)	0.7 (0.6–0.8)	0.1 (0.1–0.1)	0.1 (0.0–0.1)	0.3 (0.3–0.4)	0.2 (0.2–0.3)	0.7 (0.7–1.1)	0.3 (0.2–0.4)	0.1 (0.1–0.2)
Embankment	**16.5 (15.9–18.7)**	6.4 (4.9–6.6)	4.7 (2.6–5.3)	0.9 (0.7–1.2)	2.7 (0.5–3.1)	0.9 (0.9–1.3)	1.0 (0.8–1.4)	0.6 (0.4–1.5)	0.8 (0.7–1.3)	0.3 (0.2–0.5)
Loss of floodplains	**14.0 (13.3–14.8)**	**11.5 (10.1–12.4)**	**16.4 (15.9–17.2)**	8.6 (8.2–10.1)	9.5 (4.7–11.0)	5.9 (5.8–6.4)	5.5 (5.3–6.2)	**13.3 (11.5–13.3)**	4.4 (4.0–5.3)	**16.3 (15.9–17.0)**
Inland navigation	**10.7 (10.3–11.0)**	**23.6 (23.0–26.9)**	**20.1 (19.6–20.8)**	**33.8 (33.2–34.6)**	**25.4 (25.1–26.7)**	**18.6 (18.2–18.8)**	8.5 (8.6–9.6)	7.4 (6.5–8.9)	8.1 (7.7–9.1)	5.7 (5.0–6.0)
Organic siltation	0.1 (0.0–0.2)	0.4 (0.2–0.5)	0.1 (0.0–0.2)	**32.9 (30.8–33.6)**	0.2 (0.1–0.3)	0.5 (0.3–0.8)	0.2 (0.1–0.3)	1.2 (0.7–1.3)	0.7 (0.5–1.3)	0.0 (0.0–0.1)
Riparian vegetation	2.1 (1.5–2.4)	4.0 (3.6–4.2)	2.6 (1.3–3.3)	8.7 (7.8–9.2)	3.5 (1.6–4.1)	1.6 (1.4–1.7)	2.8 (2.5–3.0)	6.8 (6.4–7.8)	3.9 (3.8–4.5)	0.5 (0.4–0.6)
Sedimentation	**23.3 (22.6–24.3)**	7.2 (4.8–7.7)	4.9 (3.1–5.6)	5.8 (5.4–6.2)	3.8 (1.8–4.4)	2.9 (2.8–3.5)	6.7 (6.7–7.9)	**15.9 (15.3–16.7)**	7.3 (6.6–8.3)	2.5 (2.1–2.7)
Velocity increase	**18.4 (16.6–18.8)**	7.1 (6.5–7.3)	**40.0 (36.0–49.8)**	0.7 (0.6–1.2)	**48.8 (45.2–62.1)**	**54.1 (51.0–54.1)**	**68.0 (63.1–67.7)**	**18.7 (17.3–20.5)**	**61.9 (57.4–63.8)**	**70.0 (68.7–71.7)**
Model fit (R^2_{COR})	0.84 (0.84–0.85)	0.74 (0.73–0.77)	0.73 (0.73–0.76)	0.83 (0.83–0.83)	0.64 (0.63–0.67)	0.6 (0.6–0.61)	0.72 (0.71–0.72)	0.88 (0.87–0.89)	0.79 (0.78–0.79)	0.54 (0.54–0.54)

'dismo' (version 1.1–4; Hijmans et al., 2016) to calculate the BRTs, and the R package 'boot' (version 1.3–19, Canty and Ripley, 2017) to calculate bootstrap simulations. Fig. 1 was drawn using ArcMap, version 10.5.1.

3. Results

3.1. Catch composition

The 250 samplings at 76 sites in 8 large rivers yielded 148,964 fish belonging to 55 species (including three lamprey species referred to as fish in the following). The most abundant species were roach *Rutilus rutilus*, bleak *Alburnus alburnus* and perch *Perca fluviatilis*, which contributed 26%, 14% and 13% to the total catch, respectively (appendix, Table A.2). The most frequently occurring species were roach, perch and ide *Leuciscus idus* captured in 99.6%, 98.8% and 94.4% of all samplings, respectively (see appendix, Table A.2 for detailed catch statistics).

Eurytopic fish dominated the total catch with 67% of all fish. The habitat sensitive ecological guilds of rheophils, lithophils, phytophils and psammophils comprised 32%, 11%, 5% and 8% of the total catch, respectively. Eurytopic and rheophilic fish were captured in all samplings and at all sampling sites. Lithophilic, phytophilic and psammophilic fish were captured in 92% 87% and 59% of all samplings, and at 95%, 88% and 75% of all sites, respectively (see appendix, Table A.3 for detailed guild composition).

Rivers Rhine, Lek and Meuse had the lowest average densities of fish in all of the guilds studied (compare Fig. 3 for the between-river variation of guild densities and appendix, Fig. A.1 for a site-specific overview). Rivers Havel and Spree had the lowest densities of fish in the sensitive guilds of rheophils (average: ≤1.71 Ind./100 m^2) and lithophils (≤0.25 Ind./100 m^2), low densities of psammophils (≤0.06 Ind./100 m^2) and higher densities of eurytops (≥24.84 Ind./100 m^2). The rivers Rhine and Meuse had the lowest densities of psammophils (≤0.02 Ind./100 m^2). Thus, these five rivers, Rhine, Lek, Meuse, Havel and Spree experienced the highest overall degradation indicated by the guild composition. Rivers Elbe and Oder had higher densities of fish in most sensitive guilds (rheophils: ≥7.79 Ind./100 m^2, lithophils: ≥1.98 Ind./100 m^2, psammophils ≥1.87 Ind./100 m^2) than the aforementioned rivers. Phytophilic fish were more abundant in the rivers Elbe, Ems, Havel, Spree and Oder (≥1.66 Ind./100 m^2) than in the rivers Rhine, Lek and Meuse (≤0.25 Ind./100 m^2). Highest densities of rheophils (23.45 Ind./100 m^2), lithophils (12.91 Ind./100 m^2) and psammophils (9.36 Ind./100 m^2) were estimated in the River Ems. However, in the River Ems, the average Fish Region Index was below 6.5 indicating a more rhithral fish assemblage corresponding to the so-called barbel river region. All other river systems had comparable mean Fish Region Indices (>6.5) indicating similar fish assemblages corresponding to the common bream river region. Biodiversity metrics indicated degradation trends widely similar to the guild composition (e.g., lower species richness, Shannon Index, Evenness and Simpson Index and a higher Fish Region Index in the rivers Rhine, Meuse, Havel and Spree compared to the rivers Ems, Elbe and Oder) but the between-river variability was much less pronounced (Fig. 4). The River Lek had the highest Evenness of all rivers and a higher Simpson Index than the rivers Rhine, Meuse, Havel, Spree and Oder.

3.2. Modeled pressure influences

Variation between classes of single pressures was as expected rather low (Fig. 2). Across all 11 pressures considered, pressure class 1, 3 and 5 indicating little, intermediate and high alteration occurred on average at 31 ± 11% (mean ± SE), 36 ± 10% and 41 ± 14%) of the sampled sites, respectively (Table 1). Goodness-of-fit (R^2_{COR}) of 500 bootstraps of each regression tree model ranged between 0.54 and 0.88 and was highest for models fitting Evenness and the eurytopic and phytophilic guilds (means: 0.88, 0.84, 0.83, respectively) and lowest for the Fish Region Index, species richness and the psammophilic guild (0.54, 0.60, 0.64, respectively; compare Table 2).

Increased flow velocity, navigation intensity and loss of floodplains had the strongest mean relative influence (39%, 16% and 11% respectively) on all ten fish population metrics (FPM). Thereby, mean influence of increased flow velocity was higher on the five biodiversity metrics (55%) than on the five guild densities (23%) and vice versa for the influence of navigation intensity (23% on guild densities and 10% on biodiversity metrics). These three pressures as well as increased sedimentation, channelization, organic siltation, the presence of artificial embankments and the presence of barriers downstream and within a 5 km upstream segment had a relative influence >10% on at least one FPM. Thereby, each FPM was strongly influenced by one to five pressures (Table 2).

Shannon and Simpson indices were strongly influenced (68% and 62%, respectively) by one dominating pressure only: increased velocity. Species richness and the Fish Region Index were likewise dominated by the influence of increased velocity (54% and 70%), but navigation intensity had also a strong influence (19%) on species richness, and the loss of floodplains had also a strong influence on the Fish Region Index (16%). The influence of increased velocity dominated on lithophilic (40%) and psammophilic fish (49%) but these FPM were also both strongly influenced by navigation intensity (20% and 25%) and by the loss of floodplains (16% and 10%). Densities of phytophilic fish were strongly influenced by navigation intensity (34%) and organic siltation (33%). The influence of inland navigation dominated on densities of rheophilic fish (24%) but was followed by equally strong influences of barriers downstream (15%), channelization (13%), loss of floodplains (12%) and by the presence of barriers within a 5 km upstream segment (11%). The Evenness and densities of eurytopic fish were each comparably strongly influenced by five pressures (Table 2).

Six pairwise interactions between pressures affected each fish population metric (FPM, Table 3). The most frequent pairwise interactions occurred between navigation intensity and loss of floodplains and between navigation intensity and increased velocity, both affecting 80% of all FPM. Further, the 60 interactions identified in total were dominated by the pressures increased velocity (involved in 47% of the interactions), navigation intensity (38%) and loss of floodplains (35%).

Pressure impacts were both positive and negative, depending on the fish population metric affected. Fig. 5 and Fig. 6 illustrate the impacts on the guild compositions and on biodiversity metrics, respectively. For example, increased flow velocity was associated with significantly higher biodiversity, higher densities of psammophils and lithophils, a lower Fish Region Index and lower densities of eurytops, all indicating rhithralisation. Inland navigation was associated with a significant decline in densities of lithophils and phytophils already at intensities of >3000 vessels per year, corresponding to an average of >8 cargo vessels per day. Rheophils, psammophils, eurytops and biodiversity (species richness, Shannon Index, Simpson Index) significantly declined at high navigation intensities, i.e. at >33,000 vessels per year or an average of >90 vessels per day. A partial loss of floodplains was associated to significantly lower densities of rheophilic and phytophilic fish and to a higher Evenness. A total loss of floodplains was associated with significantly lower densities of eurytopic fish and higher densities of lithophilic fish. Densities of rheophilic fish significantly declined in response to the presence of barriers (both upstream and downstream).

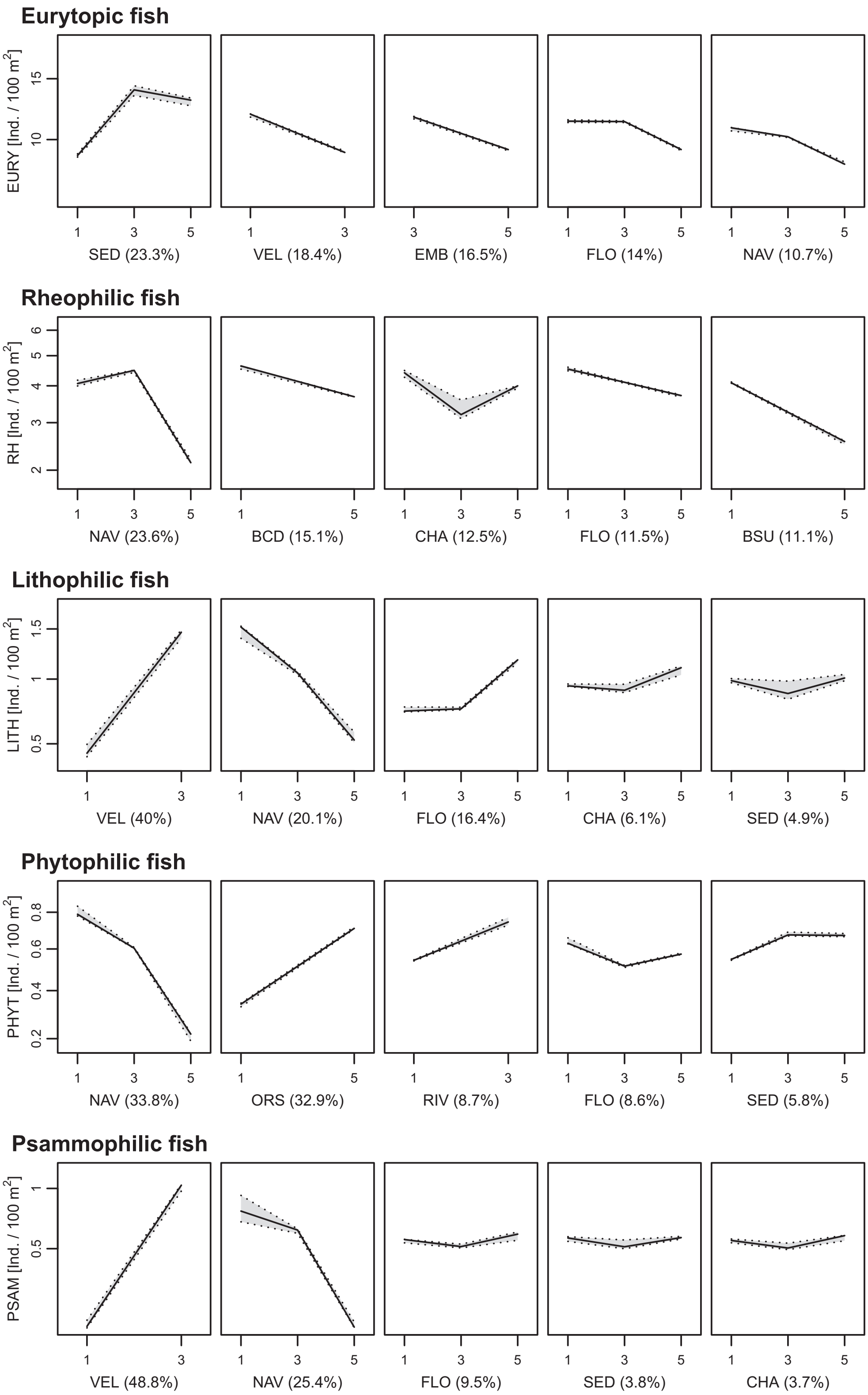
4. Discussion

This study aimed to identify key pressures and their interactions that contribute to lower densities of fish in diagnostic guilds and to lower biodiversity in European large rivers while explicitly accounting for inland navigation. It further aimed to derive diagnostic fish population metrics (FPM) for key pressures in large rivers. Increased velocities, navigation intensity and loss of floodplains had the highest influences on

Table 3
Pressure-interactions and their effect sizes on each fish population metric (FPM). Each column represents the results of one boosted regression tree model. BCD = barriers catchment downs; BSU = barriers segment up; CHA = channelization; EMB = artificial embankment; FLO = loss of floodplains; NAV = navigation intensity; ORS = organic siltation; RIV = cover of riparian vegetation; SED = increase of sedimentation; VEL = increase of flow velocity. Note: effect sizes are not comparable across different FPM.

Eurytopic fish		Rheophilic fish		Lithophilic fish		Phytophilic fish		Psammophilic fish	
Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size
CHA * SED	2.02	EMB * CHA	11.43	NAV * FLO	7.94	NAV * ORS	7.71	NAV * VEL	18.02
NAV * VEL	1.35	NAV * BSU	9.07	FLO * VEL	6.53	ORS * SED	1.4	FLO * SED	5.33
NAV * FLO	1.29	CHA * VEL	8.93	EMB * CHA	3.49	NAV * FLO	1	EMB * CHA	3.46
NAV * EMB	1.16	VEL * BSU	5.15	NAV * VEL	2.22	NAV * SED	0.63	NAV * FLO	3.11
FLO * SED	1.1	NAV * ORS	4.56	FLO * SED	0.62	ORS * RIV	0.39	FLO * EMB	0.64
NAV * BCD	0.81	NAV * VEL	4.36	VEL * BCD	0.46	ORS * CHA	0.23	SED * BCD	0.45

Species richness		Shannon index		Evenness		Simpson index		Fish region index	
Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size	Interaction	Size
NAV * VEL	316.7	NAV * VEL	10.52	CHA * VEL	0.11	CHA * VEL	0.35	FLO * VEL	1.11
NAV * FLO	170.98	FLO * VEL	8.72	SED * BCD	0.04	RIV * VEL	0.23	NAV * FLO	0.42
FLO * VEL	109.17	NAV * FLO	7.67	RIV * VEL	0.03	NAV * VEL	0.17	FLO * BCD	0.11
VEL * BSU	78.79	VEL * BCD	5.74	FLO * SED	0.02	VEL * BCD	0.12	VEL * BCD	0.08
CHA * VEL	22.39	RIV * VEL	4.05	NAV * FLO	0.01	NAV * SED	0.09	FLO * SED	0.02
FLO * RIV	16.69	CHA * VEL	2.88	NAV * VEL	0.01	FLO * VEL	0.09	SED * VEL	0.01


Eurytopic fish
EURY [Ind. / 100 m^2]
SED (23.3%)
VEL (18.4%)
EMB (16.5%)
FLO (14%)
NAV (10.7%)
Rheophilic fish
RH [Ind. / 100 m^2]
NAV (23.6%)
BCD (15.1%)
CHA (12.5%)
FLO (11.5%)
BSU (11.1%)
Lithophilic fish
LITH [Ind. / 100 m^2]
VEL (40%)
NAV (20.1%)
FLO (16.4%)
CHA (6.1%)
SED (4.9%)
Phytophilic fish
PHYT [Ind. / 100 m^2]
NAV (33.8%)
ORS (32.9%)
RIV (8.7%)
FLO (8.6%)
SED (5.8%)
Psammophilic fish
PSAM [Ind. / 100 m^2]
VEL (48.8%)
NAV (25.4%)
FLO (9.5%)
SED (3.8%)
CHA (3.7%)

FPM. Increased flow velocities resulting from shortening and straightening rivers accompanied by faster discharging runoff downstream appeared as the most dominating pressure, strongly fostering higher biodiversity and higher densities of fish relying on sediment sorting for spawning (lithophils, psammophils). Navigation intensity of more than eight vessels per day resulted in density declines of lithophilic and phytophilic fish. This finding corresponds surprisingly well with results obtained by Holland (1987) using experimental air exposure to study dewatering effects on walleye (*Stizostedion vitreum*) and pike (*Esox lucius*) larvae: A significant mortality due to dewatering events was observed at a dewatering frequency of 3 h, corresponding to the simulated passage of eight commercial tows per day (Holland, 1987). Floodplain degradation resulted in lower densities of eurytops, rheophils and phytophils. Moreover, the high influence of these three pressures was resembled in the most frequent interactions. Further important pressures identified like increased sedimentation, channelization, organic siltation, the presence of artificial embankments and migration barriers were well in line with the findings of Schinegger et al. (2012), with the latter becoming significantly improved by adding the impact of inland navigation to the pressures on large rivers. Among others, the strictly comparative analytical design as well as the special consideration of navigation intensity allowed identifying FPM that were diagnostic for certain types of human alterations in large river systems. Hence, our study contributes to disentangle the effects of multiple pressures in large rivers, even if most of the significant pressures impacted more than one fish population metric and most fish population metrics significantly responded to more than one pressure.

4.1. Limitations of the study

We acknowledge some limitations of our study in regard to the pressure variables analyzed. Several pressures had to be excluded, because their rank of severity did not vary within rivers and was also very low between rivers. In addition, the gradient of potential impacts was generally limited, because near natural and low disturbed sites were lacking in the large rivers studied. Accordingly, several pressures on river fishes reported from smaller rivers (e.g., Schinegger et al., 2012) could not be considered and analyzed here. Hence, their potential impact might have been underestimated. However, the overall rather severe degradation and little variation along river courses constitute a key character of the rather monotonous waterways. All European large rivers are highly degraded (e.g., Aarts et al., 2004), which was empirically confirmed here by very low densities of all sensitive reproduction guilds in all river systems studied.

Secondly, the classification of pressure ranks was conducted by the local water authorities and delivered with the site descriptions. In Europe, there are >100 assessment methods for river hydromorphology in use (Belletti et al., 2015). We have neither information, which particular method has been used to assess the different sites, nor on how detailed single variables have been recorded. We still know that experts can reliably discern between suitable and unsuitable habitat conditions, while they are less precise in addressing differences at finer scales (Radinger et al., 2017). Therefore, we cannot exclude that other experts would have classified a certain pressure state differently. However, at this spatial scale and reporting level on pressures, our data set still remains the best available data set for European large rivers.

4.2. Between-river variation of fish population metrics

All sampled sites, except those located in the river Ems, belonged to the same longitudinal river region (mean Fish Region Index >6.5) and therefore indicate comparable fish assemblage compositions. Hence, the observed between-river variation of the fish population metrics indicates a higher degradation of hydromorphology in the rivers Rhine, Lek, Meuse, Havel and Spree than in the rivers Elbe and Oder. Despite representing another river region, the hydromorphological degradation of the river Ems seemingly corresponds to the rivers Elbe and Oder. However, the River Ems provided the majority of sites that are not affected by commercial navigation, a rather unique situation in large rivers.

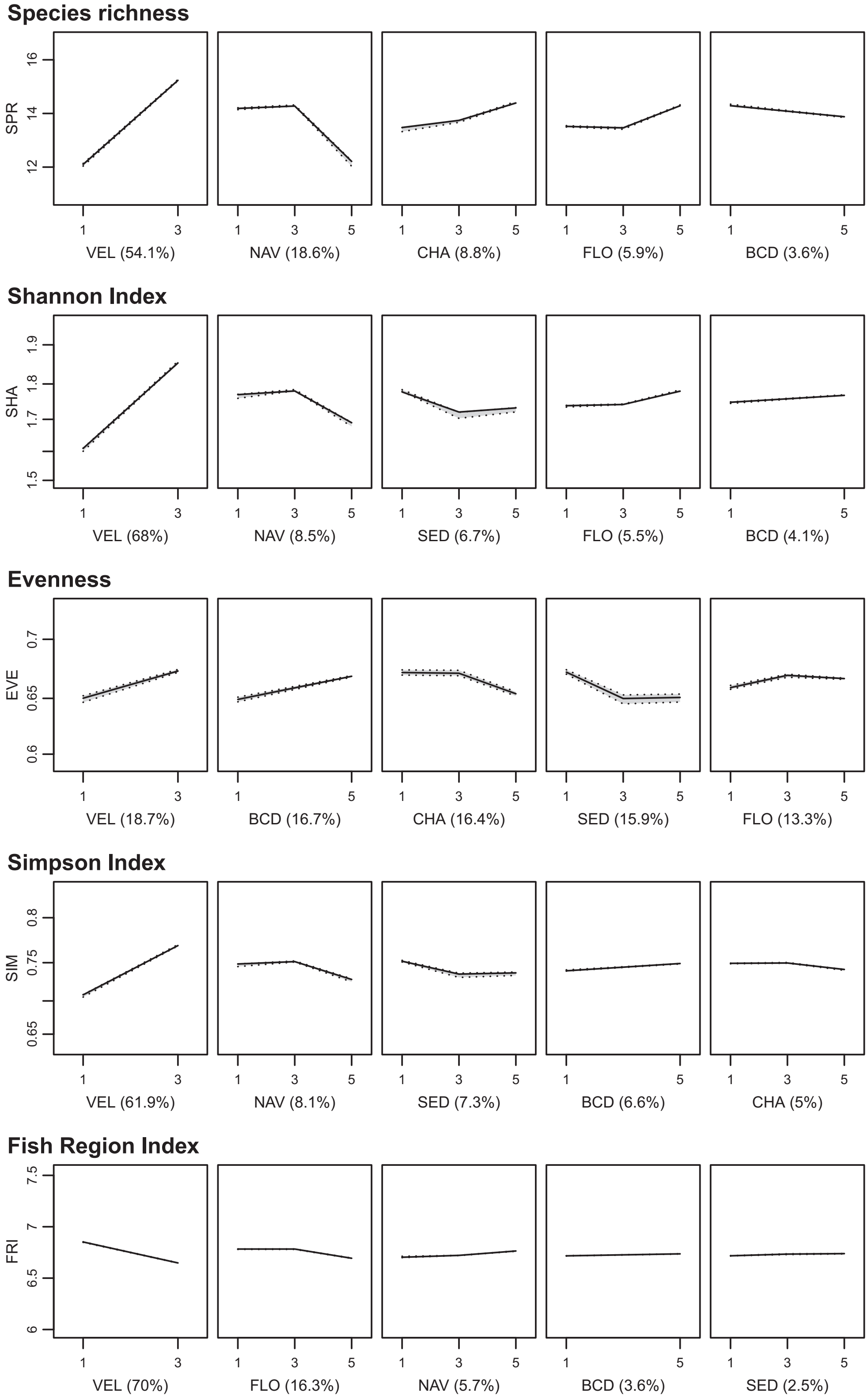
The rivers Lek, Rhine and Meuse had all the lowest densities of all sensitive reproduction guilds and comparable species richness. However, the river Lek had a higher Evenness and Simpson Index than rivers Rhine and Meuse, resembling a comparable number of species with lower densities of fish in the river Lek than in rivers Rhine and Meuse.

4.3. Highly influential pressures

The potamal region of large rivers is typically dominated by generalist species (Aarts and Nienhuis, 2003), which are well adapted to higher temperatures, nutrient loads and lower oxygen content and thus, are also successful in disturbed ecosystems (Pool et al., 2010). Nevertheless, our study indicated higher biodiversity with higher flow velocities in large rivers. High velocities can exceed the critical swimming speed of juvenile fish, with rheophilic species tolerating higher flow velocities than eurytopic species (Del Signore et al., 2014), resulting in a proportional increase of rheophils. Accordingly, increased velocities contributed to decreased density of eurytopic fish and particularly strongly to a decreased FRI which indicates rhithralisation (Wolter et al., 2013), i.e., a change from naturally slow to faster flowing conditions. Hence, increased velocities provide favorable habitat conditions for rheophilic fish species which contribute to higher diversity. Similarly, in reconnected meanders of a large river, Lorenz et al. (2016) observed increased diversity of rheophilic macroinvertebrates due to higher flow velocities therein. In our study, increased velocities were found having considerably higher influences on biodiversity metrics than on guild densities. However, lithophilic and psammophilic fish were also both strongly positively influenced by increased velocities. Hence, both lithophilic and psammophilic fish constitute indicative functional metrics for the inherent sediment sorting caused by high flow velocities. Consequently, biodiversity in large rivers (species richness, the Shannon Index, the Simpson Index) and the Fish Region Index constitute the most sensitive fish population metrics and densities of lithophils and psammophils constitute the most sensitive functional metrics for rhithralisation as a consequence of the hydrological degradation of the rather stagnant potamal region of large rivers.

The Navigation-induced Habitat Bottleneck Hypothesis (NBH, Wolter and Arlinghaus, 2003) states that littoral fish recruitment is limited in waterways due to navigation-induced hydrodynamic forces along the banks. Correspondingly, densities of all guilds requiring shallow structured habitats for reproduction most strongly declined in response to navigation intensity. Our study further refined the NBH by indicating that limited recruitment of juvenile fish along shoreline habitats propagates to lower densities of habitat-sensitive fish in the adult stages. Exemplified by the River Rhine with its prevalent floodplain loss, channelization and artificial embankments, it was further indicated

Fig. 5. Response plots of the five most important pressure variables affecting densities of fish in diagnostic guilds. Each row represents one boosted regression tree (BRT) model with a given fish metric as response. Solid lines represent results obtained from the original BRT model; dashed lines and grey areas show the 95% confidence interval based on 500 bootstrap simulations of each BRT model. X-axes show ranked pressure classes (BCD = barriers catchment down; BSU = barriers segment up; CHA = channelization; EMB = artificial embankment; FLO = loss of floodplains; NAV = navigation intensity; ORS = organic siltation; RIV = cover of riparian vegetation; SED = increase of sedimentation; VEL = increase of flow velocity) with 1 = low or no alteration; 3 = intermediate alteration; 5 = high alteration. Percentages in parenthesis indicate the relative variable importance of each pressure in the respective BRT model.


Species richness
SPR
12
14
16
VEL (54.1%)
NAV (18.6%)
CHA (8.8%)
FLO (5.9%)
BCD (3.6%)
Shannon Index
SHA
1.5
1.7
1.8
1.9
VEL (68%)
NAV (8.5%)
SED (6.7%)
FLO (5.5%)
BCD (4.1%)
Evenness
EVE
0.6
0.65
0.7
VEL (18.7%)
BCD (16.7%)
CHA (16.4%)
SED (15.9%)
FLO (13.3%)
Simpson Index
SIM
0.65
0.75
0.8
VEL (61.9%)
NAV (8.1%)
SED (7.3%)
BCD (6.6%)
CHA (5%)
Fish Region Index
FRI
6
6.5
7
7.5
VEL (70%)
FLO (16.3%)
NAV (5.7%)
BCD (3.6%)
SED (2.5%)

that commercial navigation inevitably co-occurs with these pressures mentioned and that inland navigation impacts on top of the degradation of river hydromorphology. Concomitantly, navigation intensity was part of all most frequent interactions, affecting 80% of fish population metrics in combination with increased velocity and also affecting 80% of fish population metrics in combination with the loss of floodplains. Therefore, inland navigation is a highly influential and river-type specific pressure in large rivers which moreover interacts with the degradations of river hydromorphology. Further, densities of the sensitive reproduction guilds of lithophils and phytophils were strongly influenced by commercial navigation and declined already at intensities >8 vessels per day. Densities of psammophils were also very low in all navigated rivers, indicating that psammophilic fish were similarly affected by vessel-induced hydrodynamic forces. Therefore, low densities of lithophils, phytophils and psammophils constitute most indicative metrics for the disturbance of shoreline spawning areas through both (i) wave action induced by passing vessels and (ii) hydromorphological degradation of the river channel that comes along with inland navigation. However, the influence of the solely vessel-induced wave action was shown to be strongest on phytophilic fish.

Recently, the presence of natural floodplain areas has been associated with an overall higher ecological status of European rivers (Grizzetti et al., 2017). Floodplains are less disturbed by hydraulic forces caused by inland navigation and they support the exchange of terrestrial and aquatic resources. Therefore, floodplains serve as an expansion of the littoral shoreline (Strayer and Findlay, 2010) providing additional spawning and nursery habitats that increase abundances of adult and juvenile fishes (Lorenz et al., 2013). Moreover, floodplains increase the diversity of fish larvae after flood events (Silva et al., 2017) and offer favorable conditions for macrohabitat generalists (Galat and Zweimüller, 2001; Schomaker and Wolter, 2011). High flow intensities and frequencies that result in extensive flooding of adjacent floodplains are related to higher species richness (Poff et al., 1997). Floodplains are however often degraded in large rivers and detached from the rivers' main channels by levees. Correspondingly, the loss of floodplains was associated with lower densities of eurytops, rheophils and phytophils in this study. Densities of lithophilic fish appeared to increase when floodplains were heavily degraded. This is plausible as shorelines are often stabilized with hard substrate, e.g., rip-rap structures (stones/boulders) that might at least partially serve for the reproduction of lithophilic species (Erős et al., 2008). The loss of floodplains further contributed to a decreased Fish Region Index indicating rhithralisation, mainly because levees commonly co-occur with straightened river courses, which in turn increase flow velocity, but primarily reduce habitat complexity and the availability of shelter along the banks.

Densities of eurytopic and rheophilic fish were comparably strongly influenced by five and four pressures, respectively. Eurytopic fish decreased in response to artificial embankment, increased velocity, loss of floodplains and navigation intensity. This finding firstly suggests that densities of eurytopic fish are also prone to decline if multiple pressures including inland navigation affect the potamal region of large rivers. Secondly, high densities of generalist species constitute less suitable fish population metrics to indicate the impacts of one dominating pressure. Instead, high densities of eurytops rather indicate the prevalence of multiple pressures and thus, the overall hydromorphological degradation of large rivers. However, lowered densities of eurytopic fish in the naturally slow flowing potamal river region can also indicate rhithralisation (as was indicated by a decline in densities of eurytopic fish in response to increased velocity). Rheophilic fish were comparably strongly influenced by navigation intensity, loss of floodplains, channelization and by upstream and downstream barriers. Barriers constitute a strong pressure preventing migration of rheophilic fish (e.g., Branco et al., 2017), but in their impoundments especially change the hydromorphological conditions towards lower flow velocities, sedimentation of fines, and loss of coarser spawning substrates.

4.4. Conclusions

Inland navigation constitutes a hitherto commonly neglected but highly influential pressure in European large rivers. In large rivers, inland navigation has an influence on fish assemblages comparable to hydromorphological alterations. Vessel operation contributes to declines of fish densities and biodiversity in addition to the hydromorphological degradation of the river channel and further interacts with the prevailing hydromorphological alterations. Reproduction guilds (densities of lithophilic and phytophilic fish) were most sensitive to navigation impacts but psammophils, rheophils, eurytops and biodiversity were also affected. The loss of floodplains has integral consequences for the ecological integrity of large rivers due to vanishing habitat complexity providing shelter, nursing and spawning habitats. Increased velocity as a consequence of channelization and bank stabilization results in rhithralisation of the potamal region of large rivers. Increased biodiversity (species richness, Shannon Index, Simpson Index), a decreased Fish Region Index and increased densities of lithophilic and psammophilic guilds are indicative fish population metrics for rhithralisation of the potamal region of large rivers. Declines in lithophilic, phytophilic and psammophilic guilds indicate disturbance of shoreline habitats through both (i) wave action induced by passing vessels and (ii) hydromorphological degradation of the river channel that comes along with inland navigation. High densities of the eurytopic guild indicate the influence of multiple pressures, but in large rives, eurytops can also decline as a consequence of rhithralisation. Inland navigation requires particular attention in river rehabilitation and management. Therefore, a holistic river management has to consider both river hydromorphology and inland navigation to achieve a more efficient rehabilitation of the potamal region of large rives.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.01.307.

References

Aarts, B.G.W., Nienhuis, P.H., 2003. Fish zonations and guilds as the basis for assessment of ecological integrity of large rivers. Hydrobiologia 500:157–178. https://doi.org/10.1023/A:1024638726162.

Aarts, B.G.W., Van Den Brink, F.W.B., Nienhuis, P.H., 2004. Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. River Res. Appl. 20:3–23. https://doi.org/10.1002/rra.720.

Fig. 6. Response plots of the five most important pressure variables affecting biodiversity metrics. Each row represents one boosted regression tree (BRT) model with a given biodiversity metric as response. Solid line represents results obtained from the original BRT model; dashed lines and grey area show the 95% confidence interval based on 500 bootstrap simulations of each BRT model. X-axes of each plot show ranked pressure classes (BCD = barriers catchment down; CHA = channelization; FLO = loss of floodplains; NAV = navigation intensity; SED = increase of sedimentation; VEL = increase of flow velocity) with 1 = low or no alteration; 3 = intermediate alteration; 5 = high alteration. Percentages in parenthesis indicate the relative variable importance of each pressure in the respective BRT model.

Adams, S.R., Keevin, T.M., Killgore, K.J., Hoover, J.J., 1999. Stranding potential of young fishes subjected to simulated vessel-induced drawdown. Trans. Am. Fish. Soc. 128: 1230–1234. https://doi.org/10.1577/1548-8659(1999)128<1230:SPOYFS>2.0.CO;2.
Ali, M.M., Murphy, K.J., Langendorff, J., 1999. Interrelations of river ship traffic with aquatic plants in the River Nile, Upper Egypt. In: Caffrey, J., Barrett, P.R.F., Ferreira, M.T., Moreira, I.S., Murphy, K.J., Wade, P.M. (Eds.), Biology, Ecology and Management of Aquatic Plants. Developments in Hydrobiology. Springer, Dordrecht:pp. 93–100 https://doi.org/10.1007/978-94-017-0922-4_14.
Arlinghaus, R., Engelhardt, C., Sukhodolov, A., Wolter, C., 2002. Fish recruitment in a canal with intensive navigation: implications for ecosystem management. J. Fish Biol. 61: 1386–1402. https://doi.org/10.1111/j.1095-8649.2002.tb02484.x.
Asplund, T.R., Cook, C.M., 1997. Effects of motor boats on submerged aquatic macrophytes. Lake Reservoir Manag. 13:1–12. https://doi.org/10.1080/07438149709354290.
Belletti, B., Rinaldi, M., Buijse, A.D., Gurnell, A.M., Mosselman, E., 2015. A review of assessment methods for river hydromorphology. Environ. Earth Sci. 73:2079–2100. https://doi.org/10.1007/s12665-014-3558-1.
Berg, R., Gaumert, T., Kämmereit, M., Klinger, H., Lemcke, R., Leuner, E., Wolter, C., Dußling, U., 2004. The German river typology with respect to fish-faunistic reference conditions. In: Steinberg, C., Calmano, W., Klapper, H., Wilken, R.-D. (Eds.), Handbuch Angewandte Limnologie. Ecomed-Verlag, Landsberg, pp. 12–17.
Birk, S., van Kouwen, L., Willby, N., 2012. Harmonising the bioassessment of large rivers in the absence of near-natural reference conditions – a case study of the Danube River. Freshw. Biol. 57:1716–1732. https://doi.org/10.1111/j.1365-2427.2012.02831.x.
Branco, P., Amaral, S.D., Ferreira, M.T., Santos, J.M., 2017. Do small barriers affect the movement of freshwater fish by increasing residency? Sci. Total Environ. 581–582: 486–494. https://doi.org/10.1016/j.scitotenv.2016.12.156.
Cameron, A., Windmeijer, F., 1996. R-squared measures for count data regression models with applications to health-care utilization. J. Bus. Econ. Stat. 14, 209–220.
Campbell, I.C., 2016. Integrated management of large rivers and their basins. Ecohydrol. Hydrobiol. 16:203–214. https://doi.org/10.1016/j.ecohyd.2016.09.006.
Canty, A., Ripley, B., 2017. Boot: bootstrap R (S-plus) functions [WWW document]. R package version 1.3-20. URL: https://cran.r-project.org/web/packages/boot/index.html (accessed 8.8.17).
Carpenter, J., Bithell, J., 2000. Bootstrap confidence intervals: when, which, what? A practical guide for medical statisticians. Stat. Med. 19, 1141–1164.
Clapcott, J.E., Collier, K.J., Death, R.G., Goodwin, E.O., Harding, J.S., Kelly, D., Leathwick, J.R., Young, R.G., 2012. Quantifying relationships between land-use gradients and structural and functional indicators of stream ecological integrity. Freshw. Biol. 57: 74–90. https://doi.org/10.1111/j.1365-2427.2011.02696.x.
Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. 11:1304–1315. https://doi.org/10.1111/j.1461-0248.2008.01253.x.
Dahm, V., Hering, D., 2016. A modeling approach for identifying recolonisation source sites in river restoration planning. Landsc. Ecol. 31:2323–2342. https://doi.org/10.1007/s10980-016-0402-x.
Darling, E.S., Côté, I.M., 2008. Quantifying the evidence for ecological synergies. Ecol. Lett. 11:1278–1286. https://doi.org/10.1111/j.1461-0248.2008.01243.x.
Del Signore, A., Lenders, H.J.R., Hendriks, A.J., Vonk, J.A., Mulder, C., Leuven, R.S.E.W., 2014. Size-mediated effects of water-flow velocity on riverine fish species. River Res. Appl. https://doi.org/10.1002/rra.2847.
Dußling, U., Bischoff, A., Haberbosch, R., Hoffmann, A., Klinger, H., Wolter, C., Wysujack, K., Berg, R., 2004. Ecological characters of river fish species occurring in Germany. In: Steinberg, C., Calmano, W., Klapper, H., Wilken, R.-D. (Eds.), Handbuch Angewandte Limnologie. Ecomed-Verlag, Landsberg, pp. 4–12.
EEA, 2012. European Waters – Assessment of Status and Pressures (No. EEA Report 8/2012). European Environment Agency - EEA, Copenhagen.
EFI + Consortium, 2009. Manual for the Application of the New European Fish Index – EFI +. A Fish-based Method to Assess the Ecological Status of European Running Waters in Support of the Water Framework Directive.
Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77:802–813. https://doi.org/10.1111/j.1365-2656.2008.01390.x.
Erős, T., Tóth, B., Sevcsik, A., Schmera, D., 2008. Comparison of fish assemblage diversity in natural and artificial rip-rap habitats in the littoral zone of a large river (river Danube, Hungary). Int. Rev. Hydrobiol. 93:88–105. https://doi.org/10.1002/iroh.200710976.
Feld, C.K., Segurado, P., Gutiérrez-Cánovas, C., 2016. Analysing the impact of multiple stressors in aquatic biomonitoring data: a 'cookbook' with applications in R. Sci. Total Environ. 573:1320–1339. https://doi.org/10.1016/j.scitotenv.2016.06.243.
Flotemersch, J.E., Stribling, J.B., Hughes, R.M., Reynolds, L., Paul, M.J., Wolter, C., 2011. Site length for biological assessment of boatable rivers. River Res. Appl. 27:520–535. https://doi.org/10.1002/rra.1367.
Friberg, N., Angelopoulos, N.V., Buijse, A.D., Cowx, I.G., Kail, J., Moe, T.F., Moir, H., O'Hare, M.T., Verdonschot, P.F.M., Wolter, C., 2016. Chapter eleven - effective river restoration in the 21st century: from trial and error to novel evidence-based approaches. In: Alex, J., Dumbrell, R.L.K., G.W. (Eds.), Advances in Ecological Research, Large-Scale Ecology: Model Systems to Global Perspectives. Academic Press:pp. 535–611 https://doi.org/10.1016/bs.aecr.2016.08.010.
Gabel, F., Garcia, X.F., Schnauder, I., Pusch, M.T., 2012. Effects of ship-induced waves on littoral benthic invertebrates. Freshw. Biol. 57:2425–2435. https://doi.org/10.1111/fwb.12011.
Gabel, F., Lorenz, S., Stoll, S., 2017. Effects of ship-induced waves on aquatic ecosystems. Sci. Total Environ. 601–602:926–939. https://doi.org/10.1016/j.scitotenv.2017.05.206.
Galat, D.L., Zweimüller, I., 2001. Conserving large-river fishes: is the highway analogy an appropriate paradigm? J. N. Am. Benthol. Soc. 20:266–279. https://doi.org/10.2307/1468321.
Grizzetti, B., Pistocchi, A., Liquete, C., Udias, A., Bouraoui, F., van de Bund, W., 2017. Human pressures and ecological status of European rivers. Sci. Rep. 7:205. https://doi.org/10.1038/s41598-017-00324-3.
Hering, D., Carvalho, L., Argillier, C., Beklioglu, M., Borja, A., Cardoso, A.C., Duel, H., Ferreira, T., Globevnik, L., Hanganu, J., Hellsten, S., Jeppesen, E., Kodeš, V., Solheim, A.L., Nõges, T., Ormerod, S., Panagopoulos, Y., Schmutz, S., Venohr, M., Birk, S., 2015. Managing aquatic ecosystems and water resources under multiple stress — an introduction to the MARS project. Sci. Total Environ. 503–504:10–21. https://doi.org/10.1016/j.scitotenv.2014.06.106.
Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., 2016. Dismo: species distribution modeling [WWW document]. R package version 1.1-4. URL: https://cran.r-project.org/web/packages/dismo/index.html (accessed 12.12.16).
Holland, L.E., 1987. Effect of brief navigation-related dewaterings on fish eggs and larvae. N. Am. J. Fish Manag. 7:145–147. https://doi.org/10.1577/1548-8659(1987)7<145:EOBNDO>2.0.CO;2.
Huckstorf, V., Lewin, W.-C., Mehner, T., Wolter, C., 2011. Impoverishment of YOY-fish assemblages by intense commercial navigation in a large lowland river. River Res. Appl. 27:1253–1263. https://doi.org/10.1002/rra.1420.
Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D., Chimimba, C.T., 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. Glob. Chang. Biol. 22: 180–189. https://doi.org/10.1111/gcb.13028.
Leclere, J., Belliard, J., Oberdorff, T., 2012. Young-of-the-year fish assemblages as indicators of anthropogenic disturbances in large tributaries of the Seine River Basin (France). Hydrobiologia 694:99–116. https://doi.org/10.1007/s10750-012-1135-8.
Lewin, W.-C., Mehner, T., Ritterbusch, D., Brämick, U., 2014. The influence of anthropogenic shoreline changes on the littoral abundance of fish species in German lowland lakes varying in depth as determined by boosted regression trees. Hydrobiologia 724: 293–306. https://doi.org/10.1007/s10750-013-1746-8.
Liedermann, M., Tritthart, M., Gmeiner, P., Hinterleitner, M., Schludermann, E., Keckeis, H., Habersack, H., 2014. Typification of vessel-induced waves and their interaction with different bank types, including management implications for river restoration projects. Hydrobiologia 729:17–31. https://doi.org/10.1007/s10750-014-1829-1.
Lorenz, A.W., Stoll, S., Sundermann, A., Haase, P., 2013. Do adult and YOY fish benefit from river restoration measures? Ecol. Eng. 61 (Part A):174–181. https://doi.org/10.1016/j.ecoleng.2013.09.027.
Lorenz, S., Leszinski, M., Graeber, D., 2016. Meander reconnection method determines restoration success for macroinvertebrate communities in a German lowland river. Int. Rev. Hydrobiol. 101:123–131. https://doi.org/10.1002/iroh.201501823.
Mac Nally, R., Duncan, R.P., Thomson, J.R., Yen, J.D.L., 2017. Model selection using information criteria, but is the "best" model any good? J. Appl. Ecol. 00:1–4. https://doi.org/10.1111/1365-2664.13060.
Malmqvist, B., Rundle, S., 2002. Threats to the running water ecosystems of the world. Environ. Conserv.:134–153 https://doi.org/10.1017/S0376892902000097.
Melcher, A., Schmutz, S., Haidvogl, G., Moder, K., 2007. Spatially based methods to assess the ecological status of European fish assemblage types. Fish. Manag. Ecol. 14: 453–463. https://doi.org/10.1111/j.1365-2400.2007.00583.x.
Meybeck, M., Helmer, R., 1989. The quality of rivers: from pristine stage to global pollution. Palaeogeogr. Palaeoclimatol. Palaeoecol. 75:283–309. https://doi.org/10.1016/0031-0182(89)90191-0.
Milošević, D., Mančev, D., Čerba, D., Stojković Piperac, M., Popović, N., Atanacković, A., Đuknić, J., Simić, V., Paunović, M., 2018. The potential of chironomid larvae-based metrics in the bioassessment of non-wadeable rivers. Sci. Total Environ. 616–617: 472–479. https://doi.org/10.1016/j.scitotenv.2017.10.262.
Murphy, K.J., Eaton, J.W., 1983. Effects of pleasure-boat traffic on macrophyte growth in canals. J. Appl. Ecol. 20:713–729. https://doi.org/10.2307/2403122.
Nagrodski, A., Raby, G.D., Hasler, C.T., Taylor, M.K., Cooke, S.J., 2012. Fish stranding in freshwater systems: sources, consequences, and mitigation. J. Environ. Manag. 103: 133–141. https://doi.org/10.1016/j.jenvman.2012.03.007.
Noble, R.A.A., Cowx, I.G., Goffaux, D., Kestemont, P., 2007. Assessing the health of European rivers using functional ecological guilds of fish communities: standardising species classification and approaches to metric selection. Fish. Manag. Ecol. 14:381–392. https://doi.org/10.1111/j.1365-2400.2007.00575.x.
Nõges, P., Argillier, C., Borja, Á., Garmendia, J.M., Hanganu, J., Kodeš, V., Pletterbauer, F., Sagouis, A., Birk, S., 2015. Quantified biotic and abiotic responses to multiple stress in freshwater, marine and ground waters. Sci. Total Environ. https://doi.org/10.1016/j.scitotenv.2015.06.045.
Oliver, T.H., Morecroft, M.D., 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. Wiley Interdiscip. Rev. Clim. Chang. 5:317–335. https://doi.org/10.1002/wcc.271.
Pearson, W.H., Skalski, J.R., 2011. Factors affecting stranding of juvenile salmonids by wakes from ship passage in the Lower Columbia River. River Res. Appl. 27: 926–936. https://doi.org/10.1002/rra.1397.
Petts, G.E., Möller, H., Roux, A.L., 1989. Historical Change of Large Alluvial Rivers: Western Europe. John Wiley & Sons, Chichester.
Piggott, J.J., Townsend, C.R., Matthaei, C.D., 2015. Reconceptualizing synergism and antagonism among multiple stressors. Ecol. Evol. 5:1538–1547. https://doi.org/10.1002/ece3.1465.
Pilière, A., Schipper, A.M., Breure, A.M., Posthuma, L., de Zwart, D., Dyer, S.D., Huijbregts, M.A.J., 2014. Comparing responses of freshwater fish and invertebrate community integrity along multiple environmental gradients. Ecol. Indic. 43:215–226. https://doi.org/10.1016/j.ecolind.2014.02.019.
Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime. Bioscience 47:769–784. https://doi.org/10.2307/1313099.
Pont, D., Hugueny, B., Beier, U., Goffaux, D., Melcher, A., Noble, R., Rogers, C., Roset, N., Schmutz, S., 2006. Assessing river biotic condition at a continental scale: a European

approach using functional metrics and fish assemblages. J. Appl. Ecol. 43:70–80. https://doi.org/10.1111/j.1365-2664.2005.01126.x.
Pool, T.K., Olden, J.D., Whittier, J.B., Paukert, C.P., 2010. Environmental drivers of fish functional diversity and composition in the Lower Colorado River Basin. Can. J. Fish. Aquat. Sci. 67:1791–1807. https://doi.org/10.1139/F10-095.
R Development Core Team, 2016. R: A Language and Environment for Statistical Computing [WWW Document]. R Foundation For Statistical Computing, Vienna, Austria URL: https://www.r-project.org/ (accessed 6.21.16).
Radinger, J., Hölker, F., Horký, P., Slavík, O., Dendoncker, N., Wolter, C., 2016. Synergistic and antagonistic interactions of future land use and climate change on river fish assemblages. Glob. Chang. Biol. 22:1505–1522. https://doi.org/10.1111/gcb.13183.
Radinger, J., Kail, J., Wolter, C., 2017. Differences among expert judgments of fish habitat suitability and implications for river management. River Res. Appl. 33:538–547. https://doi.org/10.1002/rra.3109.
Ridgeway, G., 2016. gbm: generalized boosted regression models [WWW document]. R package version 2.1.1. URL: https://cran.r-project.org/web/packages/gbm/index.html (accessed 12.12.16).
Sagouis, A., Jabot, F., Argillier, C., 2017. Taxonomic versus functional diversity metrics: how do fish communities respond to anthropogenic stressors in reservoirs? Ecol. Freshw. Fish 26:621–635. https://doi.org/10.1111/eff.12306.
Scharf, J., Brämick, U., Fredrich, F., Rothe, U., Schuhr, H., Tautenhahn, M., Wolter, C., Zahn, S., 2011. Fische in Brandenburg - Aktuelle Kartierung und Beschreibung der märkischen Fischfauna.
Schinegger, R., Trautwein, C., Melcher, A., Schmutz, S., 2012. Multiple human pressures and their spatial patterns in European running waters. Water Environ. J. 26: 261–273. https://doi.org/10.1111/j.1747-6593.2011.00285.x.
Schinegger, R., Trautwein, C., Schmutz, S., 2013. Pressure-specific and multiple pressure response of fish assemblages in European running waters. Limnologica - Ecology and Management of Inland Waters. 9th International Symposium on Ecohydraulics 2012 43:pp. 348–361. https://doi.org/10.1016/j.limno.2013.05.008.
Schinegger, R., Palt, M., Segurado, P., Schmutz, S., 2016. Untangling the effects of multiple human stressors and their impacts on fish assemblages in European running waters. Sci. Total Environ. 573:1079–1088. https://doi.org/10.1016/j.scitotenv.2016.08.143.
Schmutz, S., Kaufmann, M., Vogel, B., Jungwirth, M., Muhar, S., 2000. A multi-level concept for fish-based, river-type-specific assessment of ecological integrity. Hydrobiologia 422–423:279–289. https://doi.org/10.1023/A:1017038820390.
Schmutz, S., Cowx, I.G., Haidvogl, G., Pont, D., 2007. Fish-based methods for assessing European running waters: a synthesis. Fish. Manag. Ecol. 14:369–380. https://doi.org/10.1111/j.1365-2400.2007.00585.x.
Schomaker, C., Wolter, C., 2011. The contribution of long-term isolated water bodies to floodplain fish diversity. Freshw. Biol. 56:1469–1480. https://doi.org/10.1111/j.1365-2427.2011.02583.x.
Segner, H., Schmitt-Jansen, M., Sabater, S., 2014. Assessing the impact of multiple stressors on aquatic biota: the receptor's side matters. Environ. Sci. Technol. 48:7690–7696. https://doi.org/10.1021/es405082t.
Segurado, P., Branco, P., Jauch, E., Neves, R., Ferreira, M.T., 2016. Sensitivity of river fishes to climate change: the role of hydrological stressors on habitat range shifts. Sci. Total Environ. 562:435–445. https://doi.org/10.1016/j.scitotenv.2016.03.188.
Silva, C.B., Dias, J.D., Bialetzki, A., 2017. Fish larvae diversity in a conservation area of a neotropical floodplain: influence of temporal and spatial scales. Hydrobiologia 787: 141–152. https://doi.org/10.1007/s10750-016-2953-x.
Söhngen, B., Koop, J., Knight, S., Rytkönen, J., Beckwith, P., Ferrari, N., Iribarren, J., Keevin, T., Wolter, C., Maynord, S., 2008. Considerations to reduce environmental impacts of vessels (PIANC REPORT No. N° 99). PIANC Report Series. PIANC, Brussels.
Somerfield, P.J., Clarke, K.R., Warwick, R.M., 2008. Simpson index. In: Fath, B.D. (Ed.), Encyclopedia of Ecology. Academic Press, Oxford, pp. 3252–3255.
Sommerwerk, N., Wolter, C., Freyhof, J., Tockner, K., 2017. Components and drivers of change in European freshwater fish faunas. J. Biogeogr. 44:1781–1790. https://doi.org/10.1111/jbi.13019.
Spellerberg, I.F., 2008. Shannon–Wiener index. In: Fath, B.D. (Ed.), Encyclopedia of Ecology. Academic Press, Oxford, pp. 3249–3252.
Strayer, D.L., Findlay, S.E.G., 2010. Ecology of freshwater shore zones. Aquat. Sci. 72: 127–163. https://doi.org/10.1007/s00027-010-0128-9.
Trautwein, C., Schinegger, R., Schmutz, S., 2013. Divergent reaction of fish metrics to human pressures in fish assemblage types in Europe. Hydrobiologia 718:207–220. https://doi.org/10.1007/s10750-013-1616-4.
Vaughan, I.P., Diamond, M., Gurnell, A.M., Hall, K.A., Jenkins, A., Milner, N.J., Naylor, L.A., Sear, D.A., Woodward, G., Ormerod, S.J., 2009. Integrating ecology with hydromorphology: a priority for river science and management. Aquat. Conserv. Mar. Freshwat. Ecosyst. 19:113–125. https://doi.org/10.1002/aqc.895.
Welcomme, R.L., Winemiller, K.O., Cowx, I.G., 2006. Fish environmental guilds as a tool for assessment of ecological condition of rivers. River Res. Appl. 22:377–396. https://doi.org/10.1002/rra.914.
Wolter, C., Arlinghaus, R., 2003. Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. Rev. Fish Biol. Fish. 13:63–89. https://doi.org/10.1023/A:1026350223459.
Wolter, C., Vilcinskas, A., 1997. Perch (*Perca fluviatilis*) as an indicator species for structural degradation in regulated rivers and canals in the lowlands of Germany. Ecol. Freshw. Fish 6:174–181. https://doi.org/10.1111/j.1600-0633.1997.tb00160.x.
Wolter, C., Arlinghaus, R., Sukhodolov, A., Engelhardt, C., 2004. A model of navigation-induced currents in inland waterways and implications for juvenile fish displacement. Environ. Manag. 34:656–668. https://doi.org/10.1007/s00267-004-0201-z.
Wolter, C., Lorenz, S., Scheunig, S., Lehmann, N., Schomaker, C., Nastase, A., García de Jalón, D., Marzin, A., Lorenz, A.W., Krakova, M., Brabec, K., Noble, R., 2013. Review on Ecological Response to Hydromorphological Degradation and Restoration (No. Project Report REFORM D1.3).
Wolter, C., Buijse, A.D., Parasiewicz, P., 2016. Temporal and spatial patterns of fish response to hydromorphological processes. River Res. Appl. 32:190–201. https://doi.org/10.1002/rra.2980.
Zajicek, P., Wolter, C., 2018. The gain of additional sampling methods for the fish-based assessment of large rivers. Fish. Res. 197:15–24. https://doi.org/10.1016/j.fishres.2017.09.018.

Chapter three

The effects of recreational and commercial navigation on fish assemblages in large rivers

This chapter consists of the following publication:

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Authors' contributions:

PZ and CW developed the concept; PZ did the literature research; PZ developed the methods; PZ analyzed the data; PZ wrote the manuscript; PZ and CW revised the manuscript.

The appendix mentioned in this publication is provided in the appendix of this thesis.

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The effects of recreational and commercial navigation on fish assemblages in large rivers

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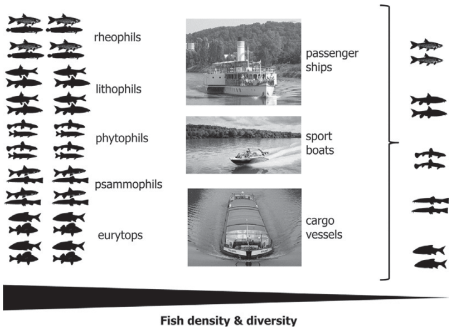
HIGHLIGHTS

- Ship traffic is pervasive in large rivers but ecological consequences are neglected.
- Habitat-sensitive fish, particularly lithophils suffer most from navigation traffic.
- Sport boats, passenger ships and cargo vessels distinctly affect fish assemblages.
- Navigation erodes bank habitats and ecological condition on top of river regulation.
- All motorized vessels impact river conservation and successful river rehabilitation.

GRAPHICAL ABSTRACT



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ABSTRACT

Recreational and commercial navigation is omnipresent, rendering European large rivers highways for cargo vessels, passenger ships and sport boats. Any types of motorized vessels create waves and drawdown eroding shallow shore areas. Consequently, inland navigation alters the living environment of fish with specific habitat requirements on nursing, hatching and spawning along shorelines. We assess the influence of recreational (sport boats) and commercial navigation (passenger ships, cargo vessels) on fish assemblages. Seven fish population metrics (FPM) were analyzed for 396 fish samplings at 88 sites in six large rivers characterized by seven different estimates of navigation intensity to identify FPM sensitive to inland navigation. Navigation intensity was characterized by frequency, total freight transported, total carrying capacity, degree of capacity utilization and by numbers of empty running vessels, aiming to approximate whether frequency, freight or draft of cargo vessels matter most. Densities of lithophilic fish were most sensitive to frequencies of sport boats, passenger ships and cargo vessels and declined as navigation traffic increased. Densities of rheophilic fish declined likewise but were less sensitive than lithophils. Frequency, freight and carrying capacity of cargo vessels had comparable effects on FPM and are equally useful in addition to frequency of sport boats and passenger ships to assess the impacts of recreational and commercial navigation on fish assemblages. Lower species richness indicated a specific influence of vessel draft on fish diversity. Our study shows that both recreational and commercial navigation impair fish assemblages in navigable rivers. Operation-related navigation impacts act on top of river regulation and engineering works to maintain fairways in the main channel. Therefore, impacts from recreational and commercial navigation must be especially addressed in addition to mitigating impacts from river regulation and hydromorphological degradation to achieve environmental objectives such as species conservation, ecological improvements and river rehabilitation.

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1. Introduction

European large rivers are extensively utilized as waterways for inland navigation: The European inland navigation network consists of 40,000 km of navigable waterways across 18 countries, a shipping fleet of 12,850 vessels, 45,000 employees, and transships 550 million tons (mt) of cargo each year (CCNR, 2016). Based on ton-kilometers, half of the European commercial navigation is located in Germany, with the largest flows between Germany, the Netherlands, France and Belgium (PINE, 2004). The River Rhine is the busiest river in the world (BVB, 2017), accounting for two third (i.e., 330 mt) of European cargo transport on inland waterways (CCNR, 2016). Concomitantly, Europe's biggest inland port Duisburg (transshipped 54 mt in the year 2015) is located at the River Rhine in Germany. Further, the River Rhine constitutes an integral North-South transport corridor across Europe, crossing Switzerland, Germany and the Netherlands (PINE, 2004). The most dense network of inland waterways is located in the Netherlands and Belgium, accounting for 40% and 20% of the countries transport performance, respectively (CCNR, 2016). Europe's biggest seaport Rotterdam, The Netherlands (450 mt cargo in 2014), is connected to the rivers Rhine, Lek and Meuse, followed by Antwerp (200 mt), Belgium, connected to the River Scheldt and Hamburg (150 mt), Germany, connected to the River Elbe (BVB, 2017). Hence, European large rivers are substantially utilized by commercial navigation.

The volume of goods transported by inland navigation was relatively stable during the last 20 years (CCNR, 2016). Despite a low modernization rate, the cargo fleet is characterized by increasingly higher powered vessels with higher carrying capacities, i.e., a higher total weight of new vessels (CCNR, 2016). Larger vessels have lower operating costs and outperform road and rail by a factor two to four in energy efficiency (Pauli, 2010). The transported goods shift from raw materials to container transport, chemical products and coal (CCNR, 2016), with the highest growth rates for container transport (PINE, 2004). Therefore, container transport by large cargo vessels is expected to increase in future. Recently, passenger navigation has started to grow likewise; for instance, the number of passenger ships (river cruises) has increased by 10% and the number of passengers (mainly international tourists) has increased by 17% from 1.13 million in 2014 to 1.33 million in 2015 (CCNR, 2016). Hence, river cruises is the fastest growing segment of inland navigation in Europe (Pauli, 2010). Consequently, the European Commission promotes inland navigation, particularly the transport of goods from the Sea ports to the hinterland to exploit the unused transportation potential of inland waterways (European Commission, 2011). Thereby, inland navigation traffic is generally perceived as being environmentally friendly. However, detrimental influences of navigation traffic on aquatic organisms (e.g., Gabel et al., 2017) and hence on the ecological quality of the riverine ecosystem remain rather unknown or neglected. Therefore, the influence of both recreational and commercial navigation requires attention in river management and further, awareness for potential ecological consequences needs to be raised.

Passing vessels transfer hydraulic forces into the water column, which affect the whole riverine ecosystem (Söhngen et al., 2008; Gabel et al., 2017), including juvenile fish (Huckstorf et al., 2011; Schludermann et al., 2013), macrophytes (Liddle and Scorgie, 1980) benthic organisms (Gabel et al., 2012; S. Lorenz et al., 2013) and morphodynamics along the shorelines (Zaggia et al., 2017). Vessel-induced waves, currents and drawdown disturb shoreline habitats (Liedermann et al., 2014), displace invertebrates (Lechner et al., 2014, 2016) and juvenile fish (Kucera-Hirzinger et al., 2008) and result in fish stranding (Adams et al., 1999; Nagrodski et al., 2012). Small and juvenile fish cannot sustain the higher flow velocities in the main channel and are therefore restricted to structured habitats along the shorelines. However, at the banks return currents and wake wash caused by passing vessels result in a habitat bottleneck for successful reproduction (Navigation-induced habitat-bottleneck hypothesis, NBH, Wolter et al., 2004). The NBH therefore predicts a decline in fish abundance as a consequence of inland navigation intensity. Shoreline erosion (Zaggia et al., 2017), alteration of sensitive habitats within the channel border area (Bhowmik et al., 1995) and dewatering significantly increase mortality of air exposed fish larvae (Holland, 1987). As a consequence, habitat-sensitive species with specific requirements on spawning substrates along shorelines lack spawning habitats in large rivers (Aarts et al., 2004; Aarts and Nienhuis, 2003). For instance, gravel and sand bars provide obligatory spawning and nursery habitats for lithophilic and psammophilic fish (A. W. Lorenz et al., 2013), but their potential use by fish is restricted. Shallow shore areas are heavily exposed to waves of passing vessels. For example, in the River Danube gravels bars in the main channel had the lowest abundances of lithophilic fish compared to groyne fields (Schludermann et al., 2013). Consequently, both lithophilic and psammophilic fish substantially declined in waterways (Wolter and Vilcinskas, 1997). Already a frequency of more than six passing vessels per day was observed altering density, spatial distribution and abundance of channel dwelling and juvenile fishes (Gutreuter et al., 2006; Huckstorf et al., 2011). Hence, hydraulic shoreline disturbance by passing vessels impoverishes juvenile fish assemblages of navigable waters (Huckstorf et al., 2011), which potentially propagates into the sub-adult and adult life stages.

Vessel shape, propulsion system and vessel draft result in distinct hydraulic forces (e.g., Kucera-Hirzinger et al., 2008; Söhngen et al., 2008). Different types of vessels are equipped with different propulsion systems (BAW, 2016; Söhngen et al., 2008), transferring variable hydraulic forces into the water column (Liedermann et al., 2014). Large vessels with deeper draft can have a higher kinetic energy than smaller vessels with lower draft at higher speeds (Pearson and Skalski, 2011). For instance, commercial barges >60 m length and loaded push tows in the River Rhine had the greatest influence on hydrodynamics and sand transport in groyne fields (Ten Brinke et al., 2004). A further consequence of passing vessels in the River Rhine were higher water level fluctuations and lower fish densities in groyne fields compared to littoral areas protected from navigation-induced hydrodynamics by a longitudinal dam (Collas et al., 2018). Hence, frequency, size and freight of commercial vessels potentially influence aquatic organisms. Both passenger ships and cargo vessels (bulk carriers, Liedermann et al., 2014) generate pronounced drawdown which is the most critical hydraulic force resulting in dewatering of banks (BAW, 2016; Mazumder et al., 1993). Passenger ships are larger and heavier than sport boats and thus have a deeper draft resulting in higher kinetic energy (Pearson and Skalski, 2011). Therefore, compared to sport boats, passenger ships create higher wake wash (Kucera-Hirzinger et al., 2008) and drawdown along shallow shore areas (Liedermann et al., 2014). Consequently, passenger ships might have a greater relevance than sport boats in affecting the fish assemblages of navigable waters, as long as both passenger ships and sport boats operate at comparable frequencies. However, sport boats often travel at very high speeds and in close proximity to the shoreline, ultimately generating powerfully propagating secondary waves (BAW, 2016; Söhngen et al., 2008), which strongly hit the littoral structures. Hence, sport boats may also have a significant influence on fish assemblages.

These hydraulic impacts of passing motorized boats are particularly pronounced, because extended complex littoral shelter structures are widely lacking due to the long history of river modification. After centuries of flood protection works cutting off floodplains by levees (e.g., Buck et al., 1993; Décamps et al., 1988), damming and river straightening was followed by river regulation (e.g., Bączyk et al., 2018; Buck et al., 1993; Raška et al., 2017), bank stabilization (Buck et al., 1993) and dredging (Haimann et al., 2018; Moog et al., 2018). Today, large rivers are so profoundly modified (e.g., Petts et al., 1989) that they resemble monotonous water channels (e.g., Diaz-Redondo et al., 2017), which are functionally decoupled from most of their floodplains (e.g., Strayer and Findlay, 2010). In addition, in the past also pollution was perceived as a key pressure (Meybeck and Helmer, 1989) and in many rivers an excess in nutrients is still relevant (Schinegger et al., 2016). Accordingly, large rivers are heavily modified and usually lack less disturbed stretches, which might serve as reference in ecological assessments (Birk et al., 2012; Melcher et al., 2007).

Furthermore, a previous analysis of the effects of multiple pressures on fish in large rivers revealed that inland navigation significantly contributed to faunal degradation on top of the pronounced impacts from hydromorphological pressures (Zajicek et al., 2018). While Zajicek et al. (2018) considered frequency of cargo vessels in three intensity classes only, this study aimed to in-depth analyze the specific factors of vessel operation (e.g., frequency, size, draft) that cause the most tremendous impacts on fishes. Hence, the objective of this study was to untangle the relation of inland navigation, both recreational and commercial, to fish assemblages in navigable large rivers. In contrast to most previous studies focusing on juvenile fishes, we assessed the adult and sub-adult fish assemblages. We compiled a comprehensive dataset on navigation intensities in major waterways of Germany and the Netherlands aiming to identify suitable navigation metrics to assess fish-based ecological responses. We differentiated between private recreational navigation (number of sport boats), commercial passenger ships and commercial freight traffic. Further, we assessed five different estimates of commercial freight traffic (e.g., number of cargo vessels, degree of capacity utilization of cargo vessels) to approximate whether both frequency and draft of cargo vessels are relevant. Finally, we analyzed the site-specific annual navigation metrics with seven fish population metrics derived from 396 representative fish samplings conducted at 88 sites in six large rivers. We hypothesized (1) that both recreational and commercial navigation contribute to impaired fish assemblages of large rivers, specifically to (2) lower densities of fish (guilds) with specific requirements on spawning and nursery habitats. Further, we assessed species richness and the Simpson Diversity Index as proxies for biodiversity although we rather expected stronger effects on guild densities than on biodiversity.

2. Methods

This study builds up on the compilation of two unique and comprehensive datasets of fish samplings and ship traffic across selected large rivers serving as waterways in Europe. First, we used a representative number of fish samplings (n = 396; sites = 88; rivers = 6) for the fish-based assessment of large rivers that we sub-sampled from an existing database consisting of 2693 fish samplings conducted at 358 sites located in 16 European large rivers (Large River Database, LRDB; described in Zajicek and Wolter, 2018). Second, we compiled a unique dataset on both recreational and commercial navigation intensities in the rivers that were representatively sampled for fish. Finally, we merged both datasets based on the year of sampling and the sampling site. The final dataset represented six large European rivers and a total of 1612 km waterways. Despite some differences in hydromorphological degradation, which was considered less severe in the rivers Oder and Elbe compared to the rivers Rhine, Lek, Meuse and Spree (compare Zajicek et al., 2018) all rivers are heavily regulated by groynes and the banks are protected mostly by rip rap.

2.1. Fish data and fish population metrics

Due to the heterogeneous nature of fish data in the LRDB, a strict standardization process (described in detail in Zajicek et al., 2018) was followed to select representative boat electrofishing samples for the fish assemblages of large rivers (Zajicek and Wolter, 2018). Electrofishing was shown best reflecting especially the littoral fish assemblage of large rivers (Zajicek and Wolter, 2018), where also the most pronounced effects of inland navigation were expected. In addition to the standardization procedure described in Zajicek et al. (2018), here we selected sites, which were sampled over a length of at least 400 m including also samplings conducted in Spring and Summer (seasonal variation was accounted for in statistical analyzes as explained further below). The resulting dataset consisted of 396 fish samplings conducted at 88 sites in six European large rivers between 1996 and 2010 (Fig. 1). 46.6% of all sites were sampled once, 47.7% were sampled >2 and <15 times and 5.7% were sampled between 16 and 32 times. The average distance between sampling sites, fished length and sampled area were 20.2 km ± 2.8 km (mean ± standard error), 1798.5 ± 72.6 m and 5549.4 ± 311.7 m^2, respectively. Consequently, selection of fish samples followed recommendations for representative assessments of running waters (e.g., Belletti et al., 2015; Dußling et al., 2004; Wolter et al., 2016; Zajicek and Wolter, 2018).

For each fish sample, we determined seven fish population metrics (FPM): densities of fish (standardized as densities per 100 m^2) belonging to the eurytopic (EURY) and rheophilic (RH) habitat guilds, to the lithophilic (LITH), phytophilic (PHYT) and psammophilic (PSAM) reproduction guilds as well as species richness (SPR) and the Simpson Diversity Index (SIM), as these FPM represent suitable bioindicators for the fish-based assessment of large rivers (Zajicek et al., 2018; Zajicek and Wolter, 2018). Specifically, eurytops tolerate a wide range of environmental conditions and have rather unspecific requirements on spawning substrates. High densities of eurytops are therefore considered indicators for an overall degraded state. In large rivers, eurytops can however also decrease in response to higher flow velocities and thereby indicate rhithralisation of the potamal river region. Rheophilic fish have a preference for faster flowing, well oxygenated waters. Lithophils, phytophils and psammophils require specific substrates for spawning and nursery, i.e., gravel (lithophils), aquatic vegetation (phytophils), and sand (psammophils). Fish of the latter three guilds particularly depend on shallow littoral areas for reproduction.

2.2. Navigation metrics

The selected 88 fish sampling sites were located between altogether 22 ship locks and one location without commercial freight traffic (referred to as "lock Linne"). For each ship lock, data on navigation intensities were provided by the Water and Navigation Authority (wsv.de) in Germany and by the Ministry of Infrastructure and the Environment (rijkswaterstaat.nl) in The Netherlands. These vessel statistics were used to calculate the navigation metrics described below. Subsequently, the lock-specific navigation metrics were assigned to all sampling sites in the influence of a given ship lock assuming that vessels which had passed the lock had also passed the fish sampling sites in the waterway serving it (compare Fig. 1). Number (NCV), freight (FCV, in metric tons) and carrying capacity (CCV, in metric tons) of cargo vessels, number of empty running (NERV) and the degree of capacity utilization (DCU) of cargo vessels were used as proxies for the intensity of commercial cargo navigation. Very few data were available on transport efficiency (relation of FCV to CCV referring to only loaded cargo vessels; partially available for rivers Havel [efficiency = 65%, n = 2], Oder [66%, n = 12] and Elbe [74%, n = 4]). Therefore, we determined the degree of capacity utilization (DCU = FCV/CCV) including empty running vessels as an estimate for the efficiency of commercial cargo navigation. Hence, high DCU serve as proxies for a high load with freight in relation to vessel size and accordingly for high draft of cargo vessels. Numbers of sport boats (NSB) served as proxies for the intensity of private recreational navigation and numbers of passenger ships (NPS) served as proxies for commercial touristic navigation. Passenger ships comprised passenger ships, passenger liners and river cruisers, i.e., vessels for touristic transportation that are usually longer than 30 m. Sport boats comprised all other small motorized boats presumably used for private recreation that are usually <15 m long. Cargo vessels embraced all types of motorized, pushing and towing vessels used to transport any type of goods. NSB, NPS, NCV, FCV, CCV and NERV were either available per year or cumulatively summed up per year (if resolution was higher) for each ship lock. Each navigation metric determined at a given ship lock for a given

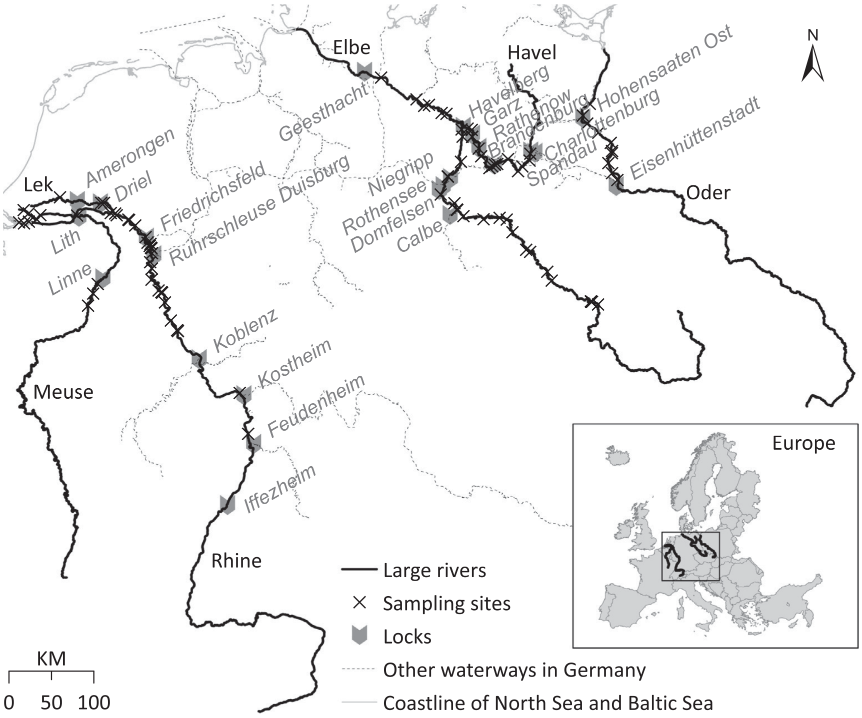

Fig. 1. Location of sampling sites and ship locks. Flow direction of all rivers is North; river Havel flows into river Elbe; river Rhine splits into rivers Lek and Waal in the Netherlands, the latter is the main branch and therefore referred to as river Rhine. Sampling sites in the river Meuse located South of lock Linne were assigned "zero" commercial navigation and unknown recreational navigation as lock Linne refers to the navigable Julianakanaal running parallel to the not-navigable river Meuse where the fish sampling sites are located.

year was assigned to all fish samplings conducted in this year at sampling sites located in the river reach covered by the ship lock.

The River Rhine has only one ship lock (Iffezheim). However, downstream of lock "Iffezheim", further ship locks are located in major tributaries just before their confluence into the River Rhine (Fig. 1). Ships passing these "confluence locks" were cumulatively summed up and added to the navigation metrics of the upstream lock (e.g., navigation metrics of the first lock downstream of Iffezheim, lock Feudenheim in the River Neckar, were added to the navigation metrics of lock Iffezheim and the navigation metrics of the next lock further downstream were added to Iffezheim + Feudenheim). This procedure was applied accordingly for all rivers with major tributaries that serve as waterways and navigation metrics were either summed up or subtracted, depending on major navigation routes and on geographic locations of confluence locks. In very few cases, navigation metrics were not available for all years in which fish samplings were conducted. In such cases, navigation metrics were estimated based on available data from previous years.

2.3. Discharge and wetted width

Discharge [m^3/s] and wetted width [m] were included as covariates in statistical modeling to account for hydrological conditions in and the size of the rivers studied (Fig. A.3, appendix). Discharge was monitored by the Water and Navigation Authority [wsv.de] in Germany and provided by the Federal Institute of Hydrology (BfG) as well as from the Ministry of Infrastructure and the Environment [rijkswaterstaat.nl] in The Netherlands. Discharge was assigned to sampling sites comparably as described for navigation metrics based on water gauge stations representative for the sampling sites. Wetted width was provided alongside with the fish samplings. Fairway depth does not vary much within a waterway and is maintained rather constant as minimum guaranteed depth and vessels usually try to travel with the maximum allowed draft.

2.4. Data analyzes and statistics

Due to variations in data availability, four data sets (ds) on navigation metrics had to be created: ds1) all seven navigation metrics including numbers of sport boats (NSB), which were only available for rivers Havel, Elbe and Oder, ds2) all navigation metrics except NSB but including numbers of passenger ships and of empty running cargo vessels, which were available for rivers Havel, Elbe, Oder and Rhine, ds3) four cargo navigation metrics including the degree of capacity utilization, which were available for Havel, Elbe, Oder, Rhine and the navigable River Meuse, and ds4) comprising the three metrics number, freight and carrying capacity of cargo vessels, which were available for all rivers and sites. Note that ds4 is the only dataset containing three sites free of commercial cargo navigation in the river Meuse which were sampled 22 times. These four datasets (Table 1) were analyzed separately. The primary intention to create four datasets was to analyze the effects of inland navigation and the different navigation metrics based on the largest available sample size at the given level of reporting detail. However, in all four datasets, we statistically assessed the effect of all navigation metrics on each fish population metric, because this procedure offered the opportunity to comparatively untangle the observed effects of recreational and commercial navigation in greater detail across the studied rivers.

The statistical effects of all navigation metrics on each fish population metric were assessed in separate mixed effects models (MEM). Separate models were required due to the inevitably correlated structure of the assessed navigation metrics that prevented the use of a global model including all predictors at once. MEM allow to taking into account random effects and are robust to non-normally distributed

Table 1
Datasets and navigation metrics, rivers and number (n) of fish samplings included in each dataset analyzed. Bold font highlights navigation metrics that were in focus of analyzes in the respective dataset as described in the methods part. NSB = number of sport boats; NPS = number of passenger ships; NCV, FCV, CCV, NERV and DCU = number, freight, carrying capacity of cargo vessels, number of empty running cargo vessels and degree of capacity utilization of cargo vessels, respectively. *ds3 includes four of the seven available sampling sites in the river Meuse; the remaining three sites in river Meuse (sampled 22 times altogether) are the only ones without commercial navigation traffic in the whole dataset and are included in ds4.

Dataset	Available navigation metrics	Rivers included in the dataset	Fish samplings (n)
ds1	**NSB**, NPS, NERV, DCU, NCV, FCV, CCV	Elbe, Havel, Oder	200
ds2	**NPS**, **NERV**, DCU, NCV, FCV, CCV	Rhine, Elbe, Havel, Oder	276
ds3	**DCU**, NCV, FCV, CCV	Rhine, Lek, (Meuse*), Elbe, Havel, Oder	365
ds4	**NCV**, **FCV**, **CCV**	Rhine, Lek, Meuse, Elbe, Havel, Oder	396

data (Zuur et al., 2009). To meet model assumptions (Zuur et al., 2010) and to improve distributional patterns, all FPM referring to guild densities and all navigation metrics were log(x + 1) transformed, discharge and wetted width were log transformed and the Simpson Index was arcsine-exponential transformed. Residual plots were inspected for normality and heteroscedasticity. Model assumptions were violated in all models fitting navigation metrics on densities of fish in the phytophilic and psammophilic guilds. We therefore refrained from statistically analyzing the latter two FPM but we provide the descriptive results. All MEM included mean annual discharge and wetted width as covariates. Season nested in year and site nested in river were both included as random effects in each MEM to account for repeated measurements in time and space. Marginal R^2 and conditional R^2 were determined for each MEM to estimate model quality (Mac Nally et al., 2017). Marginal R^2 indicates the amount of variation explained by only fixed effects whereas conditional R^2 indicates the amount of variation explained by the fixed and random effects (Nakagawa and Schielzeth, 2013). Random effects were predefined by the data structure but their contribution to the performance of each model's fit was validated by inspecting the Akaike Information Criterion (AIC, Akaike, 1981) according to Burnham and Anderson (2004) in all models in pre-runs including all plausible combinations of the four random effects.

Data were analyzed in R 3.3.3 (R Development Core Team, 2017). 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. 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 *ggplot* in the R package *ggplot2* (version 2.2.1; Wickham, 2016). Fig. 1 was drawn using ArcMap, version 10.5.1.

3. Results

3.1. Catch composition

A total of 229,666 fish (including lampreys, referred to as fish in the following) of 55 species were captured in 369 samplings at 88 sites in 6 large rivers. The most abundant species were *Rutilus rutilus*, *Perca fluviatilis* and *Alburnus alburnus* accounting for 29%, 16% and 11% of the total catch, respectively. The most frequently occurring species were *Rutilus rutilus*, *Perca fluviatilis* and *Leuciscus idus* captured at 99%, 97% and 94% of all sites, respectively. Altogether, 17 fish species were captured in all six rivers (Appendix A, Table A.1 contains detailed catch statistics). Eurytopic (EURY) and rheophilic (RH) fish comprised 70.3% and 29.2%, and lithophilic (LITH), phytophilic (PHYT) and psammophilic (PSAM) fish comprised 9.6%, 5.7% and 5.6% of the total catch, respectively. EURY and RH were captured at all sites, LITH, PHYT and PSAM were captured at 95%, 90% and 77% of all sites, respectively (Appendix A, Table A.2 contains detailed guild compositions). EURY and RH occurred in all (RH = 99.7%) samplings, LITH, PHYT and PSAM in 94%, 84% and 62% of all samplings, respectively.

Across the rivers studied, average densities of EURY, RH, LITH, PHYT and PSAM fish were 20.37 ± 6.89 (mean ± SE of river-specific means), 4.11 ± 1.25, 0.94 ± 0.26, 1.23 ± 0.53 and 0.47 ± 0.20 fish per 100 m², respectively; species richness and Simpson Index were 12.95 ± 1.12 and 0.68 ± 0.04. The River Rhine had the lowest densities of eurytops, rheophils, phytophils and psammophils as well as below average densities of lithophils and below average species richness within the rivers studied (Fig. 2). The River Lek had below average densities of fish in all reproduction guilds as well as below average species richness and Simpson Index. The River Havel had the lowest densities of lithophils and the highest densities of eurytops. The River Oder had above average densities of rheophils, lithophils, phytophils and psammophils and above average species richness.

3.2. Effects of navigation

Relevant output of all linear mixed effects models revealing significant ($p < 0.05$) fixed effects (and trends referred to as $0.05 < p < 0.1$) as described in the following subchapters is summarized in Table 2 and further details are provided in Table 3. Densities of phytophils and psammophils were not statistically analyzed (due to their low occurrence in samples) whereas the Simpson Diversity Index was not significantly affected by any of the navigation variables.

3.2.1. Effects of private recreational navigation

Annual average number of sport boats (NSB) ranged from 494 in the River Oder to 9430 in the River Elbe (Fig. 3; note: for the River Rhine were no sport boats data available), corresponding to an average vessel passage of 1–26 sport boats per day. The NSB was significantly inversely correlated with densities of eurytopic (R^2_{cond}: 0.86; R^2_{mar}: 0.10) and lithophilic (0.85; 0.18) fish (Fig. 4).

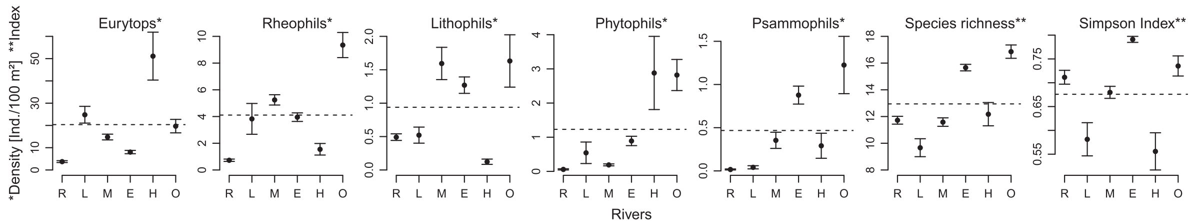

Fig. 2. River-specific estimates of fish population metrics (FPM). R = Rhine (number of samplings: 145); L = Lek (27); M = Meuse (89); E = Elbe (145); H = Havel (17); O = Oder (42). Means ± standard errors are shown, dashed lines indicate the averages of within-river sample-means. Note: y-axes [Ind. = Individuals] are differently scaled; Fig. A.1 (Appendix A) provides a site-specific overview.

Table 2
Direction (↘ = lower; ↗ = higher) of significant effects of navigation metrics (NSB = number of sport boats; NPS = number of passenger ships; NCV, FCV, CCV, NERV and DCU = number, freight, carrying capacity of cargo vessels, number of empty running cargo vessels and degree of capacity utilization of cargo vessels, respectively) on fish population metrics (FPM); "na" = navigation data not available. * includes a significantly positive effect of wetted width; ** includes a significantly negative effect of discharge; *** includes a significantly negative effect of wetted width; # trend referring to a p-value < 0.1. Note: PHYT and PSAM were not assessed statistically whereas the Simpson Index is not shown as there was no significant relation to navigation metrics, also not by trend.

Dataset	FPM	NSB	NPS	NERV	DCU	NCV	FCV	CCV
ds1	EURY	↘	↘	↗		↗		↗
ds1	RH		↘		(↘)#			
ds1	LITH	↘	↘					
ds1	SPR				(↘)#			
ds2	EURY	na	↘	↗		↗		↗
ds2	RH	na	↘		(↘)#			
ds2	LITH	na	↘					
ds2	SPR	na	(↘)#		(↘)#/***			
ds3	EURY	na	na	na		↗	↗	↗
ds3	RH	na	na	na				
ds3	LITH	na	na	na				
ds3	SPR	na	na	na	↘			
ds4	EURY	na	na	na	na			
ds4	RH	na	na	na	na	↘*	↘*	↘*
ds4	LITH	na	na	na	na	↘**	↘**	↘**
ds4	SPR	na	na	na	na			

3.2.2. Effects of commercial touristic navigation

Annual average number of passenger ships (NPS) ranged from 242 in the River Oder to 3578 in the River Rhine, corresponding to an average vessel passage of 1–10 passenger ships per day. The NPS was significantly inversely correlated with densities of eurytopic (R^2_{cond}: 0.86; R^2_{mar}: 0.08), rheophilic (0.70; 0.05) and lithophilic (0.85; 0.15) fish and by trend ($p < 0.1$) with species richness (Fig. 4). NPS was likewise significantly inversely correlated with densities of eurytops, rheophils and lithophils when using dataset ds1.

3.2.3. Effects of commercial freight traffic

3.2.3.1. Number (NCV), freight (FCV) and carrying capacity (CCV) of cargo vessels. Annual average NCV ranged from 5395 in the River Oder to 96,341 in the River Rhine, corresponding to an average vessel passage of 15–264 passenger ships per day. FCV and CCV were accordingly lowest in the River Oder (658,135 t and 1,921,552 t corresponding to 1803 t and 5265 t per day) and highest in the River Rhine (84,337,462 t and 149,291,544 t, corresponding to 231,062 t and 409,018 t per day). NCV, FCV, and CCV were all significantly inversely correlated with densities of lithophilic ([ranges] R^2_{cond}: 0.85–0.86; R^2_{mar}: 0.22–0.23) and rheophilic (0.63–0.64; 0.07–0.08) fish (Fig. 5). In addition, densities of rheophils were significantly correlated to wetted width whereas lithophils were significantly inversely correlated to discharge. Only when using datasets ds3 (NCV, FCV, and CCV), ds2 (NCV) and ds1 (NCV, CCV), increased commercial navigation was significantly correlated to higher densities of eurytopic fish.

3.2.3.2. Number of empty running cargo vessels (NERV). Annual average NERV ranged from 1390 in the River Havel to 28,250 in the River Rhine, corresponding to an average vessel passage of 4–77 empty

Table 3
Parameters of significant fixed effects (and those with a p-value < 0.01, referred to as "trend") in linear mixed effects models. Responses = fish population metrics (EURY, RH and LITH = densities eurytopic, rheophilic and lithophilic fish, respectively; SPR = species richness; SIM = Simpson Diversity Index), Predictors = navigation metrics (NSB = number of sport boats; NPS = number of passenger ships; NCV, FCV, CCV, NERV and DCU = number, freight, carrying capacity of cargo vessels, number of empty running cargo vessels and degree of capacity utilization of cargo vessels, respectively; DIS = discharge and WW = wetted width).

Model	Dataset	Response	Predictor	Intercept (±SE)	Slope (±SE)	Df	T value	p value	$R^2_{[mar]}$	$R^2_{[cond]}$
S1	ds1	EURY	NSB	0.53 (1.98)	−0.31 (0.14)	45	−2.26	0.028	0.10	0.86
S2	ds1	EURY	NPS	−0.87 (1.61)	−0.18 (0.05)	60	−3.52	<0.001	0.08	0.84
S3	ds1	EURY	NCV	−1.85 (1.73)	0.22 (0.10)	90	2.21	0.029	0.07	0.83
S4	ds1	EURY	CCV	−3.26 (1.86)	0.25 (0.10)	91	2.41	0.018	0.07	0.83
S5	ds1	EURY	NERV	−1.03 (1.63)	0.29 (0.10)	90	3.01	0.003	0.07	0.80
S6	ds1	RH	NPS	1.3 (1.11)	−0.11 (0.04)	106	−2.66	0.009	0.04	0.65
S7	ds1	RH	DCU	1.03 (1.13)	−0.79 (0.41)	59	−1.90	0.063	0.05	0.60
S8	ds1	LITH	NSB	4.03 (1.11)	−0.26 (0.08)	53	−3.29	0.002	0.18	0.85
S9	ds1	LITH	NPS	2.64 (0.99)	−0.08 (0.03)	118	−2.40	0.018	0.06	0.84
S10	ds1	SPR	DCU	24.72 (5.59)	−3.96 (1.98)	44	−2.00	0.052	0.03	0.61
S11	ds2	EURY	NPS	−0.91 (1.54)	−0.20 (0.05)	113	−4.04	<0.001	0.08	0.86
S12	ds2	EURY	NCV	−2.30 (1.71)	0.19 (0.09)	109	2.11	0.037	0.09	0.90
S13	ds2	EURY	CCV	−3.57 (1.86)	0.21 (0.09)	114	2.23	0.028	0.10	0.91
S 14	ds2	EURY	NERV	−1.80 (1.67)	0.28 (0.08)	156	3.45	<0.001	0.10	0.90
S15	ds2	RH	NPS	1.55 (0.96)	−0.11 (0.03)	162	−3.12	0.002	0.05	0.70
S16	ds2	RH	DCU	1.3 (1.01)	−0.62 (0.38)	161	−1.66	0.099	0.02	0.72
S17	ds2	LITH	NPS	2.82 (0.85)	−0.08 (0.03)	187	−2.90	0.004	0.15	0.85
S18	ds2	SPR	NPS	27.43 (5.29)	−0.33 (0.19)	148	−1.74	0.083	0.07	0.70
			WW		−2.53 (0.96)	52	−2.63	0.011		
S19	ds2	SPR	DCU	26.9 (5.14)	−3.23 (1.86)	83	−1.73	0.087	0.05	0.64
			WW		−2.29 (0.96)	54	−2.38	0.021		
S20	ds3	EURY	NCV	0.23 (1.17)	0.24 (0.08)	143	3.06	0.003	0.05	0.74
S21	ds3	EURY	FCV	0.04 (1.30)	0.17 (0.07)	155	2.44	0.016	0.05	0.74
S22	ds3	EURY	CCV	−1.32 (1.45)	0.25 (0.08)	138	3.08	0.003	0.06	0.77
S23	ds3	SPR	DCU	21.05 (3.59)	−4.58 (1.27)	33	−3.60	0.001	0.28	0.62
S24	ds4	RH	NCV	1.24 (0.58)	−0.06 (0.03)	77	−2.24	0.028	0.07	0.64
			WW		0.24 (0.10)	77	2.41	0.018		
S25	ds4	RH	FCV	1.17 (0.57)	−0.05 (0.02)	70	−2.80	0.007	0.08	0.63
			WW		0.27 (0.10)	75	2.76	0.007		
S26	ds4	RH	CCV	1.23 (0.57)	−0.04 (0.02)	70	−2.71	0.008	0.08	0.64
			WW		0.27 (0.10)	76	2.71	0.008		
S27	ds4	LITH	NCV	2.92 (0.53)	−0.08 (0.02)	87	−3.39	0.001	0.22	0.86
			DIS		−0.34 (0.10)	136	−3.47	<0.001		
S28	ds4	LITH	FCV	2.83 (0.52)	−0.05 (0.01)	79	−3.66	<0.001	0.23	0.85
			DIS		−0.32 (0.10)	126	−3.35	0.001		
S29	ds4	LITH	CCV	2.90 (0.52)	−0.05 (0.01)	81	−3.43	<0.001	0.22	0.85
			DIS		−0.33 (0.10)	130	−3.41	<0.001		

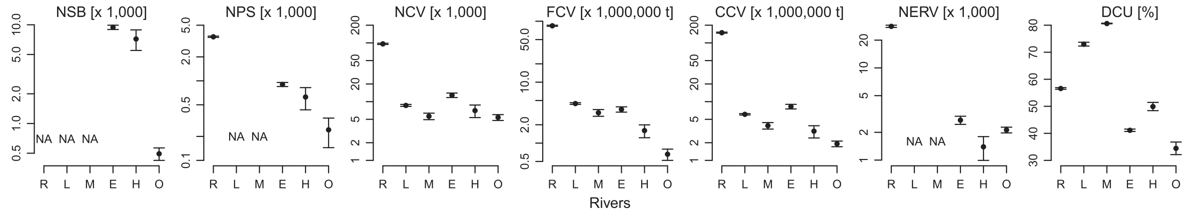

Fig. 3. River-specific estimates of navigation metrics. NSB = Number of sport boats; NPS = Number of passenger ships; NCV = Number of cargo vessels; FCV = Freight of cargo vessels; CCV = Carrying capacity of cargo vessels; NERV = Number of empty running cargo vessels; DCU = Degree of capacity utilization. Rivers: R = Rhine (n: for NPS: 13, for all others: 27); L = Lek (7); M = Meuse (5); E = Elbe (32); H = Havel (8); O = Oder (14). Means ± standard errors are shown. Note: y-axes are on different log-scales (despite DCU-graph); Fig. A.2 (appendix) provides a site-specific overview.

running cargo vessels per day. Higher NERV was significantly correlated with higher densities of eurytopic fish (R^2_{cond}: 0.90; R^2_{mar}: 0.10, Fig. A.4, Appendix A), also when using ds1.

3.2.3.3. Degree of capacity utilization of cargo vessels (DCU). Annual average DCU ranged from 29% in the River Oder to 81% in the River Meuse. DCU was significantly inversely correlated to species richness (R^2_{cond}: 0.62; R^2_{mar}: 0.28; Fig. 6), but positively to densities of eurytopic fish (the latter only by using dataset ds2). A trend ($p < 0.1$) towards lower densities of rheophilic fish with higher DCU was indicated in the datasets ds2 and ds1.

4. Discussion

This study aimed to assess the influence of common modes of navigation traffic on fish assemblages in large rivers. Our study shows that both recreational and commercial navigation negatively alter densities of both habitat-sensitive and habitat-insensitive fish. Several responses of fish population metrics were identified to private recreational navigation (sport boats), commercial touristic navigation (river cruises) and commercial freight transport (cargo vessels). Thereby, lithophilic fish were distinctly affected by all modes of navigation and declined in response to high vessel frequencies, which is well in line with Schludermann et al. (2013), who attributed juvenile lithophilic fish as most sensitive to shoreline disturbance caused by wakes of passing vessels. A variable response of lithophils, rheophils and eurytops to frequency, freight and carrying capacity of cargo vessels when considering sites with and without cargo traffic indicated that navigation traffic adds on top of the influence of river regulation. The degree of capacity utilization of cargo vessels was inversely correlated to species richness, indicating a distinct influence of fully loaded cargo vessels with higher draft, blockage ratio and physical forces induced during passage (Söhngen et al., 2008). Hence, our study demonstrates how the power of vessel-induced waves and drawdown (Bhowmik et al., 1995; Mazumder et al., 1993) affects entire fish assemblages. Moreover, this is the first study that analyzed the impacts of inland navigation on fishes by using different estimates of navigation intensities across a substantial number of fish samplings and sites in major European rivers. It comparatively and quantitatively substantiates the commonly unseen ecological drawbacks of inland navigation. Further, it fortifies that both recreational and commercial navigation impact on the ecological status of large rivers in addition to the prevailing hydromorphological degradations of the river channel substantiating previous findings of Zajicek et al. (2018).

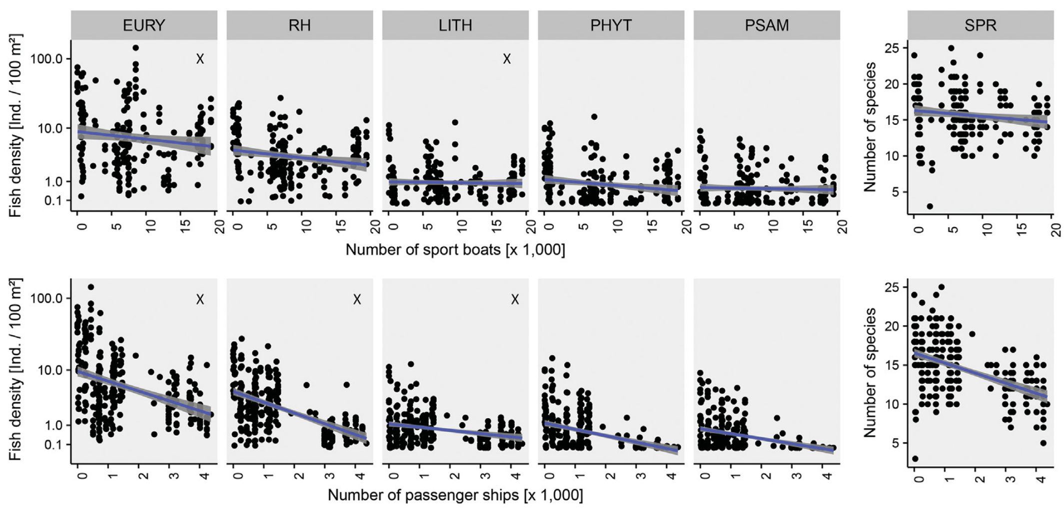

Fig. 4. Response of fish population metrics (EURY = eurytopic guild, RH = rheophilic guild, LITH = lithophilic guild, PHYT = phytophilic guild, PSAM = psammophilic guild; SPR = species richness) to recreational navigation (number of sport boats refers to ds1 and includes rivers Elbe, Havel and Oder; number of passenger ships refers to ds2 and includes additionally river Rhine). Raw data are shown and a linear smoother line (blue) with standard errors (grey) is included for visualization. "X" denotes significant ($p < 0.05$) effects of the respective navigation metric on the respective fish population metric (note: y-axes [Ind. = Individuals] representing guild densities are log-scaled; PHYT and PSAM were not assessed statistically whereas the Simpson Index is not shown as there was no significant [$p > 0.05$] relation to navigation metrics, also not by trend [$p > 0.1$]). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

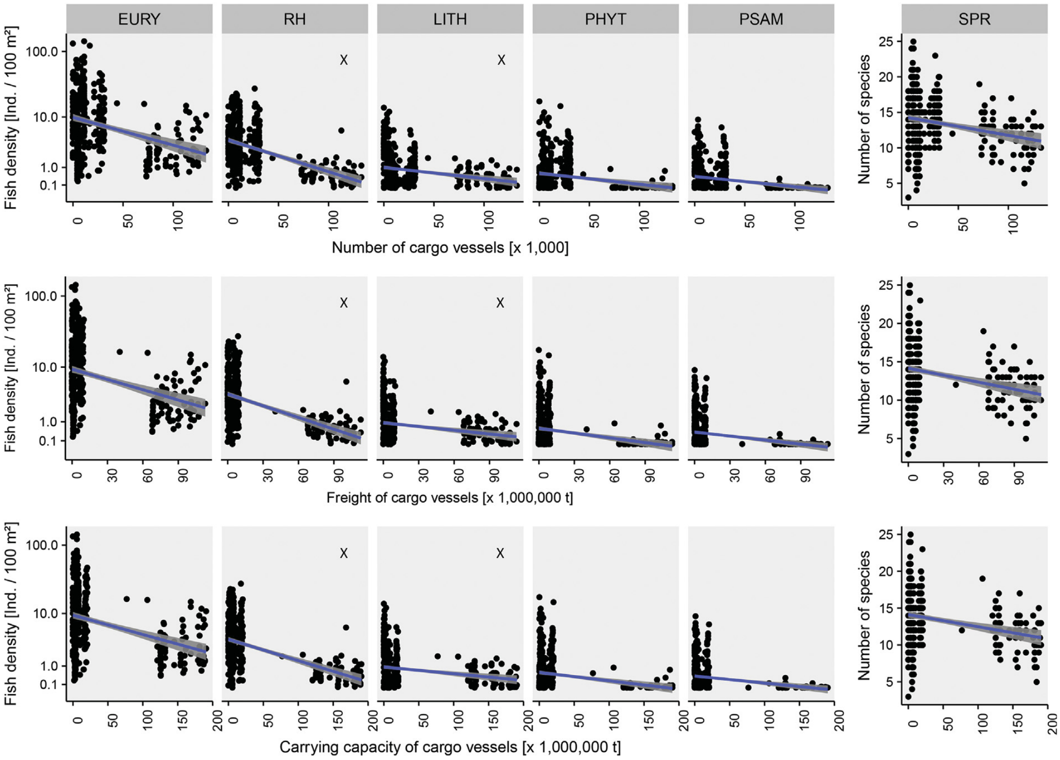

Fig. 5. Response of fish population metrics (EURY = eurytopic guild, RH = rheophilic guild, LITH = lithophilic guild, PHYT = phytophilic guild, PSAM = psammophilic guild; SPR = species richness) to commercial navigation (referring to ds4, the full dataset comprising all sampling sites in all six rivers [Elbe, Havel, Oder, Rhine, Lek, Meuse]). Raw data are shown and a linear smoother line (blue) with standard errors (grey) is included for visualization. "X" denotes significant ($p < 0.05$) effects of the respective navigation metric on the respective fish population metric (note: y-axes [Ind. = Individuals] representing guild densities are log-scaled; PHYT and PSAM were not assessed statistically whereas the Simpson Index is not shown as there was no significant [$p > 0.05$] relation to navigation metrics, also not by trend [$p > 0.1$]). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1. Limitations of this study

We assessed a unique compilation of field data on fish samplings and on navigation traffic as they occur across six European large rivers. Hence, all assessed rivers are used as waterways by both recreational and commercial navigation. For some rivers, we did not have data on the numbers of sport boats and on numbers of passenger ships. Therefore, each navigation metric was assessed using separate models and estimates of model quality were provided as indicators for the relevance of each predictor considered. In addition, navigation metrics were stepwise excluded in four different datasets to untangle the influence of the different navigation metrics that were available only within the respective dataset, also allowing for consideration of a rising number of rivers and sites and hence greater sample sizes.

Commercial cargo and passenger navigation and recreational sport boats share the same navigable waters. Therefore, reference conditions without the one or the other mode of navigation barely exist. The commercial cargo fleet runs much larger and more powerful vessels and

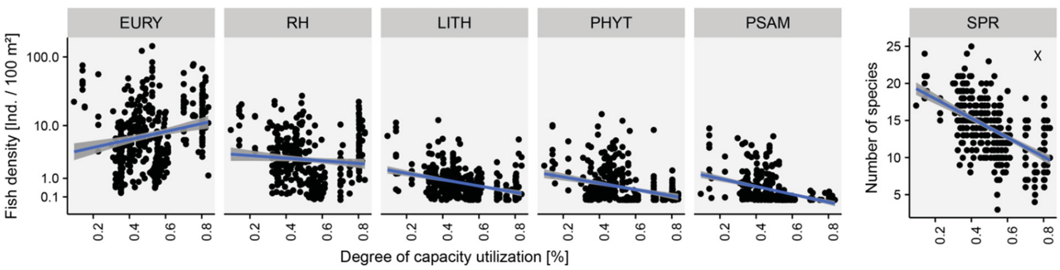

Fig. 6. Response of fish population metrics (EURY = eurytopic guild, RH = rheophilic guild, LITH = lithophilic guild, PHYT = phytophilic guild, PSAM = psammophilic guild; SPR = species richness) to the degree of capacity utilization of loaded cargo vessels. This figure refers to ds3 and includes the rivers Havel, Oder, Elbe, Rhine, Lek and sites located in the navigable river Meuse. Raw data are shown and a linear smoother line (blue) with standard errors (grey) is included for visualization. "X" denotes significant ($p < 0.05$) effects. Note: y-axes [Ind. = Individuals] representing guild densities are log-scaled; PHYT and PSAM were not assessed statistically whereas the Simpson Index is not shown as there was no significant [$p > 0.05$] relation to navigation metrics, also not by trend [$p > 0.1$]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

thus typically generates higher hydraulic forces dominating the impact on aquatic communities in the littoral (e.g., Arlinghaus et al., 2002). However, passenger ships and recreational sport boats typically create higher secondary waves and thus, induce higher wake wash (Söhngen et al., 2008). We applied a stepwise analytical and comparative approach, which allowed us to identify a distinct influence of recreational and commercial navigation on fish assemblages in large rivers. For instance, densities of eurytopic fish declined in response to sport boats and passenger ships whereas they increased in response to cargo vessels using dataset ds1. Likewise, densities of lithophils declined in response to sport boats and passenger ships whereas no significant effect was observed in response to cargo vessels using dataset ds1. Hence, although we encounter the above outlined limitations, we could show distinct responses of some fish population metrics in the rivers studied.

4.2. Indicative navigation metrics

Frequency of passenger ships affected most of the studied fish population metrics showing the specific and strong influence of commercial river cruises on fish assemblages. Therefore, frequency of passenger vessels constitutes a highly efficient navigation metric to study navigation-driven consequences of commercial water tourism on fish. Given that an average of one to ten passenger ships per day across the rivers studied resulted in a strong response in the fish assemblage, an expected increase in water tourism could seriously negate efforts to increase ecological quality in European running waters.

Frequency, freight and carrying capacity of commercial cargo traffic affected most habitat-sensitive fish guilds but had rather similar estimates of model quality within identical guilds. Therefore, all of the latter three estimates for cargo traffic appear equally suitable to study navigation-driven consequences of cargo transport on fish. Future studies might accordingly select whether to assess frequency, freight or carrying capacity of cargo vessels, depending on availability or accessibility of the estimates. Further, average frequencies of freight transporters corresponded at least to 15 vessels per day within the rivers studied, which is well beyond the threshold of six to eight passing cargo vessels impoverishing juvenile fish assemblages (Gutreuter et al., 2006; Huckstorf et al., 2011). Hence, low ecological effect levels of commercial freight transport were clearly exceeded in the studied rivers. Therefore, commercial navigation requires specific management consideration to improve ecological status of economically relevant waterways.

The degree of capacity utilization of cargo vessels (DCU) had a distinct influence on the fish assemblage by affecting species richness. A higher DCU corresponds to more efficiently loaded vessels and hence to a higher draft resulting in higher physical forces during vessel passage (Söhngen et al., 2008). Hence, the DCU provides an additional useful estimate of commercial cargo navigation to reveal diversity-related responses of the fish assemblage. Further, enhancement of the river cross-sections to allow for higher vessel drafts might require additional measures mitigating increased hydraulic forces to maintain fish faunal diversity.

The number of empty running cargo vessels (NERV) showed a similar trend as number and carrying capacity of cargo vessels using datasets ds1 and ds2. We therefore expect similar effects of empty running vessels as were shown for the frequency of all cargo vessels (including loaded vessels). However, due to limited availability of data, empty running vessels might not be a suitable navigation metric for future studies.

The number of sport boats had a distinct influence on the habitat sensitive lithophils and the habitat-insensitive eurytops compared to all estimates of commercial cargo traffic in the same rivers. Hence, frequency of sport boats constitutes an important metric to study consequences of private recreational motorboats on fish. Moreover, across the rivers studied, the average frequency of sport boats corresponded to one to 26 passing boats per day, which impacted even on densities of habitat generalists. The latter findings clearly indicate that in economically less important waterways, private recreational motorized vessels could substitute or even outcompete commercial freight traffic, not only in numbers but more importantly, in ecological consequences. This finding is highly relevant in regard to the envisioned improvement of recreational uses of the commercially less important waterways. For example, in Germany the waterway network has been recently divided into three classes according to their average traffic volume, i.e., to their commercial importance. Minor waterways with low traffic volume are considered candidates for the Federal initiative "The Blue Band" (http://www.blaues-band.bund.de, 2018). This initiative aims at enhancing the ecological status of waterways and the improvement of water-bound recreation and water tourism at the same time. According to our results, this approach has a high potential for failure, because improving recreational navigation to a certain degree contradicts ecological rehabilitation. Both commercial touristic vessels and recreational boats impact on littoral aquatic communities comparably to commercial freight traffic, in particular due to the significant wake wash induced at the banks. However, more research is needed on the ecological effects of recreational sport boats and touristic passenger cruises as well as on their successful mitigation. Hence, detailed research and monitoring using the outlined navigation metrics in this study should provide appropriate advice on mitigation measures (e.g., Weber and Wolter, 2017) so that ecological quality and recreational utility could go hand in hand.

4.3. Indicative fish population metrics

Densities of lithophilic and rheophilic fish declined in response to number of passenger ships and cargo traffic (number, freight and carrying capacity of cargo vessels). Lithophils additionally declined in response to number of sport boats. Further, lithophils were most affected out of all five statistically tested fish population metrics as indicated by model quality. Correspondingly, Zajicek et al. (2018) identified lithophils as most sensitive to disturbance of shoreline habitats and Schludermann et al. (2013) attributed lowest densities of juvenile lithophils to ship-induced waves. Consequently, the density of lithophilic fish constitutes the most sensitive fish population metric responding to disturbance by passing motorized vessels, ships and boats.

Densities of both rheophilic and lithophilic fish declined in relation to increasing traffic by commercial navigation (number, freight and carrying capacity of cargo vessels) whereas densities of eurytopic fish increased. The decline of rheophils and lithophils was only significant when the full dataset also including sites free of commercial cargo traffic was analyzed whereas significance in the increase of eurytops then vanished. These findings clearly indicate two causalities for the impacts of inland navigation on fishes. First, rivers had been modified by engineering works, which resulted in river regulation (high densities of eurytops). Secondly, inland navigation results in physical forces induced by moving vessels (reduced densities of rheophils), which were in depth analyzed here, and that add on top of the construction related impact. Therefore, inland navigation had a substantial lowering effect on densities of rheophils and lithophils in addition to river-engineering related alterations of the river channel that a priori caused high densities of eurytops. Hence, commercial navigation is an important driver downgrading the ecological status of navigable large rivers in addition to river engineering to facilitate inland navigation.

We could not test the influence of navigation traffic on densities of phytophilic and psammophilic fish due to their low occurrence in samples. However, phytophils and psammophils have been shown to be most sensitive besides lithophils to disturbance of shoreline habitats (Zajicek et al., 2018). Therefore, we expect that densities of phytophils and psammophils are comparably affected by sport boats, passenger ships and cargo vessels as was shown for lithophils in this study.

4.4. New opportunities and challenges for river management and research

This study found that any mode of motorized ship traffic impairs ecological quality using functional and taxonomic traits of fish assemblages in large rivers. Moreover, this navigation-induced ecological degrading takes place in addition to the impacts resulting from river regulation and channel modifications. Correspondingly, Zajicek et al. (2018) outlined that among the most prevailing pressures, cargo vessels impacted on fish assemblages comparably to hydromorphological degradation, increased flow velocities and the loss of floodplains in large rivers. Recent river restoration acknowledges a holistic perspective on the riverine landscape that takes into account, for example, the different river types, hydromorphology and habitat availability (Friberg et al., 2016). Hence, large navigable rivers constitute a specific type of running waters exposed to particular impacts from vessel traffic as well as river engineering and maintenance to improve inland navigation. Besides the physical modifications and embankments, in waterways rehabilitation efforts have to address also all kinds of motorized boat traffic, from commercial cargo vessels to river cruises and recreational sport boats.

In large navigable rivers, densities of typical riverine fish are often already so low that the identification of pressure impacts is challenging or even impossible. Here, it was the case for phytophilic and psammophilic fish, which were too rare to draw any conclusions from their distribution observed. This is a particular challenge and opportunity for river management and research at the same time. Specific rehabilitation measures such alternative bank protection measures that account for inland navigation (e.g., Weber et al., 2012, 2016; Weber and Wolter, 2017) or even longitudinal protective dams within the navigable river channel (e.g., Collas et al., 2018) provide potential solutions that open up new research opportunities. However, a multitude of pressures and their potential interactions that are prevalent in any large river (Zajicek et al., 2018) need to be taken into account, at both scales regarding the local river reach and the overall catchment (Wolter et al., 2016). Aside from waterways, especially recreational sport boats might impose an overlooked threat to any near-natural water body, which again opens up future management challenges and research opportunities.

4.5. Conclusions

Rivers had been modified to waterways by river regulation and engineering works resulting in significant declines of river fishes. In addition to these construction related degradation of fish communities, all kinds of vessel operation cause additional impacts on aquatic communities. Cargo vessels, river cruises and even private sport boats have distinct impacts on fish assemblages. Thereby, recreational boating and passenger ships negatively affect densities of habitat-sensitive fish similarly to large commercial freight transporters. In addition, sport boat and passenger ship traffic even lower densities of habitat-insensitive fish. Therefore, any mode of recreational and commercial navigation requires specific attention in river management; specifically in species conservation and river rehabilitation because even pleasure boats or river cruises can override rehabilitation efforts in waterways. Therefore, the promotion of water tourism might counteract efforts to increase ecological quality. As a consequence, restoration of habitat structures alone, neglecting influence of passing vessels, may not achieve the desired ecological outcomes in any type of navigable water body. Frequencies of sport boats and passenger ships constitute navigation metrics that allow identifying responses in fish densities. For commercial cargo traffic, frequencies, total freight transported and total carrying capacity are equally suitable and should be chosen upon availability or accessibility. The degree of capacity utilization of cargo vessels is beneficial to reveal effects of cargo traffic on species richness. An average frequency of one to 26 sport boats and only one to ten passenger ships per day already affected the fish assemblages. Hence, more research is needed on the impacts of passenger vessels and recreational boating as the intended improvement of water bound tourism may further interfere with the desired enhancement of the ecological status of rivers.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.07.403.

References

Aarts, B.G.W., Nienhuis, P.H., 2003. Fish zonations and guilds as the basis for assessment of ecological integrity of large rivers. Hydrobiologia 500, 157–178. https://doi.org/10.1023/A:1024638726162.

Aarts, B.G.W., Van Den Brink, F.W.B., Nienhuis, P.H., 2004. Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. River Res. Appl. 20, 3–23. https://doi.org/10.1002/rra.720.

Adams, S.R., Keevin, T.M., Killgore, K.J., Hoover, J.J., 1999. Stranding potential of young fishes subjected to simulated vessel-induced drawdown. Trans. Am. Fish. Soc. 128, 1230–1234. https://doi.org/10.1577/1548-8659(1999)128<1230:SPOYFS>2.0.CO;2.

Akaike, H., 1981. Likelihood of a model and information criteria. J. Econ. 16, 3–14. https://doi.org/10.1016/0304-4076(81)90071-3.

Arlinghaus, R., Engelhardt, C., Sukhodolov, A., Wolter, C., 2002. Fish recruitment in a canal with intensive navigation: implications for ecosystem management. J. Fish Biol. 61, 1386–1402. https://doi.org/10.1111/j.1095-8649.2002.tb02484.x.

Bączyk, A., Wagner, M., Okruszko, T., Grygoruk, M., 2018. Influence of technical maintenance measures on ecological status of agricultural lowland rivers – Systematic review and implications for river management. Sci. Total Environ. 627, 189–199. https://doi.org/10.1016/j.scitotenv.2018.01.235.

Barton, K., 2016. MuMIn: multi-model inference [WWW document]. R package version 1.15.6. URL. https://CRAN.R-project.org/package=MuMIn, Accessed date: 25 June 2016.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01.

BAW (Ed.), 2016. Driving Dynamics of Inland Vessels, Published in German Language by VBW in July 2013; Translation and Revision by BAW in July 2016. BAW - Bundesanstalt für Wasserbau (Federal Warterways Engineering Research Institute).

Belletti, B., Rinaldi, M., Buijse, A.D., Gurnell, A.M., Mosselman, E., 2015. A review of assessment methods for river hydromorphology. Environ. Earth Sci. 73, 2079–2100. https://doi.org/10.1007/s12665-014-3558-1.

Bhowmik, N.G., Xia, R., Mazumder, Bijoy S., Soong, Ta W., 1995. Return flow in rivers due to navigation traffic. J. Hydraul. Eng. 121, 914–918. https://doi.org/10.1061/(ASCE)0733-9429(1995)121:12(914).

Birk, S., van Kouwen, L., Willby, N., 2012. Harmonising the bioassessment of large rivers in the absence of near-natural reference conditions – a case study of the Danube River. Freshw. Biol. 57, 1716–1732. https://doi.org/10.1111/j.1365-2427.2012.02831.x.

Buck, W., Felkel, K., Gerhard, H., Kalweit, H., van Malde, J., Nippes, K.-R., Ploeger, B., Schmitz, W., 1993. Der Rhein unter der Einwirkung des Menschen - Ausbau, Schifffahrt, Wasserwirtschaft (No. Bericht Nr. I-11 der KHR), KHR-Arbeitsgruppe "Anthropogene Einflüsse auf das Abflußregime." Internationale Kommission für die Hydrologie des Rheingebietes, Lelystad, NL.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Methods Res. 33, 261–304. https://doi.org/10.1177/0049124104268644.

BVB, 2017. The Power of Inland navigation. Dutch Inland navigation Information Agency (BVB).

CCNR, 2016. Inland Navigation in Europe (No. Annual Report 2016). Central Commission for the Navigation of the Rhine, Strasbourg.

Collas, F.P.L., Buijse, A.D., van den Heuvel, L., van Kessel, N., Schoor, M.M., Eerden, H., Leuven, R.S.E.W., 2018. Longitudinal training dams mitigate effects of shipping on environmental conditions and fish density in the littoral zones of the river Rhine. Sci. Total Environ. 619–620, 1183–1193. https://doi.org/10.1016/j.scitotenv.2017.10.299.

Décamps, H., Fortuné, M., Gazelle, F., Pautou, G., 1988. Historical influence of man on the riparian dynamics of a fluvial landscape. Landsc. Ecol. 1, 163–173. https://doi.org/10.1007/BF00162742.

Diaz-Redondo, M., Egger, G., Marchamalo, M., Hohensinner, S., Dister, E., 2017. Benchmarking fluvial dynamics for process-based river restoration: the upper

Rhine river (1816–2014). River Res. Appl. 33, 403–414. https://doi.org/10.1002/rra.3077.
Dußling, U., Bischoff, A., Haberbosch, R., Hoffmann, A., Klinger, H., Wolter, C., Wysujack, K., Berg, R., 2004. The fish-based assessment system - description of the German approach. In: Steinberg, C., Calmano, W., Klapper, H., Wilken, R.-D. (Eds.), Handbuch Angewandte Limnologie. Ecomed-Verlag, Landsberg, pp. 27–38.
European Commission (Ed.), 2011. White Paper on Transport: Roadmap to a Single European Transport Area - Towards a Competitive and Resource-efficient Transport System. Publ. Off. of the Europ. Union, Luxembourg.
Friberg, N., Angelopoulos, N.V., Buijse, A.D., Cowx, I.G., Kail, J., Moe, T.F., Moir, H., O'Hare, M.T., Verdonschot, P.F.M., Wolter, C., 2016. Chapter eleven - effective river restoration in the 21st century: from trial and error to novel evidence-based approaches. In: Dumbrell, Alex J., R.L.K., G.W. (Eds.), Advances in Ecological Research, Large-scale Ecology: Model Systems to Global Perspectives. Academic Press, pp. 535–611 https://doi.org/10.1016/bs.aecr.2016.08.010.
Gabel, F., Garcia, X.F., Schnauder, I., Pusch, M.T., 2012. Effects of ship-induced waves on littoral benthic invertebrates. Freshw. Biol. 57, 2425–2435. https://doi.org/10.1111/fwb.12011.
Gabel, F., Lorenz, S., Stoll, S., 2017. Effects of ship-induced waves on aquatic ecosystems. Sci. Total Environ. 601–602, 926–939. https://doi.org/10.1016/j.scitotenv.2017.05.206.
Gutreuter, S., Vallazza, J.M., Knights, B.C., 2006. Persistent disturbance by commercial navigation alters the relative abundance of channel-dwelling fishes in a large river. Can. J. Fish. Aquat. Sci. 63, 2418–2433. https://doi.org/10.1139/f06-129.
Haimann, M., Hauer, C., Tritthart, M., Prenner, D., Leitner, P., Moog, O., Habersack, H., 2018. Monitoring and modelling concept for ecological optimized harbour dredging and fine sediment disposal in large rivers. Hydrobiologia 814, 89–107. https://doi.org/10.1007/s10750-016-2935-z.
Holland, L.E., 1987. Effect of brief navigation-related dewaterings on fish eggs and larvae. N. Am. J. Fish Manag. 7, 145–147. https://doi.org/10.1577/1548-8659(1987)7<145:EOBNDO>2.0.CO;2.
http://www.blaues-band.bund.de, 2018. Bundesprogramm Blaues Band Deutschland [WWW Document]. Bundesprogramm Blaues Band Deutschland. (URL). http://www.blaues-band.bund.de/Projektseiten/Blaues_Band/DE/00_Home/home_node.html, Accessed date: 23 May 2018.
Huckstorf, V., Lewin, W.-C., Mehner, T., Wolter, C., 2011. Impoverishment of YOY-fish assemblages by intense commercial navigation in a large Lowland river. River Res. Appl. 27, 1253–1263. https://doi.org/10.1002/rra.1420.
Kucera-Hirzinger, V., Schludermann, E., Zornig, H., Weissenbacher, A., Schabuss, M., Schiemer, F., 2008. Potential effects of navigation-induced wave wash on the early life history stages of riverine fish. Aquat. Sci. 71, 94–102. https://doi.org/10.1007/s00027-008-8110-5.
Kuznetsova, A., Brockhoff, B., Christensen, H.B., 2016. lmerTest: tests in linear mixed effects models [WWW document]. R package version 2.0-32. (URL). https://CRAN.R-project.org/package=lmerTest, Accessed date: 23 June 2016.
Lechner, A., Keckeis, H., Schludermann, E., Humphries, P., McCasker, N., Tritthart, M., 2014. Hydraulic forces impact larval fish drift in the free flowing section of a large European river. Ecohydrology 7, 648–658. https://doi.org/10.1002/eco.1386.
Lechner, A., Keckeis, H., Humphries, P., 2016. Patterns and processes in the drift of early developmental stages of fish in rivers: a review. Rev. Fish Biol. Fish. 26, 471–489. https://doi.org/10.1007/s11160-016-9437-y.
Liddle, M.J., Scorgie, H.R.A., 1980. The effects of recreation on freshwater plants and animals: a review. Biol. Conserv. 17, 183–206. https://doi.org/10.1016/0006-3207(80)90055-5.
Liedermann, M., Tritthart, M., Gmeiner, P., Hinterleitner, M., Schludermann, E., Keckeis, H., Habersack, H., 2014. Typification of vessel-induced waves and their interaction with different bank types, including management implications for river restoration projects. Hydrobiologia 729, 17–31. https://doi.org/10.1007/s10750-014-1829-1.
Lorenz, A.W., Stoll, S., Sundermann, A., Haase, P., 2013. Do adult and YOY fish benefit from river restoration measures? Ecol. Eng. 61 (Part A), 174–181. https://doi.org/10.1016/j.ecoleng.2013.09.027.
Lorenz, S., Gabel, F., Dobra, N., Pusch, M.T., 2013. Modelling the effects of recreational boating on self-purification activity provided by bivalve mollusks in a lowland river. Freshw Sci 32, 82–93. https://doi.org/10.1899/12-054.1.
Mac Nally, R., Duncan, R.P., Thomson, J.R., Yen, J.D.L., 2017. Model selection using information criteria, but is the "best" model any good? J. Appl. Ecol. 00, 1–4. https://doi.org/10.1111/1365-2664.13060.
Mazumder, B.S., Bhowmik, N.G., Soong, T.W., 1993. Turbulence in rivers due to navigation traffic. J. Hydraul. Eng. 119, 581–597. https://doi.org/10.1061/(ASCE)0733-9429(1993)119:5(581).
Melcher, A., Schmutz, S., Haidvogl, G., Moder, K., 2007. Spatially based methods to assess the ecological status of European fish assemblage types. Fish. Manag. Ecol. 14, 453–463. https://doi.org/10.1111/j.1365-2400.2007.00583.x.
Meybeck, M., Helmer, R., 1989. The quality of rivers: from pristine stage to global pollution. Palaeogeogr. Palaeoclimatol. Palaeoecol. 75, 283–309. https://doi.org/10.1016/0031-0182(89)90191-0.
Moog, O., Stubauer, I., Haimann, M., Habersack, H., Leitner, P., 2018. Effects of harbour excavating and dredged sediment disposal on the benthic invertebrate fauna of River Danube (Austria). Hydrobiologia 814, 109–120. https://doi.org/10.1007/s10750-015-2476-x.
Nagrodski, A., Raby, G.D., Hasler, C.T., Taylor, M.K., Cooke, S.J., 2012. Fish stranding in freshwater systems: sources, consequences, and mitigation. J. Environ. Manag. 103, 133–141. https://doi.org/10.1016/j.jenvman.2012.03.007.
Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.
Pauli, G., 2010. Sustainable transport: a case study of Rhine navigation. Nat. Res. Forum 34, 236–254. https://doi.org/10.1111/j.1477-8947.2010.01309.x.
Pearson, W.H., Skalski, J.R., 2011. Factors affecting stranding of juvenile salmonids by wakes from ship passage in the lower Columbia River. River Res. Appl. 27, 926–936. https://doi.org/10.1002/rra.1397.
Petts, G.E., Möller, H., Roux, A.L., 1989. Historical Change of Large Alluvial Rivers: Western Europe. John Wiley & Sons, Chichester.
PINE, 2004. Prospects of Inland Navigation Within the Enlarged Europe (No. Final Concise Report), Prospects of Inland Navigation Within the Enlarged Europe.
R Development Core Team, 2017. R: A Language and Environment for Statistical Computing [WWW Document]. R Foundation for Statistical Computing, Vienna, Austria (URL). https://www.r-project.org/, Accessed date: 21 February 2018.
Raška, P., Dolejš, M., Hofmanová, M., 2017. Effects of damming on long-term development of Fluvial Islands, Elbe River (N Czechia). River Res. Appl. 33, 471–482. https://doi.org/10.1002/rra.3104.
Schinegger, R., Palt, M., Segurado, P., Schmutz, S., 2016. Untangling the effects of multiple human stressors and their impacts on fish assemblages in European running waters. Sci. Total Environ. 573, 1079–1088. https://doi.org/10.1016/j.scitotenv.2016.08.143.
Schludermann, E., Liedermann, M., Hoyer, H., Tritthart, M., Habersack, H., Keckeis, H., 2013. Effects of vessel-induced waves on the YOY-fish assemblage at two different habitat types in the main stem of a large river (Danube, Austria). Hydrobiologia 729, 3–15. https://doi.org/10.1007/s10750-013-1680-9.
Söhngen, B., Koop, J., Knight, S., Rytkönen, J., Beckwith, P., Ferrari, N., Iribarren, J., Keevin, T., Wolter, C., Maynord, S., 2008. Considerations to Reduce Environmental Impacts of Vessels (PIANC REPORT No. No 99), PIANC Report Series. PIANC, Brussels.
Strayer, D.L., Findlay, S.E.G., 2010. Ecology of freshwater shore zones. Aquat. Sci. 72, 127–163. https://doi.org/10.1007/s00027-010-0128-9.
Ten Brinke, W.B.M., Schulze, F.H., van Der Veer, P., 2004. Sand exchange between groyne-field beaches and the navigation channel of the Dutch Rhine: the impact of navigation versus river flow. River Res. Appl. 20, 899–928. https://doi.org/10.1002/rra.809.
Weber, A., Wolter, C., 2017. Habitat rehabilitation for juvenile fish in urban waterways: a case study from Berlin, Germany. J. Appl. Ichthyol. 33, 136–143. https://doi.org/10.1111/jai.13212.
Weber, A., Lautenbach, S., Wolter, C., 2012. Improvement of aquatic vegetation in urban waterways using protected artificial shallows. Ecol. Eng. 42, 160–167. https://doi.org/10.1016/j.ecoleng.2012.01.007.
Weber, A., Zhang, J., Nardin, A., Sukhodolov, A., Wolter, C., 2016. Modelling the influence of aquatic vegetation on the hydrodynamics of an alternative bank protection measure in a navigable waterway. River Res. Appl. 32, 2071–2080. https://doi.org/10.1002/rra.3052.
Wickham, H., 2016. Ggplot2: Elegant Graphics for Data Analysis. Second edition. Use R! Springer, Cham.
Wolter, C., Vilcinskas, A., 1997. Characterization of the typical fish community of inland waterways of the north-eastern lowlands in Germany. Regul. Rivers Res. Manag. 13, 335–343. https://doi.org/10.1002/(SICI)1099-1646(199707)13:4<335::AID-RRR443>3.0.CO;2-G.
Wolter, C., Arlinghaus, R., Sukhodolov, A., Engelhardt, C., 2004. A model of navigation-induced currents in inland waterways and implications for juvenile fish displacement. Environ. Manag. 34, 656–668. https://doi.org/10.1007/s00267-004-0201-z.
Wolter, C., Buijse, A.D., Parasiewicz, P., 2016. Temporal and spatial patterns of fish response to hydromorphological processes. River Res. Appl. 32, 190–201. https://doi.org/10.1002/rra.2980.
Zaggia, L., Lorenzetti, G., Manfé, G., Scarpa, G.M., Molinaroli, E., Parnell, K.E., Rapaglia, J.P., Gionta, M., Soomere, T., 2017. Fast shoreline erosion induced by ship wakes in a coastal lagoon: Field evidence and remote sensing analysis. PLoS One 12, e0187210. https://doi.org/10.1371/journal.pone.0187210.
Zajicek, P., Wolter, C., 2018. The gain of additional sampling methods for the fish-based assessment of large rivers. Fish. Res. 197, 15–24. https://doi.org/10.1016/j.fishres.2017.09.018.
Zajicek, P., Radinger, J., Wolter, C., 2018. Disentangling multiple pressures on fish assemblages in large rivers. Sci. Total Environ. 627, 1093–1105. https://doi.org/10.1016/j.scitotenv.2018.01.307.
Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology With R. Springer, New York NY.
Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.

General discussion

Summary of major findings

The overall aim of this doctoral thesis was to comprehensively investigate fish assemblages in large rivers, how fish samples are to be derived representatively (chapter one), how fish assemblages are influenced by multiple pressures while specifically assessing the role of inland navigation as an additional pressure (chapter two) and how different modes of ship traffic such as sport boats, river cruises and cargo vessels influence fish assemblages in detail (chapter three). Ultimately, recommendations for river management were derived and discussed throughout this thesis.

Chapter one

Study one aimed to identify benefits, drawbacks and overall suitability of fishing gears for the fish-based assessment of large rivers. Identical river reaches sampled with different fishing gears and identical river stretches sampled with two different gears were selected. Data requirements on fish samples comprised, for instance, representative fished length and numbers of fishes captured. The major outcomes of study one confirmed the overall hypotheses, showing that electrofishing catches most fish species and highest fish densities. Electrofishing is therefore a well-suited sampling method to representatively assess large rivers` fish assemblages. Nevertheless, it was also shown that additional methods such as trawling have additional gains for fish-based assessments in completing the species inventory and capturing more migratory species, potamal fish and larger fish. Beyond that, it was shown and discussed that the differences in the catch composition of each sampling method do not only reflect gear-based selectivity (e.g., Blabolil et al., 2018; Mueller et al., 2017), but also the habitat-dependent variability in fish density and species composition of large rivers (e.g., Muška et al., 2018). A study on plankton environments in rivers just recently concluded that "*the ability to delineate nearshore and main channel environments supports the notion that along the river there are at least two* *physically distinct water column ecosystems […] that have different chemical and physical characteristics relevant to the ecological functioning of rivers*” (Ball et al., 2018), which is well in line with the discussed macro-habitats in regard to fishes and fish-sampling gears in chapter one of this thesis. Nevertheless, electrofishing sufficiently well represents the overall fish assemblages of large rivers. Albeit, it was confirmed in chapter one that appropriate sampling gears should be selected in accordance to the research objectives of any study (e.g., De Leeuw et al., 2007; Flotemersch et al., 2011), such as electrofishing to evaluate environmental restoration along shallow areas or trawling in addition to electrofishing to assess biodiversity, rare, potamal and large fishes. These findings are also in line with a recent study (Fischer et al., 2018) in a large temperate river bordering Canada and the USA. Fischer et al. (2018) have shown that electrofishing captures more species and individuals than gillnets and minnow traps. Further, Fischer et al. (2018) also highlighted suitability of electrofishing to assess shoreline remediation and the latter authors likewise outlined better comprehensiveness of assessments when also applying the other fishing gears tested in their study in addition to electrofishing. Study one of this thesis further highlights that identical sampling gears should be selected in studies covering large spatial and temporal scales (e.g., Goffaux et al., 2005). The key findings of this study are highly relevant to assess the ecological status of large rivers based on their fish assemblages and provide a sound basis for future fish based-assessments of large rivers. Consequently, electrofishing was selected in studies two and three to estimate representative fish population metrics for large rivers` fish assemblages.

Chapter two

Study two aimed to identify the most influential pressures and their interactions while explicitly assessing the influence of inland navigation as an additional pressure. Only electrofishing catches were selected at sites representing a gradient in several degradation variables. Major outcomes of study two confirmed the key hypothesis, that inland navigation has an influence on fish assemblages comparable to other major human alterations of the river channel. Inland navigation appeared as one of the most influential pressures (together with increased flow velocity and the loss of floodplains) and also frequently interacted with those. Hence, inland navigation constitutes a highly relevant pressure on riverine fishes. As improving ecological quality predominantly focuses on hydromorphological degradation (Friberg et al., 2016), inland navigation constitutes a yet overseen additional challenge in river rehabilitation. The key findings of study two were for the first time derived under field conditions in large rivers, covering a substantial amount of sampling sites and accounting for the commercial transportation of goods via water-based navigation. The identified pressures inventory well corresponds to pressures that were identified for smaller and alpine rivers and streams (Schinegger et al., 2018, 2016, 2013, 2012; Trautwein et al., 2013) with the latter becoming significantly improved by adding the impact of inland navigation to the pressure inventory of large rivers. The major results of study two are highly relevant for fish-based ecological assessments and the management of large rivers as they

(i) outline the high influence of inland navigation in relation to other pressures,

(ii) identify highly influential pressures and their interactions that predominantly relate to hydromorphological degradation and inland navigation and

(iii) derive fish population metrics such as densities of lithophilic fish that are well suitable to identify distinct human alterations of large rivers.

Moreover, the highly significant influence of inland navigation intensity on the fish assemblage underlined the necessity to study the effects of ship traffic in more detail.

Chapter three

Study three aimed to determine the intensity of common modes of inland navigation and their influence on fish assemblages in large rivers. Sampling sites representing a gradient in navigation intensities of sport boats, river cruises and cargo vessels were selected and the fish assemblages at the selected sites were assessed using electrofishing. Major outcomes of study three confirmed the main hypotheses in so far that

(i) both recreational and commercial inland navigation and even draft of cargo vessels had distinct impacts on fish assemblages, and

(ii) habitat-sensitive lithophilic fish were most affected by any type of passing motorized vessels, ships and boats.

In line with former local-scale studies demonstrating the influence of waves and drawdown caused by passing vessels on juvenile fish (Arlinghaus et al., 2002; Kucera-Hirzinger et al., 2008; Liedermann et al., 2014), study three shows for the first time on a large spatial scale, how the power of vessel-induced waves and drawdown alters entire fish assemblages. Even more importantly, study three shows that even recreational sport boats significantly and negatively affect fish assemblages, which has major implications for the restoration, rehabilitation and conservation of aquatic environments. It further substantiates results of study two by outlining the interplay of inland navigation and the accompanying engineering-based modifications of the river channel, which corresponds very well to the outcomes of a recent review of the impacts of day-to-day technical maintenance measures in agricultural lowland rivers (Bączyk et al., 2018). Moreover, study three identifies responsive fish population metrics to both recreational and commercial navigation, again (as in study two) showing the high sensitivity of lithophilic fish to impairments of habitats within the shallow shorelines. Key findings of study three are highly relevant for the adaptive management of waterways, in particular for economically less important waterways that are primarily deemed for water-based recreation such as motorized sport boats, as these can impact efforts to increase ecological quality.

Consequences arising from the ecological degradation of large rivers

Centuries of river modifications resulted in a multitude of persistent pressures stretching across river reaches and even across entire river catchments. The occurrence of multiple pressures challenges a clear identification of principal cause-effect chains (e.g., Craig et al., 2017) in large rivers for two major reasons. On the one hand, the overall degradation that prevails in large rivers does not offer ideal gradients in environmental conditions ranging from well-structured, natural river reaches to heavily degraded ones. Hence, natural reference conditions are missing in European large rivers (e.g., Birk et al., 2012b; Brabender et al., 2016; Melcher et al., 2007; Ramos-Merchante and Prenda, 2018). On the other hand, as a consequence of the persistent degradation, the composition of the fish assemblages across the different river reaches is often comparable (ecological simplification and faunal homogenization; Peipoch et al., 2015; Sommerwerk et al., 2017), also lacking an ideal gradient in the derived fish population metrics (e.g., study three; Zajicek and Wolter, 2019). In turn, a clear identification of specific pressure-responses proves difficult. Comparable challenges (regarding gradients in the data) are encountered even in smaller streams and rivers, so that studies addressing multiple pressures in any kind of running waters cover as many water bodies and even entire catchments to identify cause-effect chains (e.g., Bierschenk et al., 2019; Mueller et al., 2018; Schinegger et al., 2018, 2016, 2012; Trautwein et al., 2013). Hence, current research outlines the necessity of long-term monitoring programs to create large datasets to better understand large rivers' ecology in future. Within this thesis, a unique dataset (the Large River Fish Database) was analyzed that consisted of 2693 sites spread across various river reaches and several hundreds of river-kilometers in several European large rivers. Due to this substantial amount of data across a large spatial extent, gradients in most of the metrics analyzed throughout this thesis could be established. For instance, in study two, gradients in both pressure (between slight, moderate and strong expressions of each pressure) and fish population metrics could be identified and therefore some robust correlations among them established. A clear effect of inland navigation could be identified because sites in the River Rhine with extremely strong ship traffic (on average >= 90 cargo vessels per day at the sampled sites) were compared to sites in rivers with moderate ship traffic (> 8 and < 90; rank 3) and to sites in rivers with slight ship traffic (< 8; rank 1). Moreover, at each site, a set of ten gradually ranked (rank orders 1-3-5) pressure variables persisting at all of the selected sites were accounted for. Ultimately, multiple pressures could be disentangled while accounting for inland navigation. As a major drawback resulting from the monotonous degradation of the studied rivers, 62% of the initially preselected 26 pressure variables lacked a gradient between pressure ranks and had to be excluded prior analyzes. As a major strength resulting from the careful selection and the large amount of data, the derived results and conclusions can be considered conservative and generalizable for European large rivers.

Implications for fish-based assessments of large rivers

Fish-based assessments of large rivers are a challenging task because of the complexity and the spatial extent of the riverine ecosystem as well as due to limitations brought about by the application of any fishing gear (Zajicek and Wolter, 2018). Study one provides potential solutions for the existing challenges in fish-based assessments of large rivers:

(i) Electrofishing well represents the fish assemblages of large rivers and is therefore generally suitable for ecological assessments,

(ii) electrofishing is particularly suitable to assess hydromorphological degradation and remediation of the river channel,

(iii) additional fishing gears such as trawling complement the species inventory and are therefore valuable for species conservation and biodiversity assessments.

As shown in chapter one, each fishing gear has benefits for fish-based assessments with electrofishing catching most fish species and highest fish densities along the banks while additional methods also covering the main channel capture additional (rare and migratory) fish species as well as larger fish that more frequently occupy the main river channel (e.g., Foubert et al., 2018). Consequently, a prerequisite for successful fish based assessments is a clear definition of the study objectives and goals that are to be assessed or achieved. While electrofishing is very well suited to capture changes in fish densities and of taxonomic richness in response to hydromorphological rehabilitation measures along the banks (ecological assessments), complementary sampling using additional gears in the main channel is required for a full inventory of taxonomic diversity (species conservation and biodiversity) and size and age classes of large river fishes (Erős et al., 2017). Rare species can disproportionately contribute to the functional structure of species assemblages (Leitão et al., 2016; Mouillot et al., 2013), again outlining the necessity to apply complementary fishing gears in assessments of biodiversity and ecosystem functioning. If sampling data cover large spatial scales and were therefore assembled by various agencies or within different research projects, a constant data standardization procedure needs to be followed (such as suggested in chapter one; Zajicek and Wolter, 2018) to determine representative fish population metrics while maintaining reasonable sample sizes. Likewise, comprehensive long-term datasets need to be assembled and made available (Wetzel et al., 2018) to derive robust estimates of the fish assemblage and hence, to reliably evaluate restoration outcomes (Höckendorff et al., 2017; Schmutz et al., 2016). Electrofishing is a well suitable method for the long-term monitoring of hydromorphological alterations and rehabilitation in large rivers.

Implications of multiple pressures in large rivers

A multitude of pressures influencing fish assemblages in large rivers was identified in study two (Zajicek et al., 2018): The most influential pressures referred to river hydrology (increased flow velocity), river morphology (loss of floodplains) and inland navigation (navigation intensity). The most frequent pairwise interactions consisted of a combination of the former three pressures. Further, increased sedimentation, channelization, organic siltation, the presence of artificial embankments and migration barriers were additional pressures (and also involved in numerous pairwise interactions) with a significant influence on at least one fish population metric. The multitude of influential pressures, as well as the multitude of pressure interactions identified within this thesis is in line with recent studies aiming to improve ecological quality in running waters that frequently outline

(i) the significant role of hydromorphological dynamics in the riverine environment (e.g., Arias et al., 2018; Ball et al., 2018; Colin et al., 2018; Staentzel et al., 2018);

(ii) both the river channel and the surrounding floodplains as an entity and prerequisite for natural hydromorphological processes (e.g., Diaz-Redondo et al., 2017; Hauer et al., 2016; Hayes et al., 2018)

(iii) longitudinal connectivity as an integral part of the riverine ecosystem (e.g., Benitez et al., 2015; Brinker et al., 2018; Radinger et al., 2018b), and hence,

(iv) the need for an integrative management approach also accounting for potential pressure interactions (e.g., Hein et al., in press).

Hence, results of this thesis underline that measures of river rehabilitation need to account for potential pressure influences stemming from both local river reaches and also from the entire river catchment (Drake et al., 2018; Jourdan et al., in press; Pilotto et al., 2019; Van Looy et al., in press; Wolter et al., 2016) that can result in hydromorphological alterations at the reach scale and ultimately in unexpected ecological outcomes (Ormerod et al., 2010). Likewise, connectivity to floodplains, side-arms and oxbows is essential (e.g., Naus and Adams, 2018; Seliger and Zeiringer, 2018; Spurgeon et al., 2018; Van Oorschot et al., 2018) to provide diverse hydromorphological conditions. Within the multitude of pressures in large rivers, inland navigation stands out as a pressure that can further modify hydromorphological processes along the banks and shallow areas in addition to hydromorphological degradation of the river channel and therefore, requires particular attention in river management. Consequently, river management and river rehabilitation in large rivers need to maintain river hydrology (provide adequate river flows), provide access to floodplains (enable flooding of floodplains) as well as mitigate for inland navigation (protect shallow shore areas from hydraulic forces of passing vessels).

Study two quantitatively shows for the first time that on fish assemblages, inland navigation forms an additional pressure that is as influential as other most influential pressures within the pressure pool of large rivers. In support of this finding, juvenile fish assemblages (0+) had lower fish densities and species diversity in river stretches exposed to commercial navigation as compared to river stretches closed to cargo vessels in the upper river Elbe in the Czech Republic (Valova et al., 2014). Even more importantly, study two revealed that inland navigation has the potential to be as detrimental as the hydromorphological degradation of the river channel. The latter finding has major implications for the rehabilitation of all freshwater systems that are utilized as waterways, because targeting solely hydromorphology (e.g., Buijse et al., 2003) might not achieve the desired ecological outcomes. Hence, "*reestablishing geomorphological and hydrological processes that cause river ecosystems to be dynamic and diverse*" (Buijse et al., 2003) as a key focus of river management and rehabilitation (Buijse et al., 2003) needs to be expanded by simultaneously accounting and mitigating for navigation traffic. As another consequence of hitherto neglected navigation-related impacts, inland navigation could even explain past failures of restoration measures that did not account for navigation traffic (e.g., Kail et al., 2015; Schmutz et al., 2015), likely even in other taxa than fishes (e.g., invertebrates; England and Wilkes, 2018; Gabel et al., 2008). Consequently, navigation traffic and the inherent engineering works to maintain fairway depth and to stabilize shorelines set significant boundaries for successful river rehabilitation and amelioration of ecological quality. Therefore, inland navigation (ship traffic and accompanying engineering works) require particular attention in river rehabilitation planning (e.g., Weber and Wolter,

2017) to increase rehabilitation success and ecological quality (e.g., Collas et al., 2018).

Implications of recreational and commercial navigation

The results of the impact analyses of the interactive effects from multiple pressures and the identification of the prominent effects from inland navigation have led to an in depth analysis of the various facets of inland navigation and vessel-induced impacts (presented in chapter three, Zajicek and Wolter, 2019): Any types of motorized boats, be it recreational sport boats, touristic river cruises, commercial cargo vessels and even the draft of commercial cargo vessels, were shown to distinctly influence the adult fish assemblages of large rivers. These findings are strikingly novel as they for the first time show that

(i) any mode of motorized navigation traffic matters, even recreational sport boats,

(ii) the impacts of recreational sport boats and commercial river cruises appeared in waterways, i.e., in commercial fairways and thus in addition to commercial cargo traffic, and,

(iii) sport boats can outcompete the effects of commercial cargo vessels in economically less important waterways.

Besides the former major findings, it was shown that even draft of cargo vessels has an impact and that navigation traffic acts in addition to river-engineering related alterations of the river channel. Moreover, lithophilic fishes were identified as most sensitive to passing vessels, ships and boats.

Recreational sport boats, commercial passenger ships and commercial cargo vessels were revealed to have distinct influences on the fish assemblages. Impacts of vessels, ships and boats are distinctive because hydrodynamics caused by each mode of navigation are distinctive as was reviewed and summarized in Söhngen et al. (2008) and BAW (2016) [but see also e.g., Kucera-Hinziger et al. (2008) and Schiemer (2001)]: Depending on vessel type (in European rivers), speed and draught of cargo vessels vary between 10 km/h and 18 km/h and 1.8 m and 4.0 m, respectively. Passenger ships sail at 15 - 19 km/h and with a draught of 1.0 -2.0 m. Sport boats (yachts) achieve speeds of up to 40 km/h and have a draught of 1.1 – 1.5 m. Hence, cargo vessels typically sail at lowest speeds but with the highest draught (highest total weight). Passenger ships typically sail with a lower draught (lower total weight) but at higher speed than cargo vessels. Sport boats sail at highest speeds but with lowest draught (lowest total weight). As a consequence, each vessel type generates distinctive hydrodynamic forces during vessel passage: Based on vessel draught, speed, shape and distance to the shores, cargo vessels can cause significant drawdown ranging from 0.1 m to 0.4 m. Deep draft vessels also produce the highest displacement flow velocities and stern heavy loaded vessels result in largest primary waves (i.e., a sequence of bow wave, drawdown and stern wave). Partially loaded cargo vessels can travel at higher speeds and thereby cause more drawdown and higher waves. The latter issue is highly relevant as cargo vessels do mostly not operate at full capacity as was indicated in chapter three of this thesis. Whereas primary waves loose energy with distance to the shores, secondary waves (regular wavelets) propagate and hit the shores with almost full power even over great distances. Importantly, the biggest secondary waves are caused by fast-moving recreational sport boats and passenger ships rather than by commercial cargo vessels (BAW, 2016). Hence, primary waves such as drawdown are most relevant for cargo vessels whereas secondary waves are most relevant for recreational sport boats. Passenger ships induce both relevant drawdown and secondary waves. Sport boats often sail closer to the shores due to their low draught and to avoid collision with commercial ship traffic. Hydrodynamical power of motorized sport boats is therefore fully discharged along the shores. Consequently, "*in large waterways with intense water sports activities the stress on the banks from recreational craft can exceed that from commercial navigation*" (BAW, 2016), which is overwhelmingly in line with the main result of study three of this thesis. The distinctive hydrodynamics of the different vessel categories, very well correspond to the distinctive impacts of sport boats, passenger ships and cargo vessels on fish assemblages identified in this thesis. It is therefore indispensable to consider any type of ship traffic, as well cargo vessels, passenger ships and also recreational sport boats in river management and rehabilitation.

A major strength in assessing distinct effects of recreational and commercial navigation in study three was the fact that all types of inland navigation mostly persisted in all studied rivers. Therefore, it could be revealed that the most relevant hydrodynamics such as drawdown for cargo vessels and regular wavelets for sport boats each distinctly impacted on the fish assemblage: For instance, distinct influence of sport boats compared to cargo vessels were identified in identical rivers with both known frequencies on sport boats and cargo vessels. Likewise, resulting from the opportunity to consider a few sites with and without cargo traffic, vessel-based impacts were shown to act on top of the hydromorphological degradation of the river channel, which is well in line to results from study two. In large rivers, hydromorphological degradation of the main river channel is superimposed through engineering works to maintain the navigation fairway (e.g., Bączyk et al., 2018). Therefore, study three uncovers distinct influences of different types of inland navigation and indicates in addition that inland navigation acts on top of river engineering. Hence, even in highly degraded large rivers where maintenance-related engineering works take place, ecological quality would benefit from mitigating for navigation traffic, also for recreational sport boats or passenger ships if cargo traffic is negligible.

The underlying mechanism of hydrodynamics caused by passing vessels, ships and boats relate to morphological degradation along the shores (e.g., Zaggia et al., 2017). Hydraulic forces cause a significant loss of habitats for aquatic organisms (Arlinghaus et al., 2002; Gabel et al., 2017; Wolter et al., 2004a). Drawdown causes dewatering and air exposure (Schiemer et al., 2001) which mainly affects the smallest and weakest fishes. For instance, vessel-induced return currents exceed the critical swimming speed of juvenile fish (Wolter and Arlinghaus, 2003) and result in fish stranding and even in direct mortality (Adams et al., 1999; Nagrodski et al., 2012; Pearson and Skalski, 2011). Accordingly, hydraulic forces of passing vessels cause a significant decline in juvenile fishes (e.g., Huckstorf et al., 2011). Taking into account that the afore referenced studies have shown a major impact on juvenile fish and that inland navigation acts on top of hydromorphological degradation (as shown here), a depletion of nursery habitats due to hydraulic forces of passing vessels appears as the most plausible mechanism for declines in fish densities in navigable rivers. An additional depletion of potential spawning and nursery habitats due to ship traffic is detrimental, particularly in large rivers, because structural habitat complexity required by many riverine fish species is already scarce as a result of the hydromorphological degradation of the river channel (e.g., Friberg et al., 2016; Zajicek et al., 2018). In light of the general scarcity of fish-nursery habitats in large rivers and the significant damage to those due to ship traffic, speed limits for any type of motorized vessels might be a first approach to protect the remainder living environment for juvenile fishes. Speed limits in waterways would reduce strength of hydraulic forces, morphological damage along shorelines and even maintenance costs (BAW, 2016) and improve habitat suitability for riverine fishes.

The reported findings reveal hitherto unknown or neglected ecological consequences of navigation traffic on fish assemblages and have major implications for a) the management and rehabilitation of particularly economically less important waterways that are under consideration for both ecological rehabilitation and the promotion of water based recreation at the same time (e.g., recreational sport boats; www.blaues-band.bund.de, accessed 26.09.2018) as well as b) waterways that are under consideration for expansion of commercial navigation capacity (e.g., expansion of cross-section, increase of navigable depth; Ławicki et al., 2017). In case of a), commercial, touristic river cruises as well as recreational sport boats will hamper restoration efforts and further contribute to the failure of river rehabilitation and hence counteract the improvement of ecological quality in economically less important waterways. The establishment of shallow, riparian areas was significantly beneficial for many juvenile and small riverine fishes, in particular for the sensitive reproductive guilds of lithophils and psammophils in sixth-order rivers (i.e., presumably in rivers without any ship traffic, Lorenz et al., 2013). Ship traffic such as passages of motorized sport boats and river cruises could adversely affect such restoration efforts in any navigated water body and countervail restoration success. Ship traffic is therefore highly relevant for consideration within the Blue Band Initiative. In case of b) increased draft and frequency of cargo vessels will add on top of the additional degradation of the river channel via construction and engineering works (e.g., Henning and Hentschel, 2013). Moreover, cargo vessels, river cruises and sport boats will lower ecological quality and thereby contradict the prescriptions and goals of the European Water Framework Directive to increase ecological quality or potential in all navigable European surface water bodies. Therefore, appropriate mitigation measures (e.g., BAW, 2016; Collas et al., 2018; Weber and Wolter, 2017) need to be established in any navigable water body to account for navigation traffic: Speed limits (BAW, 2016), longitudinal dams (Collas et al., 2018) and alternative bank protection measures (Weber and Wolter, 2017) are potential solutions to increase habitat availability in large rivers and other waterways.

However, intense navigation traffic and fairway maintenance might significantly limit the application of mitigation measures within the main river channel. Therefore, mitigation measures providing additional nursery habitats such as the reconnection of side-arms, backwaters and tributaries to the main river channel (e.g., Lorenz et al., 2016; Milner et al., 2019) might be required in addition if mitigation measures are limited within the main river channel. The availability of differently structured habitats ("habitat mosaics", Pander et al., 2018), both inside and outside the main channel is of key importance for riverine fishes (e.g., Pander et al., 2018; Pander and Geist, 2018). Multiple mitigation measures addressing hydromorphology, navigation traffic and additional habitat availability would result in multiple benefits for also other aquatic organisms (e.g., macroinvertebrates; Brabender et al., 2016; Gabel et al., 2012; Lemm and Feld, 2017; Shell and Collier, 2018; Stoll et al., 2016) and such living at the aquatic-terrestrial borderline (e.g., apex predators; Holland et al., 2018), aquatic vegetation (e.g., Seer et al., 2018) as well as stipulate positive feedbacks amongst organisms and ecosystems (e.g., Lusardi et al., 2018).

Utility of diagnostic fish population metrics

Lithophilic fish appeared as most sensitive to both hydromorphological alteration and the impact of waves and drawdown caused by any type of passing motorized vessel, ship and boat. Lithophilic fish strongly rely on hydromorphodynamics consisting of high flow velocities and the inherent sediment sorting providing coarse gravel substrates (Duerregger et al., 2018). Interestingly, Duerregger et al. (2018) showed that eggs and hatched fish larvae of the lithophilic nase (*Chondrostoma nasus*) reside, likely shelter, in the deep (up to 30 cm for eggs) permeable interstitial of coarse sediments. Thereby, accumulation of fine sediments correlated to lower hatch rates, emphasizing the necessity of the intact flow providing fresh and oxygenated water into the deep layers of gravel substratum (Duerregger et al., 2018). In regulated rivers, gravel bars are often scarce (dredged to maintain sufficient depth within the navigation channel) and if available then in shallower parts of the river bed (where hydraulic forces of passing vessels discharge), explaining the high sensitivity of lithophils to hydromorphological degradation and inland navigation revealed here. In further support of the high sensitivity of lithophils to habitat degradation, Mueller et al. (2018) identified the most negative trends for particularly gravel spawners within the fish community in medium sized and large rivers of Bavaria (Germany) using historical and current data covering more than 30 years. The authors further outlined that abundance of each of the gravel spawning *Thymallus thymallus*, *Chondrostoma nasus* and *Barbus barbus* has not increased in rivers and streams across the entire state of Bavaria since the 1990s (Mueller et al., 2018). Consequently, there is profound evidence that lithophilic fishes are the most sensitive habitat specialists to environmental degradation and ship traffic in running waters, which is well in line with the results derived in this thesis. Therefore, increasing densities of lithophilic fish provide a viable bioindicator for the successful rehabilitation of hydromorphodynamics and successful mitigation for ship traffic. On the other hand, depleted densities of lithophils indicate degraded hydromorphology in rivers without ship traffic and both consequences of hydromorphological degradation and ship traffic in navigable rivers.

Within this thesis, ten fish population metrics were derived and tested in total, five referring to biodiversity and five referring to densities of fish with similar life history traits. Functional groups (guilds) of fishes with similar life history traits responded to distinct types of river degradation and to all modes of inland navigation. Functional guilds accordingly constitute well-suited diagnostic fish population metrics to assess the success or failure of river rehabilitation. This finding is in line with very recent research, which outlines the responsiveness of structural taxonomic and functional life-history traits of fishes to environmental modifications in the aquatic environment (e.g., Colin et al., 2018; Lima et al., 2017; Pilotto et al., 2019; Sagouis et al., 2017). However, life-history traits appeared more responsive to human alterations than diversity metrics, which specifically is in line to stronger responses of functional traits than taxonomic structures to human alterations, as e.g. observed in the Colorado River (Pool et al., 2010). Further, functional life history traits are just recently being recognized as more valuable (i.e., more responsive regarding e.g., hydromorphological changes) tools for ecological assessments (England and Wilkes, 2018; Pander et al., 2017; Schmutz et al., 2015). Accordingly, life-history traits referring to the obligate selection of spawning habitats of fishes were, as expected, confirmed most sensitive to hydromorphological degradation within this thesis and should be considered as important ecological bioindicators in fish-based assessments, particularly in the evaluation of restoration projects (e.g., Schmutz et al., 2016). Indeed, an increase of habitat specialist species relying on complex structures for spawning was recently observed following the structural restoration of a formerly degraded small stream (Favata et al., 2018). Hence, densities of fish in habitat-sensitive functional guilds, in particular those of phytophils and psammophils in addition to lithophils provide well suited bioindicators for fish-based ecological assessments and should overall increase after successful river rehabilitation.

Each of the reproduction guilds of lithophils, phytophils and psammophils consisted of remarkably low densities of fish compared to the overabundant habitat generalists of eurytopic fish in any of the three studies conducted within this thesis. Amongst the latter guilds, densities of phytophils and especially of psammophils were so low, that they even could not be statistically analyzed in the third study of this thesis (Zajicek and Wolter, 2019). Tremendously low densities of all sensitive spawners and even declines in habitat generalists and rheophilic fish were identified throughout this thesis and reflect the overall highly degraded state of large rivers (EEA, 2018). Accordingly, sensitive functional guilds to specific habitat structures as well as to flow velocities, and even changes in the densities of generalists might constitute suitable fish population metrics to determine failure or success of river rehabilitation and habitat restoration. For instance, mitigation measures that would restore and protect or just protect shallow shore areas from waves and drawdown of passing vessels should result in a distinct response in fish density. In particular, densities of lithophilic but also of psammophilic and phytophilic fish were expected to increase if the respective substrata were present within the restored and protected areas. Rheophils and eurytops are strongly influenced by a multitude of pressures and therefore less sensitive to single mitigation measures. Although a comparably high sensitivity of phytophils and psammophils was clearly indicated in study two of this thesis, it could not be validated statistically for the different types of inland navigation assessed in chapter three. Hence, further detailed research is needed on dynamics of phytophilic and psammophilic fish in large rivers, in particular also in waterways with significant volumes of sport boats and river cruises. As outlined before, an increase in densities of phytophils and psammophils following successful rehabilitation and mitigation for passing vessels is hypothesized. This hypothesis might be best testable in secondary waterways, side-arms and tributaries of large rivers that provide more abundant sandy substrates and aquatic vegetation compared to the main river channel. Another opportunity to test this hypothesis might be offered by longitudinal dams, which protect shallow areas from hydraulic forces of passing vessels (Collas et al., 2018).

Responses of biodiversity metrics to pressures and inland navigation were much less pronounced than responses of life-history traits. Correspondingly, high taxonomic diversity could not be related to a good ecological status in assessments of ecological quality using fish (Foubert et al., 2018; Maire et al., 2017) and macrophytes (Vukov et al., 2018) as bioindicators. However, the latter notions should be taken with care because

(i) in large rivers, sites with good ecological quality do not exist and hence

(ii) taxonomic diversity is overall already degraded and accordingly low.

As a result, high taxonomic diversity cannot be detected because of the lack of a gradient in species richness but could be more relevant in case of more natural conditions; for instance, after successful rehabilitation measures. Further, the Shannon Index in the large rivers Elbe and Oder almost reached a value of three around 1850, i.e., before major channel modifications took place (Wolter et al., 2003). Within this thesis, also including rivers Elbe and Oder, the Shannon Index barely exceeded a value of two in any of the rivers studied, again indicating little variance in biodiversity due to prevalent degradation. Therefore, a profound increase in ecological quality should result in an increase of biodiversity. Moreover, biodiversity metrics such as species richness, Shannon Index, Simpson Index and the Fish Region Index indicated rhithralisation in potamal large rivers as was shown in chapter two (Zajicek et al., 2018). Therefore, particularly the latter biodiversity metrics provide viable taxonomic bioindicators for fish-based ecological assessments.

Implications for the rehabilitation of large rivers and waterways

Europe-wide, the Water Framework Directive (WFD) has set up the legal framework to improve ecological quality in all water bodies, initially within six years until 2015 and ultimately prolonged until 2021 and finally until 2027 (Hering et al., 2010; Poikane et al., 2014). Unprecedented challenges in implementing goals of the WFD were encountered (Hering et al., 2010), resulting in broad criticism of the WFD (reviewed in Voulvoulis et al., 2017). However, on the example of European large rivers, failure of improving ecological quality (rather ecological potential in terms of heavily modified water bodies), within a few years is not surprising at all. Large rivers have been profoundly modified over centuries, hence, river alterations spreading over hundreds of kilometers – basically over the entire river extent – (and their ecological consequences) can impossibly be reversed within a few years (e.g., Buijse et al., 2003; Eschbach et al., 2018). Even the rehabilitation of some lotic dynamics resulting in, for instance, island development, takes significant time to develop (e.g., Angelopoulos et al., 2018; Gurnell and Petts, 2002). Moreover, economical importance of large rivers as waterways and socio-economic issues such as persistence of industrial, urbanized and agricultural centers along the river courses or the fear of damage through flooding (e.g., Angelopoulos et al., 2018) prevent a complete restoration of large rivers (Buijse et al., 2002; Gore and Shields, 1995; Leyer et al., 2012). Therefore, "*restoration of large rivers to a pristine condition is probably not practical, but there is considerable potential for rehabilitation, that is, the partial restoration of riverine habitats and ecosystems*" (Gore and Shields, 1995). Trade-offs between human demands on satisfaction of social and economic needs and the growing demand on preserving and fostering biodiversity and ultimately ecological quality are insurmountable (Gordon et al., 2018). Indeed, these challenges render extensive river restoration of large rivers to formerly natural conditions utopian (Buijse et al., 2003; Geist and Hawkins, 2016). In addition, negative consequences of ship traffic have been totally neglected to date, although they significantly contribute to the degradation of essential habitats for aquatic organisms. Therefore, in large rivers, spatially inclusive and comprehensive shifts (e.g., covering the whole Europe) in ecological quality or potential (towards the better) as prescribed by the WFD are highly unrealistic, if not utopian, both today and likely also in the long run (e.g., Pander et al., 2015). Therefore, achieving an ecological quality comparable to (hypothetical) undisturbed reference conditions is highly questionable (Geist, 2014). Increasing ecological quality might be more feasible in secondary river channels in less populated areas (Pander et al., 2015) or at some carefully selected local river reaches within the primary channel (Buijse et al., 2003). However, consequences of ship traffic need to be acknowledged for and appropriate mitigation needs to be established (e.g., Díaz-Redondo et al., 2018), both in primary and secondary river channels. In secondary river channels, sport boat traffic and river cruises require as much attention as cargo vessels in primary channels.

A very recent conceptual review of the WFD (Carvalho et al., 2019) has revealed that future improvements of the WFD would strongly benefit from evidence of multiple pressures on aquatic ecosystems and from new diagnosis tools. The latter authors have further outlined that "*whilst the knowledge base on multiple stressors is developing, it remains a challenge for river basin managers to use these insights to establish a practical 'stressor-hierarchy' in management and decide which stressors to tackle first, or when it is necessary to tackle multiple stressors simultaneously*" (Carvalho et al., 2019). Concerning large rivers, this doctoral thesis at hand clearly provides potential solutions to these challenges raised by Carvalho et al. (2019):

(i) Electrofishing was proven as a suitable assessment method to conduct fish-based ecological assessments in large rivers.

(ii) Clear evidence of multiple pressures and their interactions has been provided suggesting that multiple pressures need to be tackled perpetually.

(iii) A hitherto unknown or neglected but highly influential pressure has been quantitatively tested and confirmed: Inland navigation.

(iv) A hierarchy of pressures has been established with flow velocity, navigation intensity and the loss of floodplains dominating over others.

(v) Ten diagnostic tools were tested and their benefits for fish based-assessments were discussed. For instance, habitat-sensitive spawners, in particular lithophilic fish, are highly sensitive to hydromorphological degradation and to ship traffic.

(vi) Moreover, it was shown that recreational ship traffic requires likewise as commercial river cruises and cargo vessels additional attention in river management to render goals of the WFD more feasible in any navigable water body.

Within the WFD, ecological status of water bodies is determined in comparison to a reference state that resembles natural and pristine environmental and ecological conditions. However, in European large rivers pristine and hence, reference conditions are not available (Birk et al., 2012b). All large rivers and in particular those serving as waterways are highly degraded and impacted by multiple pressures as has been outlined within this thesis. Reference conditions of such heavily modified water bodies are often derived from sporadically documented historical reports. However, even ecological conditions reported in historical reports have likely been derived from already altered environments (Wolter et al., 2003) and are consequently rather speculative. Moreover, fish assemblages in rivers have profoundly adapted to current environmental conditions (e.g. invasive species; Brandner et al., 2018; Radinger et al., 2019; Wolter and Röhr, 2010). Hence, re-shaping (rehabilitating) current fish assemblage compositions to historically derived states appears rather unattainable (Geist, 2014). Therefore, achieving the goals of increasing ecological status or potential in large rivers compared to a pristine reference conditions as prescribed by the WFD appears, likewise, rather unattainable. A comparison to historically derived reference conditions might be a misleading approach (Belliard et al., 2018) and an unachievable objective to measure the achieved improvement in ecological status. Rather, ecological improvements might be more sensitively measurable based on a comparison to the currently highly degraded conditions: Thus, the current ecological conditions in heavily modified water bodies can provide a negative reference. The major advantage of using a negative reference is that any improvement resulting from river rehabilitation and even the failure of thereof become measurable compared to a known state. In the simplest case, conditions before rehabilitation can serve as a negative reference. In this way, success rates, also to specific forms of river rehabilitation, can be determined and set in relation to the known negative reference. Therefore, it is suggested here, that in heavily modified water bodies such as large rivers and other engineered waterways for inland navigation, a negative reference mirroring the current, highly degraded state is a better means compared to a historically derived condition to detect changes and improvements in ecological status after rehabilitation. Accordingly, it is hypothesized here that a negative reference will constitute a sensitive indicator for rehabilitation success and both future research and river management are encouraged to elaborate on this issue.

Germany-wide, the initiative “The Blue Band” (www.blaues-band.bund.de) aims to rehabilitate secondary waters while promoting water based recreation at the same time and therefore follows strongly contradictory goals. On one hand, secondary waterways that have little relevance for commercial cargo transport should be dismantled and more natural environmental conditions should be re-established. On the other hand, the societal value of these water bodies should be increased at the same time by promoting water based tourism such as pleasure boating. According to the results of this thesis, in particular as derived in study three, The Blue Band initiative is likely to encounter failure in increasing ecological quality as long as motorized ship traffic such as pleasure boating and river cruising persist or even increase in rehabilitated river reaches. Speed limits (BAW, 2016) or additional mitigation measures (e.g., Collas et al., 2018; Weber et al., 2012; Weber and Wolter, 2017) need to be implemented along with the restoration of environmental conditions to protect shallow spawning, nursery and living habitats of aquatic organisms, in particular lithophilic, phytophilic and psammophilic fish, from hydraulic forces induced by passing vessels. Mitigating for ship traffic will strongly increase the likelihood for a successful rehabilitation of secondary waterways by the Blue Band Initiative.

Conclusions

Electrofishing is well suitable to representatively assess both functional and structural fish population metrics in large rivers but trawling complements the full species inventory. Functional fish population metrics such as densities of fish in habitat-sensitive reproduction guilds (predominantly lithophils but also psammophils and phytophils) provide valuable diagnostic tools outperforming taxonomic traits in assessing the environmental impacts of specific pressures. Multiple pressures are prevailing in large rivers but increased flow velocities, navigation intensities, the loss of floodplains and interactions amongst the latter clearly stand out. Remarkably, commercial cargo navigation is as detrimental as hydromorphological degradation of the river channel. Even more strikingly, recreational sport boats and commercial river cruises distinctly affect fish assemblages to cargo vessels. Any form of motorized ship traffic constitutes a substantial but hitherto neglected pressure that requires additional attention in river management and to complement comprehensive river rehabilitation. As a result of multiple pressures including inland navigation, large rivers progressively undergo habitat simplification and faunal homogenization which is well reflected in the overall fish community of the large rivers analyzed: Typical riverine and habitat sensitive fish are delimited whereas habitat generalists expand.

References

Aarts, B.G.W., Nienhuis, P.H., 2003. Fish zonations and guilds as the basis for assessment of ecological integrity of large rivers. Hydrobiologia 500, 157–178. https://doi.org/10.1023/A:1024638726162

Aarts, B.G.W., Van Den Brink, F.W.B., Nienhuis, P.H., 2004. Habitat loss as the main cause of the slow recovery of fish faunas of regulated large rivers in Europe: the transversal floodplain gradient. River Res. Applic. 20, 3–23. https://doi.org/10.1002/rra.720

Adams, S.R., Keevin, T.M., Killgore, K.J., Hoover, J.J., 1999. Stranding potential of young fishes subjected to simulated vessel-induced drawdown. Transactions of the American Fisheries Society 128, 1230–1234. https://doi.org/10.1577/1548-8659(1999)128<1230:SPOYFS>2.0.CO;2

Angelopoulos, N.V., Harvey, J.P., Bolland, J.D., Nunn, A.D., Noble, R.A.A., Smith, M.A., Taylor, M.J., Masters, J.E.G., Moxon, J., Cowx, I.G., 2018. Overcoming the dichotomy of implementing societal flood risk management while conserving instream fish habitat – A long-term study from a highly modified urban river. Journal of Environmental Management 224, 69–76. https://doi.org/10.1016/j.jenvman.2018.07.030

Aparicio, E., Carmona-Catot, G., Moyle, P.B., García-Berthou, E., 2011. Development and evaluation of a fish-based index to assess biological integrity of Mediterranean streams. Aquatic Conserv: Mar. Freshw. Ecosyst. 21, 324–337. https://doi.org/10.1002/aqc.1197

Arias, M.E., Wittmann, F., Parolin, P., Murray-Hudson, M., Cochrane, T.A., 2018. Interactions between flooding and upland disturbance drives species diversity in large river floodplains. Hydrobiologia 814, 5–17. https://doi.org/10.1007/s10750-016-2664-3

Arlinghaus, R., Engelhardt, C., Sukhodolov, A., Wolter, C., 2002. Fish recruitment in a canal with intensive navigation: implications for ecosystem management. Journal of Fish Biology 61, 1386–1402. https://doi.org/10.1111/j.1095-8649.2002.tb02484.x

Athammer, W. (Ed.), 1969. Die Donau als Verkehrsweg Südosteuropas und die Großschiffahrtsstraße Rhein-Main-Donau, Südosteuropa-Studien. Eigenverlag der Südosteuropa-Gesellschaft München, München.

Bączyk, A., Wagner, M., Okruszko, T., Grygoruk, M., 2018. Influence of technical maintenance measures on ecological status of agricultural lowland rivers – Systematic review and implications for river management. Science of The Total Environment 627, 189–199. https://doi.org/10.1016/j.scitotenv.2018.01.235

Ball, E.E., Smith, D.E., Anderson, E.J., Skufca, J.D., Twiss, M.R., 2018. Water velocity modeling can delineate nearshore and main channel plankton environments in a large river. Hydrobiologia 815, 125–140. https://doi.org/10.1007/s10750-018-3556-5

Balon, E.K., 1981. Additions and amendments to the classification of reproductive styles in fishes. Environ Biol Fish 6, 377–389. https://doi.org/10.1007/BF00005769

Balon, E.K., 1975. Reproductive guilds of fishes: A proposal and definition. J. Fish. Res. Bd. Can. 32, 821–864. https://doi.org/10.1139/f75-110

Baumgartner, M.T., Oliveira, A.G. de, Agostinho, A.A., Gomes, L.C., 2018. Fish functional diversity responses following flood pulses in the upper Paraná River floodplain. Ecology of Freshwater Fish 27, 910–919. https://doi.org/10.1111/eff.12402

BAW, 2016. Driving Dynamics of Inland Vessels, published in German language by VBW in July 2013; translation and revision by BAW in July 2016. ed. BAW - Bundesanstalt für Wasserbau (Federal Warterways Engineering Research Institute).

Beier, U., Degerman, E., Melcher, A., Rogers, C., Wirlöf, H., 2007. Processes of collating a European fisheries database to meet the objectives of the European Union Water Framework Directive. Fisheries Management and Ecology 14, 407–416. https://doi.org/10.1111/j.1365-2400.2007.00579.x

Belliard, J., Beslagic, S., Delaigue, O., Tales, E., 2018. Reconstructing long-term trajectories of fish assemblages using historical data: the Seine River basin (France) during the last two centuries. Environ Sci Pollut Res 25, 23430–23450. https://doi.org/10.1007/s11356-016-7095-1

Benejam, L., Angermeier, P.L., Munné, A., García-Berthou, E., 2010. Assessing effects of water abstraction on fish assemblages in Mediterranean streams. Freshwater Biology 55, 628–642. https://doi.org/10.1111/j.1365-2427.2009.02299.x

Benitez, J.-P., Dierckx, A., Nzau Matondo, B., Rollin, X., Ovidio, M., 2018. Movement behaviours of potamodromous fish within a large anthropised river after the reestablishment of the longitudinal connectivity. Fisheries Research 207, 140–149. https://doi.org/10.1016/j.fishres.2018.06.008

Benitez, J.-P., Matondo, B.N., Dierckx, A., Ovidio, M., 2015. An overview of potamodromous fish upstream movements in medium-sized rivers, by means of fish passes monitoring. Aquat Ecol 49, 481–497. https://doi.org/10.1007/s10452-015-9541-4

Berg, R., Gaumert, T., Kämmereit, M., Klinger, H., Lemcke, R., Leuner, E., Wolter, C., Dußling, U., 2004. The German river typology with respect to fish-faunistic reference conditions, in: Steinberg, C., Calmano, W., Klapper, H., Wilken, R.-D. (Eds.), Handbuch Angewandte Limnologie. Ecomed-Verlag, Landsberg, pp. 12–17.

Bierschenk, A.M., Mueller, M., Pander, J., Geist, J., 2019. Impact of catchment land use on fish community composition in the headwater areas of Elbe, Danube and Main. Science of The Total Environment 652, 66–74. https://doi.org/10.1016/j.scitotenv.2018.10.218

Birk, S., Bonne, W., Borja, A., Brucet, S., Courrat, A., Poikane, S., Solimini, A., van de Bund, W., Zampoukas, N., Hering, D., 2012a. Three hundred ways to assess Europe's surface waters: An almost complete overview of biological methods to implement the Water Framework Directive. Ecological Indicators 18, 31–41. https://doi.org/10.1016/j.ecolind.2011.10.009

Birk, S., van KOUWEN, L., Willby, N., 2012b. Harmonising the bioassessment of large rivers in the absence of near-natural reference conditions – a case study of the Danube River. Freshwater Biology 57, 1716–1732. https://doi.org/10.1111/j.1365-2427.2012.02831.x

Blabolil, P., Duras, J., Jůza, T., Kočvara, L., Matěna, J., Muška, M., Říha, M., Vejřík, L., Holubová, M., Peterka, J., 2018. Assessment of burbot Lota lota (L. 1758) population sustainability in central European reservoirs. Journal of Fish Biology 92, 1545–1559. https://doi.org/10.1111/jfb.13610

Blondel, J., 2003. Guilds or functional groups: does it matter? Oikos 100, 223–231. https://doi.org/10.1034/j.1600-0706.2003.12152.x

Bohlin, T., Hamrin, S., Heggberget, T., Rasmussen, G., Saltveit, S., 1989. Electrofishing — theory and practice with special emphasis on salmonids. Hydrobiologia 173, 9–43. https://doi.org/10.1007/BF00008596

Bonar, S.A., Mercado-Silva, N., Hubert, W.A., Beard, T.D., Dave, G., Kubečka, J., Graeb, B.D.S., Lester, N.P., Porath, M., Winfield, I.J., 2017. Standard Methods for Sampling Freshwater Fishes: Opportunities for International Collaboration. Fisheries 42, 150–156. https://doi.org/10.1080/03632415.2017.1276352

Boys, C.A., Thoms, M.C., 2006. A large-scale, hierarchical approach for assessing habitat associations of fish assemblages in large dryland rivers. Hydrobiologia 572, 11–31. https://doi.org/10.1007/s10750-005-0004-0

Brabender, M., Weitere, M., Anlanger, C., Brauns, M., 2016. Secondary production and richness of native and non-native macroinvertebrates are driven by human-altered shoreline morphology in a large river. Hydrobiologia 776, 51–65. https://doi.org/10.1007/s10750-016-2734-6

Branco, P., Amaral, S.D., Ferreira, M.T., Santos, J.M., 2017. Do small barriers affect the movement of freshwater fish by increasing residency? Science of The Total Environment 581–582, 486–494. https://doi.org/10.1016/j.scitotenv.2016.12.156

Brandner, J., Cerwenka, A.F., Schliewen, U.K., Geist, J., 2018. Invasion strategies in round goby (Neogobius melanostomus): Is bigger really better? PLOS ONE 13, e0190777. https://doi.org/10.1371/journal.pone.0190777

Brinker, A., Chucholl, C., Behrmann-Godel, J., Matzinger, M., Basen, T., Baer, J., 2018. River damming drives population fragmentation and habitat loss of the threatened Danube streber (Zingel streber): Implications for conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 28, 587–599. https://doi.org/10.1002/aqc.2878

Britton, J.R., Pegg, J., 2011. Ecology of European Barbel Barbus Barbus: Implications for river, fishery, and conservation management. Reviews in Fisheries Science 19, 321–330. https://doi.org/10.1080/10641262.2011.599886

Buck, W., Felkel, K., Gerhard, H., Kalweit, H., van Malde, J., Nippes, K.-R., Ploeger, B., Schmitz, W., 1993. Der Rhein unter der Einwirkung des Menschen - Ausbau, Schifffahrt, Wasserwirtschaft (No. Bericht Nr. I-11 der KHR), KHR-Arbeitsgruppe “Anthropogene Einflüsse auf das Abflußregime.” Internationale Kommission für die Hydrologie des Rheingebietes, Lelystad, NL.

Buijse, A.D., Coops, H., Staras, M., Jans, L.H., Van Geest, G.J., Grift, R.E., Ibelings, B.W., Oosterberg, W., Roozen, F.C.J.M., 2002. Restoration strategies for river floodplains along large lowland rivers in Europe. Freshwater Biology 47, 889–907. https://doi.org/10.1046/j.1365-2427.2002.00915.x

Buijse, A.D., Klijn, F., Leuven, R.S.E.W., Middelkoop, H., Schiemer, F., Thorp, J.H., Wolfert, H.P., 2003. Rehabilitation of large rivers: references, achievements and integration into river management. Large Rivers 715–738. https://doi.org/10.1127/lr/15/2003/715

Bunn, S.E., Arthington, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. Environ Manage 30, 492–507.

BVB, 2017. The power of inland navigation. Dutch Inland navigation Information Agency (BVB).

Carvalho, L., Mackay, E.B., Cardoso, A.C., Baattrup-Pedersen, A., Birk, S., Blackstock, K.L., Borics, G., Borja, A., Feld, C.K., Ferreira, M.T., Globevnik, L., Grizzetti, B., Hendry, S., Hering, D., Kelly, M., Langaas, S., Meissner, K., Panagopoulos, Y., Penning, E., Rouillard, J., Sabater, S., Schmedtje, U., Spears, B.M., Venohr, M., van de Bund, W., Solheim, A.L., 2019. Protecting and restoring Europe’s waters: An analysis of the future development needs of the Water Framework Directive. Science of The Total Environment 658, 1228–1238. https://doi.org/10.1016/j.scitotenv.2018.12.255

CCNR, 2016. Inland navigation in Europe (No. Annual Report 2016). Central Commission for the Navigation of the Rhine, Strasbourg.

Colin, N., Villéger, S., Wilkes, M., de Sostoa, A., Maceda-Veiga, A., 2018. Functional diversity measures revealed impacts of non-native species and habitat degradation on species-poor freshwater fish assemblages. Science of The Total Environment 625, 861–871. https://doi.org/10.1016/j.scitotenv.2017.12.316

Collas, F.P.L., Buijse, A.D., van den Heuvel, L., van Kessel, N., Schoor, M.M., Eerden, H., Leuven, R.S.E.W., 2018. Longitudinal training dams mitigate effects of shipping on environmental conditions and fish density in the littoral zones of the river Rhine. Science of The Total Environment 619–620, 1183–1193. https://doi.org/10.1016/j.scitotenv.2017.10.299

Craig, L.S., Olden, J.D., Arthington, A.H., Entrekin, S., Hawkins, C.P., Kelly, J.J., Kennedy, T.A., Maitland, B.M., Rosi, E.J., Roy, A.H., Strayer, D.L., Tank, J.L., West, A.O., Wooten, M.S., 2017. Meeting the challenge of interacting threats in freshwater ecosystems: A call to scientists and managers. Elem Sci Anth 5, 72. https://doi.org/10.1525/elementa.256

Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters 11, 1304–1315. https://doi.org/10.1111/j.1461-0248.2008.01253.x

Darling, E.S., Côté, I.M., 2008. Quantifying the evidence for ecological synergies. Ecology Letters 11, 1278–1286. https://doi.org/10.1111/j.1461-0248.2008.01243.x

Darwall, W., Bremerich, V., Wever, A.D., Dell, A.I., Freyhof, J., Gessner, M.O., Grossart, H.-P., Harrison, I., Irvine, K., Jähnig, S.C., Jeschke, J.M., Lee, J.J., Lu, C., Lewandowska, A.M., Monaghan, M.T., Nejstgaard, J.C., Patricio, H., Schmidt-Kloiber, A., Stuart, S.N., Thieme, M., Tockner, K., Turak, E., Weyl, O., 2018. The Alliance for Freshwater Life: A global call to unite efforts for freshwater biodiversity science and conservation. Aquatic Conservation: Marine and Freshwater Ecosystems 28, 1015–1022. https://doi.org/10.1002/aqc.2958

Davis, A.M., Pusey, B.J., Pearson, R.G., 2018. Big floods, big knowledge gap: Food web dynamics in a variable river system. Ecology of Freshwater Fish 27, 898–909. https://doi.org/10.1111/eff.12401

De Leeuw, J.J., Buijse, A.D., Haidvogl, G., Lapinska, M., Noble, R., Repecka, R., Virbickas, T., Wiśniewolski, W., Wolter, C., 2007. Challenges in developing fish-based ecological assessment methods for large floodplain rivers. Fisheries Management and Ecology 14, 483–494. https://doi.org/10.1111/j.1365-2400.2007.00576.x

Décamps, H., Fortuné, M., Gazelle, F., Pautou, G., 1988. Historical influence of man on the riparian dynamics of a fluvial landscape. Landscape Ecol 1, 163–173. https://doi.org/10.1007/BF00162742

Dembkowski, D.J., Wuellner, M.R., Willis, D.W., 2012. Sampling glacial lake littoral fish assemblages with four gears. North American Journal of Fisheries Management 32, 1160–1166. https://doi.org/10.1080/02755947.2012.728176

Dettmers, J.M., Gutreuter, S., Wahl, D.H., Soluk, D.A., 2001. Patterns in abundance of fishes in main channels of the upper Mississippi River system. Can. J. Fish. Aquat. Sci. 58, 933–942. https://doi.org/10.1139/f01-046

Díaz-Redondo, M., Egger, G., Marchamalo, M., Damm, C., Oliveira, R.P. de, Schmitt, L., 2018. Targeting lateral connectivity and morphodynamics in a large river-floodplain system: The upper Rhine River. River Research and Applications 34, 734–744. https://doi.org/10.1002/rra.3287

Diaz-Redondo, M., Egger, G., Marchamalo, M., Hohensinner, S., Dister, E., 2017. Benchmarking fluvial dynamics for process-based river restoration: The upper Rhine river (1816–2014). River Research and Applications 33, 403–414. https://doi.org/10.1002/rra.3077

Drake, D.C., Gray, B.R., Forbes, N., 2018. Aquatic vegetation responses to island construction (habitat restoration) in a large floodplain river. River Research and Applications 34, 765–776. https://doi.org/10.1002/rra.3307

Duerregger, A., Pander, J., Palt, M., Mueller, M., Nagel, C., Geist, J., 2018. The importance of stream interstitial conditions for the early-life-stage development of the European nase (Chondrostoma nasus L.). Ecology of Freshwater Fish 27, 920–932. https://doi.org/10.1111/eff.12403

Dußling, U., 2009. Handbuch zu fiBS, Schriftenreihe des Verbandes Deutscher Fischereiverwaltungsbeamter und Fischereiwissenschaftler e.V. Verband Deutscher Fischereiverwaltungsbeamter und Fischereiwissenschaftler e.V., Offenbach am Main.

Dußling, U., Bischoff, A., Haberbosch, R., Hoffmann, A., Klinger, H., Wolter, C., Wysujack, K., Berg, R., 2004. The fish-based assessment system - description of the German approach, in: Steinberg, C., Calmano, W., Klapper, H., Wilken, R.-D. (Eds.), Handbuch Angewandte Limnologie. Ecomed-Verlag, Landsberg, pp. 27–38.

Dynesius, M., Nilsson, C., 1994. Fragmentation and flow regulation of river systems in the Northern third of the world. Science 266, 753–762. https://doi.org/10.1126/science.266.5186.753

EEA, 2018. European waters – assessment of status and pressures 2018 (No. EEA report 7/2018). European Environment Agency - EEA, Copenhagen.

England, J., Wilkes, M.A., 2018. Does river restoration work? Taxonomic and functional trajectories at two restoration schemes. Science of The Total Environment 618, 961–970. https://doi.org/10.1016/j.scitotenv.2017.09.014

Erős, T., Bammer, V., György, Á.I., Pehlivanov, L., Schabuss, M., Zornig, H., Weiperth, A., Szalóky, Z., 2017. Typology of a great river using fish assemblages: Implications for the bioassessment of the Danube river. River Research and Applications 33, 37–49. https://doi.org/10.1002/rra.3060

Erős, T., Kuehne, L., Dolezsai, A., Sommerwerk, N., Wolter, C., 2019. A systematic review of assessment and conservation management in large floodplain rivers – Actions postponed. Ecological Indicators 98, 453–461. https://doi.org/10.1016/j.ecolind.2018.11.026

Erős, T., Tóth, B., Sevcsik, A., Schmera, D., 2008. Comparison of fish assemblage diversity in natural and artificial rip-rap habitats in the littoral zone of a large river (river Danube,

Hungary). International Review of Hydrobiology 93, 88–105. https://doi.org/10.1002/iroh.200710976
Eschbach, D., Schmitt, L., Imfeld, G., May, J.-H., Payraudeau, S., Preusser, F., Trauerstein, M., Skupinski, G., 2018. Long-term temporal trajectories to enhance restoration efficiency and sustainability on large rivers: an interdisciplinary study. Hydrology and Earth System Sciences 22, 2717–2737. https://doi.org/10.5194/hess-22-2717-2018
Favata, C.A., Maia, A., Pant, M., Nepal, V., Colombo, R.E., 2018. Fish assemblage change following the structural restoration of a degraded stream. River Research and Applications 34, 927–936. https://doi.org/10.1002/rra.3336
Fischer, J.L., Roseman, E.F., Mayer, C.M., Qian, S., 2018. Effectiveness of shallow water habitat remediation for improving fish habitat in a large temperate river. Ecological Engineering 123, 54–64. https://doi.org/10.1016/j.ecoleng.2018.07.022
Flotemersch, J.E., Stribling, J.B., Hughes, R.M., Reynolds, L., Paul, M.J., Wolter, C., 2011. Site length for biological assessment of boatable rivers. River Res. Applic. 27, 520–535. https://doi.org/10.1002/rra.1367
Förster, K., 1964. Die Bedeutung der Rheinregion für den Doanauraum und des Donauraums für die Rheinregion, in: Vogel, R. (Ed.), Südosteuropa-Studien. Südosteuropa-Verlagsgesellschaft m.b.H., München, p. 23.
Foubert, A., Lecomte, F., Legendre, P., Cusson, M., 2018. Spatial organisation of fish communities in the St. Lawrence River: a test for longitudinal gradients and spatial heterogeneities in a large river system. Hydrobiologia 809, 155–173. https://doi.org/10.1007/s10750-017-3457-z
Freyhof, J., Brooks, E., 2011. European red list of freshwater fishes, IUCN red list of threatened species. Regional assessments. Publications Office of the European Union ; IUCN, Luxembourg : [Gland, Switzerland].
Friberg, N., Angelopoulos, N.V., Buijse, A.D., Cowx, I.G., Kail, J., Moe, T.F., Moir, H., O'Hare, M.T., Verdonschot, P.F.M., Wolter, C., 2016. Chapter eleven - effective river restoration in the 21st century: From trial and error to novel evidence-based approaches, in: Alex J. Dumbrell, R.L.K. and G.W. (Ed.), Advances in Ecological Research, Large-Scale Ecology: Model Systems to Global Perspectives. Academic Press, pp. 535–611. https://doi.org/10.1016/bs.aecr.2016.08.010
Gabel, F., Garcia, X.-F., Brauns, M., Sukhodolov, A., Leszinski, M., Pusch, M.T., 2008. Resistance to ship-induced waves of benthic invertebrates in various littoral habitats. Freshwater Biology 53, 1567–1578. https://doi.org/10.1111/j.1365-2427.2008.01991.x
Gabel, F., Garcia, X.F., Schnauder, I., Pusch, M.T., 2012. Effects of ship-induced waves on littoral benthic invertebrates. Freshwater Biology 57, 2425–2435. https://doi.org/10.1111/fwb.12011
Gabel, F., Lorenz, S., Stoll, S., 2017. Effects of ship-induced waves on aquatic ecosystems. Science of The Total Environment 601–602, 926–939. https://doi.org/10.1016/j.scitotenv.2017.05.206
Geist, J., 2014. Trends and Directions in Water Quality and Habitat Management in the Context of the European Water Framework Directive. Fisheries 39, 219–220. https://doi.org/10.1080/03632415.2014.903838
Geist, J., Hawkins, S.J., 2016. Habitat recovery and restoration in aquatic ecosystems: current progress and future challenges. Aquatic Conservation: Marine and Freshwater Ecosystems 26, 942–962. https://doi.org/10.1002/aqc.2702
Goffaux, D., Grenouillet, G., Kestemont, P., 2005. Electrofishing versus gillnet sampling for the assessment of fish assemblages in large rivers. Archiv für Hydrobiologie 162, 73–90. https://doi.org/10.1127/0003-9136/2005/0162-0073
Gordon, T. a. C., Harding, H.R., Clever, F.K., Davidson, I.K., Davison, W., Montgomery, D.W., Weatherhead, R.C., Windsor, F.M., Armstrong, J.D., Bardonnet, A., Bergman, E., Britton, J.R., Côté, I.M., D'agostino, D., Greenberg, L.A., Harborne, A.R., Kahilainen, K.K., Metcalfe, N.B., Mills, S.C., Milner, N.J., Mittermayer, F.H., Montorio, L., Nedelec, S.L., Prokkola, J.M., Rutterford, L.A., Salvanes, A.G.V., Simpson, S.D., Vainikka, A., Pinnegar, J.K., Santos, E.M., 2018. Fishes in a changing world: learning from the past to promote

sustainability of fish populations. Journal of Fish Biology 92, 804–827. https://doi.org/10.1111/jfb.13546
Gore, J.A., Shields, F.D., 1995. Can large rivers be restored? BioScience 45, 142–152. https://doi.org/10.2307/1312553
Gregory, K.J., 2006. The human role in changing river channels. Geomorphology, 37th Binghamton Geomorphology Symposium 79, 172–191. https://doi.org/10.1016/j.geomorph.2006.06.018
Gurnell, A.M., Petts, G.E., 2002. Island-dominated landscapes of large floodplain rivers, a European perspective. Freshwater Biology 47, 581–600. https://doi.org/10.1046/j.1365-2427.2002.00923.x
Haidvogl, G., 2018. Historic Milestones of Human River Uses and Ecological Impacts, in: Schmutz, S., Sendzimir, J. (Eds.), Riverine Ecosystem Management: Science for Governing Towards a Sustainable Future, Aquatic Ecology Series. Springer International Publishing, Cham, pp. 19–39. https://doi.org/10.1007/978-3-319-73250-3_2
Hauer, F.R., Locke, H., Dreitz, V.J., Hebblewhite, M., Lowe, W.H., Muhlfeld, C.C., Nelson, C.R., Proctor, M.F., Rood, S.B., 2016. Gravel-bed river floodplains are the ecological nexus of glaciated mountain landscapes. Science Advances 2, e1600026. https://doi.org/10.1126/sciadv.1600026
Hayes, D.S., Brändle, J.M., Seliger, C., Zeiringer, B., Ferreira, T., Schmutz, S., 2018. Advancing towards functional environmental flows for temperate floodplain rivers. Science of The Total Environment 633, 1089–1104. https://doi.org/10.1016/j.scitotenv.2018.03.221
Hein, T., Funk, A., Pletterbauer, F., Graf, W., Zsuffa, I., Haidvogl, G., Schinegger, R., Weigelhofer, G., in press. Management challenges related to long-term ecological impacts, complex stressor interactions, and different assessment approaches in the Danube River Basin. River Research and Applications 0. https://doi.org/10.1002/rra.3243
Henning, M., Hentschel, B., 2013. Sedimentation and flow patterns induced by regular and modified groynes on the River Elbe, Germany. Ecohydrology 6, 598–610. https://doi.org/10.1002/eco.1398
Hering, D., Borja, A., Carstensen, J., Carvalho, L., Elliott, M., Feld, C.K., Heiskanen, A.-S., Johnson, R.K., Moe, J., Pont, D., Solheim, A.L., de Bund, W. van, 2010. The European Water Framework Directive at the age of 10: A critical review of the achievements with recommendations for the future. Science of The Total Environment 408, 4007–4019. https://doi.org/10.1016/j.scitotenv.2010.05.031
Hering, D., Carvalho, L., Argillier, C., Beklioglu, M., Borja, A., Cardoso, A.C., Duel, H., Ferreira, T., Globevnik, L., Hanganu, J., Hellsten, S., Jeppesen, E., Kodeš, V., Solheim, A.L., Nõges, T., Ormerod, S., Panagopoulos, Y., Schmutz, S., Venohr, M., Birk, S., 2015. Managing aquatic ecosystems and water resources under multiple stress — An introduction to the MARS project. Science of The Total Environment 503–504, 10–21. https://doi.org/10.1016/j.scitotenv.2014.06.106
Hjältén, J., Nilsson, C., Jørgensen, D., Bell, D., 2016. Forest–stream links, anthropogenic stressors, and climate change: Implications for restoration planning. BioScience 66, 646–654. https://doi.org/10.1093/biosci/biw072
Höckendorff, S., Tonkin, J.D., Haase, P., Bunzel-Drüke, M., Zimball, O., Scharf, M., Stoll, S., 2017. Characterizing fish responses to a river restoration over 21 years based on species' traits. Conservation Biology 31, 1098–1108. https://doi.org/10.1111/cobi.12908
Hohensinner, S., Hauer, C., Muhar, S., 2018. River Morphology, Channelization, and Habitat Restoration, in: Schmutz, S., Sendzimir, J. (Eds.), Riverine Ecosystem Management: Science for Governing Towards a Sustainable Future, Aquatic Ecology Series. Springer International Publishing, Cham, pp. 41–65. https://doi.org/10.1007/978-3-319-73250-3_3
Holland, A.M., Schauber, E.M., Nielsen, C.K., Hellgren, E.C., 2018. Stream community richness predicts apex predator occupancy dynamics in riparian systems. Oikos 127, 1422–1436. https://doi.org/10.1111/oik.05085
Holland, L.E., Sylvester, J.R., 1983. Distribution of Larval Fishes Related to Potential Navigation Impacts on the Upper Mississippi River, Pool 7. Transactions of the American Fisheries

Society 112, 293–301. https://doi.org/10.1577/1548-8659(1983)112<293:DOLFRT>2.0.CO;2

http://www.blaues-band.bund.de, 2018. Bundesprogramm Blaues Band Deutschland [WWW Document]. Bundesprogramm Blaues Band Deutschland. URL http://www.blaues-band.bund.de/Projektseiten/Blaues_Band/DE/00_Home/home_node.html (accessed 5.23.18).

Huckstorf, V., Lewin, W.-C., Mehner, T., Wolter, C., 2011. Impoverishment of YOY-fish assemblages by intense commercial navigation in a large Lowland river. River Res. Applic. 27, 1253–1263. https://doi.org/10.1002/rra.1420

Illies, J., 1961. Versuch einer allgemeinen biozönotischen Gliederung der Fließgewässer. Int. Revue ges. Hydrobiol. Hydrogr. 46, 205–213. https://doi.org/10.1002/iroh.19610460205

Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D., Chimimba, C.T., 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. Glob Change Biol 22, 180–189. https://doi.org/10.1111/gcb.13028

Jager, N.R.D., Houser, J.N., 2016. Patchiness in a large floodplain river: Associations among hydrology, nutrients, and fish communities. River Research and Applications 32, 1915–1926. https://doi.org/10.1002/rra.3026

Jourdan, J., Plath, M., Tonkin, J.D., Ceylan, M., Dumeier, A.C., Gellert, G., Graf, W., Hawkins, C.P., Kiel, E., Lorenz, A.W., Matthaei, C.D., Verdonschot, P.F.M., Verdonschot, R.C.M., Haase, P., in press. Reintroduction of freshwater macroinvertebrates: challenges and opportunities. Biological Reviews 0. https://doi.org/10.1111/brv.12458

Jungwirth, M., Haidvogl, G., Hohensinner, S., Muhar, S., Schmutz, S., Waidbacher, H., 2003. Leitbild-specific measures for the rehabilitation of the heavily modified Austrian Danube River. Large Rivers 17–36. https://doi.org/10.1127/lr/15/2003/17

Kail, J., Brabec, K., Poppe, M., Januschke, K., 2015. The effect of river restoration on fish, macroinvertebrates and aquatic macrophytes: A meta-analysis. Ecological Indicators 58, 311–321. https://doi.org/10.1016/j.ecolind.2015.06.011

Karr, J.R., 1981. Assessment of biotic integrity using fish communities. Fisheries 6, 21–27. https://doi.org/10.1577/1548-8446(1981)006<0021:AOBIUF>2.0.CO;2

Karr, J.R., Dudley, D.R., 1981. Ecological perspective on water quality goals. Environmental Management 5, 55–68. https://doi.org/10.1007/BF01866609

Kucera-Hirzinger, V., Schludermann, E., Zornig, H., Weissenbacher, A., Schabuss, M., Schiemer, F., 2008. Potential effects of navigation-induced wave wash on the early life history stages of riverine fish. Aquat. Sci. 71, 94–102. https://doi.org/10.1007/s00027-008-8110-5

Lamouroux, N., Olivier, J.-M., Persat, H., PouilLy, M., Souchon, Y., Statzner, B., 1999. Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. Freshwater Biology 42, 275–299. https://doi.org/10.1046/j.1365-2427.1999.444498.x

Lapointe, N.W.R., 2014. Effects of shoreline type, riparian zone and instream microhabitat on fish species richness and abundance in the Detroit River. Journal of Great Lakes Research, Conservation and Management of Fisheries and Aquatic Communities in Great Lakes Connecting Channels 40, 62–68. https://doi.org/10.1016/j.jglr.2013.02.004

Ławicki, Ł., Pawlaczyk, P., Świerkosz, K., Żurek, R., 2017. Poland: Central European large river ecosystems under unprecedented threat. Oryx 51, 397–397. https://doi.org/10.1017/S0030605317000722

Lechner, A., Keckeis, H., Schludermann, E., Loisl, F., Humphries, P., Glas, M., Tritthart, M., Habersack, H., 2014. Shoreline configurations affect dispersal patterns of fish larvae in a large river. ICES J. Mar. Sci. 71, 930–942. https://doi.org/10.1093/icesjms/fst139

Leclere, J., Belliard, J., Oberdorff, T., 2012. Young-of-the-year fish assemblages as indicators of anthropogenic disturbances in large tributaries of the Seine River Basin (France). Hydrobiologia 694, 99–116. https://doi.org/10.1007/s10750-012-1135-8

Leitão, R.P., Zuanon, J., Villéger, S., Williams, S.E., Baraloto, C., Fortunel, C., Mendonça, F.P., Mouillot, D., 2016. Rare species contribute disproportionately to the functional structure of species assemblages. Proc. Biol. Sci. 283. https://doi.org/10.1098/rspb.2016.0084

Lemm, J.U., Feld, C.K., 2017. Identification and interaction of multiple stressors in central European lowland rivers. Sci. Total Environ. 603–604, 148–154. https://doi.org/10.1016/j.scitotenv.2017.06.092

Leyer, I., Mosner, E., Lehmann, B., 2012. Managing floodplain-forest restoration in European river landscapes combining ecological and flood-protection issues. Ecological Applications 22, 240–249. https://doi.org/10.1890/11-0021.1

Liedermann, M., Tritthart, M., Gmeiner, P., Hinterleitner, M., Schludermann, E., Keckeis, H., Habersack, H., 2014. Typification of vessel-induced waves and their interaction with different bank types, including management implications for river restoration projects. Hydrobiologia 729, 17–31. https://doi.org/10.1007/s10750-014-1829-1

Lima, A.C., Wrona, F.J., Soares, A.M.V.M., 2017. Fish traits as an alternative tool for the assessment of impacted rivers. Rev Fish Biol Fisheries 27, 31–42. https://doi.org/10.1007/s11160-016-9446-x

Loisl, F., Singer, G., Keckeis, H., 2013. Method-integrated fish assemblage structure at two spatial scales along a free-flowing stretch of the Austrian Danube. Hydrobiologia 729, 77–94. https://doi.org/10.1007/s10750-013-1588-4

Lorenz, A.W., Stoll, S., Sundermann, A., Haase, P., 2013. Do adult and YOY fish benefit from river restoration measures? Ecological Engineering 61, Part A, 174–181. https://doi.org/10.1016/j.ecoleng.2013.09.027

Lorenz, S., Leszinski, M., Graeber, D., 2016. Meander reconnection method determines restoration success for macroinvertebrate communities in a German lowland river. Internat. Rev. Hydrobiol. 101, 123–131. https://doi.org/10.1002/iroh.201501823

Love, S.A., Phelps, Q.E., Tripp, S.J., Herzog, D.P., 2017. The Importance of Shallow-Low Velocity Habitats to Juvenile Fish in the Middle Mississippi River. River Research and Applications 33, 321–327. https://doi.org/10.1002/rra.3075

Lusardi, R.A., Jeffres, C.A., Moyle, P.B., 2018. Stream macrophytes increase invertebrate production and fish habitat utilization in a California stream. River Research and Applications 34, 1003–1012. https://doi.org/10.1002/rra.3331

Lyon, J.P., Bird, T., Nicol, S., Kearns, J., O'Mahony, J., Todd, C.R., Cowx, I.G., Bradshaw, C.J.A., 2014. Efficiency of electrofishing in turbid lowland rivers: implications for measuring temporal change in fish populations. Can. J. Fish. Aquat. Sci. 71, 878–886. https://doi.org/10.1139/cjfas-2013-0287

Maire, A., Laffaille, P., Maire, J.-F., Buisson, L., 2017. Identification of priority areas for the conservation of stream fish assemblages: Implications for river management in France. River Research and Applications 33, 524–537. https://doi.org/10.1002/rra.3107

Malmqvist, B., Rundle, S., 2002. Threats to the running water ecosystems of the world. Environmental Conservation null, 134–153. https://doi.org/10.1017/S0376892902000097

Melcher, A., Schmutz, S., Haidvogl, G., Moder, K., 2007. Spatially based methods to assess the ecological status of European fish assemblage types. Fisheries Management and Ecology 14, 453–463. https://doi.org/10.1111/j.1365-2400.2007.00583.x

Meybeck, M., Helmer, R., 1989. The quality of rivers: From pristine stage to global pollution. Palaeogeography, Palaeoclimatology, Palaeoecology 75, 283–309. https://doi.org/10.1016/0031-0182(89)90191-0

Milner, V.S., Yarnell, S.M., Peek, R.A., 2019. The ecological importance of unregulated tributaries to macroinvertebrate diversity and community composition in a regulated river. Hydrobiologia 829, 291–305. https://doi.org/10.1007/s10750-018-3840-4

Morandi, B., Piégay, H., Lamouroux, N., Vaudor, L., 2014. How is success or failure in river restoration projects evaluated? Feedback from French restoration projects. Journal of Environmental Management 137, 178–188. https://doi.org/10.1016/j.jenvman.2014.02.010

Mouillot, D., Bellwood, D.R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C.E.T., Renaud, J., Thuiller, W., 2013. Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. PLOS Biology 11, e1001569. https://doi.org/10.1371/journal.pbio.1001569

Mueller, M., Pander, J., Geist, J., 2018. Comprehensive analysis of >30 years of data on stream fish population trends and conservation status in Bavaria, Germany. Biological Conservation 226, 311–320. https://doi.org/10.1016/j.biocon.2018.08.006
Mueller, M., Pander, J., Knott, J., Geist, J., 2017. Comparison of nine different methods to assess fish communities in lentic flood-plain habitats. J Fish Biol 91, 144–174. https://doi.org/10.1111/jfb.13333
Musil, J., Horký, P., Slavík, O., Zbořil, A., Horká, P., 2012. The response of the young of the year fish to river obstacles: Functional and numerical linkages between dams, weirs, fish habitat guilds and biotic integrity across large spatial scale. Ecological Indicators 23, 634–640. https://doi.org/10.1016/j.ecolind.2012.05.018
Muška, M., Tušer, M., Frouzová, J., Mrkvička, T., Ricard, D., Seďa, J., Morelli, F., Kubečka, J., 2018. Real-time distribution of pelagic fish: combining hydroacoustics, GIS and spatial modelling at a fine spatial scale. Scientific Reports 8, 5381. https://doi.org/10.1038/s41598-018-23762-z
Nagrodski, A., Raby, G.D., Hasler, C.T., Taylor, M.K., Cooke, S.J., 2012. Fish stranding in freshwater systems: Sources, consequences, and mitigation. Journal of Environmental Management 103, 133–141. https://doi.org/10.1016/j.jenvman.2012.03.007
Naus, C.J., Adams, S.R., 2018. Fish nursery habitat function of the main channel, floodplain tributaries and oxbow lakes of a medium-sized river. Ecol Freshw Fish 27, 4–18. https://doi.org/10.1111/eff.12319
Nilsson, C., Reidy, C.A., Dynesius, M., Revenga, C., 2005. Fragmentation and Flow Regulation of the World’s Large River Systems. Science 308, 405–408. https://doi.org/10.1126/science.1107887
Noble, R. a. A., Cowx, I.G., Goffaux, D., Kestemont, P., 2007. Assessing the health of European rivers using functional ecological guilds of fish communities: standardising species classification and approaches to metric selection. Fisheries Management and Ecology 14, 381–392. https://doi.org/10.1111/j.1365-2400.2007.00575.x
Nõges, P., Argillier, C., Borja, Á., Garmendia, J.M., Hanganu, J., Kodeš, V., Pletterbauer, F., Sagouis, A., Birk, S., 2015. Quantified biotic and abiotic responses to multiple stress in freshwater, marine and ground waters. Science of The Total Environment. https://doi.org/10.1016/j.scitotenv.2015.06.045
Oliveira, A.G., Baumgartner, M.T., Gomes, L.C., Dias, R.M., Agostinho, A.A., 2018. Long-term effects of flow regulation by dams simplify fish functional diversity. Freshwater Biology 63, 293–305. https://doi.org/10.1111/fwb.13064
Ormerod, S.J., Dobson, M., Hildrew, A.G., Townsend, C.R., 2010. Multiple stressors in freshwater ecosystems. Freshwater Biology 55, 1–4. https://doi.org/10.1111/j.1365-2427.2009.02395.x
Pander, J., Geist, J., 2018. The contribution of different restored habitats to fish diversity and population development in a highly modified river: A case study from the River Günz. Water 10, 1202. https://doi.org/10.3390/w10091202
Pander, J., Mueller, M., Geist, J., 2018. Habitat diversity and connectivity govern the conservation value of restored aquatic floodplain habitats. Biological Conservation 217, 1–10. https://doi.org/10.1016/j.biocon.2017.10.024
Pander, J., Mueller, M., Geist, J., 2015. Succession of fish diversity after reconnecting a large floodplain to the upper Danube River. Ecological Engineering 75, 41–50. https://doi.org/10.1016/j.ecoleng.2014.11.011
Pander, J., Mueller, M., Knott, J., Egg, L., Geist, J., 2017. Is it worth the money? The functionality of engineered shallow stream banks as habitat for juvenile fishes in heavily modified water bodies. River Research and Applications 33, 63–72. https://doi.org/10.1002/rra.3065
Paukert, C.P., 2004. Comparison of electrofishing and trammel netting variability for sampling native fishes. Journal of Fish Biology 65, 1643–1652. https://doi.org/10.1111/j.0022-1112.2004.00575.x
Pauli, G., 2010. Sustainable transport: A case study of Rhine navigation. Natural Resources Forum 34, 236–254. https://doi.org/10.1111/j.1477-8947.2010.01309.x

Pearson, W.H., Skalski, J.R., 2011. Factors affecting stranding of juvenile salmonids by wakes from ship passage in the Lower Columbia River. River Res. Applic. 27, 926–936. https://doi.org/10.1002/rra.1397

Peipoch, M., Brauns, M., Hauer, F.R., Weitere, M., Valett, H.M., 2015. Ecological simplification: Human influences on riverscape complexity. BioScience 65, 1057–1065. https://doi.org/10.1093/biosci/biv120

Petts, G.E., Möller, H., Roux, A.L., 1989. Historical change of large alluvial rivers: western Europe. John Wiley & Sons, Chichester.

Pilotto, F., Tonkin, J.D., Januschke, K., Lorenz, A.W., Jourdan, J., Sundermann, A., Hering, D., Stoll, S., Haase, P., 2019. Diverging response patterns of terrestrial and aquatic species to hydromorphological restoration. Conservation Biology 33, 132–141. https://doi.org/10.1111/cobi.13176

Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 1246752. https://doi.org/10.1126/science.1246752

PINE, 2004. Prospects of Inland Navigation within the enlarged Europe (No. Final Concise Report), Prospects of Inland Navigation within the enlarged Europe.

Piria, M., Simonović, P., Zanella, D., Ćaleta, M., Šprem, N., Paunović, M., Tomljanović, T., Gavrilović, A., Pecina, M., Špelić, I., Matulić, D., Rezić, A., Aničić, I., Safner, R., Treer, T., 2019. Long-term analysis of fish assemblage structure in the middle section of the Sava River – The impact of pollution, flood protection and dam construction. Science of The Total Environment 651, 143–153. https://doi.org/10.1016/j.scitotenv.2018.09.149

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime. BioScience 47, 769–784. https://doi.org/10.2307/1313099

Poff, N.L., Zimmerman, J.K.H., 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. Freshwater Biology 55, 194–205. https://doi.org/10.1111/j.1365-2427.2009.02272.x

Poikane, S., Zampoukas, N., Borja, A., Davies, S.P., van de Bund, W., Birk, S., 2014. Intercalibration of aquatic ecological assessment methods in the European Union: Lessons learned and way forward. Environmental Science & Policy 44, 237–246. https://doi.org/10.1016/j.envsci.2014.08.006

Pool, T.K., Olden, J.D., Whittier, J.B., Paukert, C.P., 2010. Environmental drivers of fish functional diversity and composition in the Lower Colorado River Basin. Can. J. Fish. Aquat. Sci. 67, 1791–1807. https://doi.org/10.1139/F10-095

Porreca, A.P., Pederson, C.L., Laursen, J.R., Colombo, R.E., 2013. A comparison of electrofishing methods and fyke netting to produce reliable abundance and size metrics. Journal of Freshwater Ecology 28, 585–590. https://doi.org/10.1080/02705060.2013.810555

Puijenbroek, P.J.T.M. van, Buijse, A.D., Kraak, M.H.S., Verdonschot, P.F.M., 2019. Species and river specific effects of river fragmentation on European anadromous fish species. River Research and Applications 35, 68–77. https://doi.org/10.1002/rra.3386

Radinger, J., Alcaraz-Hernández, J.D., García-Berthou, E., 2019. Environmental filtering governs the spatial distribution of alien fishes in a large, human-impacted Mediterranean river. Diversity and Distributions 0. https://doi.org/10.1111/ddi.12895

Radinger, J., Alcaraz-Hernández, J.D., García-Berthou, E., 2018a. Environmental and spatial correlates of hydrologic alteration in a large Mediterranean river catchment. Science of The Total Environment 639, 1138–1147. https://doi.org/10.1016/j.scitotenv.2018.05.227

Radinger, J., Hölker, F., Horký, P., Slavík, O., Dendoncker, N., Wolter, C., 2016. Synergistic and antagonistic interactions of future land use and climate change on river fish assemblages. Glob Change Biol 22, 1505–1522. https://doi.org/10.1111/gcb.13183

Radinger, J., Hölker, F., Horký, P., Slavík, O., Wolter, C., 2018b. Improved river continuity facilitates fishes' abilities to track future environmental changes. Journal of

Environmental Management 208, 169–179. https://doi.org/10.1016/j.jenvman.2017.12.011
Radinger, J., Wolter, C., 2014. Patterns and predictors of fish dispersal in rivers. Fish Fish 15, 456–473. https://doi.org/10.1111/faf.12028
Ramos-Merchante, A., Prenda, J., 2018. The Ecological and Conservation Status of The Guadalquivir River Basin (s Spain) Through The Application Of A Fish-based Multimetric Index. Ecological Indicators 84, 45–59. https://doi.org/10.1016/j.ecolind.2017.08.034
Randall, R.G., Minns, C.K., Cairns, V.W., Moore, J.E., 1996. The relationship between an index of fish production and submerged macrophytes and other habitat features at three littoral areas in the Great Lakes. Can. J. Fish. Aquat. Sci. 53, 35–44. https://doi.org/10.1139/f95-271
Raška, P., Dolejš, M., Hofmanová, M., 2017. Effects of Damming on Long-Term Development of Fluvial Islands, Elbe River (N Czechia). River Research and Applications 33, 471–482. https://doi.org/10.1002/rra.3104
Ravn, H.D., Lauridsen, T.L., Jepsen, N., Jeppesen, E., Hansen, P.G., Hansen, J.G., Berg, S., in press. A comparative study of three different methods for assessing fish communities in a small eutrophic lake. Ecology of Freshwater Fish 0. https://doi.org/10.1111/eff.12457
Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P.A., Johnson, P.T.J., Kidd, K.A., MacCormack, T.J., Olden, J.D., Ormerod, S.J., Smol, J.P., Taylor, W.W., Tockner, K., Vermaire, J.C., Dudgeon, D., Cooke, S.J., in press. Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 0. https://doi.org/10.1111/brv.12480
Root, R.B., 1967. The niche exploitation pattern of the blue-gray Gnatcatcher. Ecological Monographs 37, 317–350. https://doi.org/10.2307/1942327
Sagouis, A., Jabot, F., Argillier, C., 2017. Taxonomic versus functional diversity metrics: how do fish communities respond to anthropogenic stressors in reservoirs? Ecol Freshw Fish 26, 621–635. https://doi.org/10.1111/eff.12306
Sala, O.E., Chapin, F.S., Iii, Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774. https://doi.org/10.1126/science.287.5459.1770
Schiemer, F., Bartl, E., Hirzinger, V., Weissenbacher, A., Zornig, H., 2001. Der Einfluss des schifffahrtsbedingten Wellenschlages auf die Entwicklung der Fischfauna der Donau (Studie in Auftrag gegeben vom Fischereirevierverband II – Korneuburg). Nationalpark Donau-Auen GmbH.
Schinegger, R., Palt, M., Segurado, P., Schmutz, S., 2016. Untangling the effects of multiple human stressors and their impacts on fish assemblages in European running waters. Science of The Total Environment 573, 1079–1088. https://doi.org/10.1016/j.scitotenv.2016.08.143
Schinegger, R., Pucher, M., Aschauer, C., Schmutz, S., 2018. Configuration of multiple human stressors and their impacts on fish assemblages in Alpine river basins of Austria. Science of The Total Environment 616–617, 17–28. https://doi.org/10.1016/j.scitotenv.2017.10.283
Schinegger, R., Trautwein, C., Melcher, A., Schmutz, S., 2012. Multiple human pressures and their spatial patterns in European running waters. Water Environ J 26, 261–273. https://doi.org/10.1111/j.1747-6593.2011.00285.x
Schinegger, R., Trautwein, C., Schmutz, S., 2013. Pressure-specific and multiple pressure response of fish assemblages in European running waters. Limnologica - Ecology and Management of Inland Waters, 9th International Symposium on Ecohydraulics 2012 43, 348–361. https://doi.org/10.1016/j.limno.2013.05.008
Schletterer, M., Kuzovlev, V.V., Zhenikov, Y.N., Tuhtan, J.A., Haidvogl, G., Friedrich, T., Górski, K., Füreder, L., 2018. Fish fauna and fisheries of large European rivers: examples from the Volga and the Danube. Hydrobiologia 814, 45–60. https://doi.org/10.1007/s10750-017-3370-5

Schletterer, M., Shaporenko, S.I., Kuzovlev, V.V., Minin, A.E., Geest, G.J.V., Middelkoop, H., Górski, K., in press. The Volga: Management issues in the largest river basin in Europe. River Research and Applications 0. https://doi.org/10.1002/rra.3268

Schludermann, E., Liedermann, M., Hoyer, H., Tritthart, M., Habersack, H., Keckeis, H., 2013. Effects of vessel-induced waves on the YOY-fish assemblage at two different habitat types in the main stem of a large river (Danube, Austria). Hydrobiologia 729, 3–15. https://doi.org/10.1007/s10750-013-1680-9

Schmutz, S., Bakken, T.H., Friedrich, T., Greimel, F., Harby, A., Jungwirth, M., Melcher, A., Unfer, G., Zeiringer, B., 2015. Response of fish communities to hydrological and morphological alterations in hydropeaking rivers of Austria. River Res. Applic. 31, 919–930. https://doi.org/10.1002/rra.2795

Schmutz, S., Jurajda, P., Kaufmann, S., Lorenz, A.W., Muhar, S., Paillex, A., Poppe, M., Wolter, C., 2016. Response of fish assemblages to hydromorphological restoration in central and northern European rivers. Hydrobiologia 769, 67–78. https://doi.org/10.1007/s10750-015-2354-6

Schmutz, S., Kaufmann, M., Vogel, B., Jungwirth, M., Muhar, S., 2000. A multi-level concept for fish-based, river-type-specific assessment of ecological integrity. Hydrobiologia 422–423, 279–289. https://doi.org/10.1023/A:1017038820390

Schmutz, S., Moog, O., 2018. Dams: Ecological Impacts and Management, in: Schmutz, S., Sendzimir, J. (Eds.), Riverine Ecosystem Management: Science for Governing Towards a Sustainable Future, Aquatic Ecology Series. Springer International Publishing, Cham, pp. 111–127. https://doi.org/10.1007/978-3-319-73250-3_6

Seer, F.K., Brunke, M., Schrautzer, J., 2018. Mesoscale river restoration enhances the diversity of floodplain vegetation. River Research and Applications 34, 1013–1023. https://doi.org/10.1002/rra.3330

Segner, H., Schmitt-Jansen, M., Sabater, S., 2014. Assessing the impact of multiple stressors on aquatic biota: the receptor's side matters. Environ. Sci. Technol. 48, 7690–7696. https://doi.org/10.1021/es405082t

Seliger, C., Zeiringer, B., 2018. River Connectivity, Habitat Fragmentation and Related Restoration Measures, in: Schmutz, S., Sendzimir, J. (Eds.), Riverine Ecosystem Management: Science for Governing Towards a Sustainable Future, Aquatic Ecology Series. Springer International Publishing, Cham, pp. 171–186. https://doi.org/10.1007/978-3-319-73250-3_9

Shannon, C.E., 1948. A mathematical theory of communication. Bell System Technical Journal 27, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

Shannon, C.E., Weaver, W., 1949. The mathematical theory of communication, The Mathematical Theory of Communication. University of Illinois Press, Illinois.

Shell, T.M., Collier, K.J., 2018. Partitioning of macroinvertebrate communities in a large New Zealand river highlights the role of multiple shore-zone habitat types. River Research and Applications 34, 993–1002. https://doi.org/10.1002/rra.3344

Simpson, E.H., 1949. Measurement of Diversity. Nature 163, 688. https://doi.org/10.1038/163688a0

Sindilariu, P.-D., Freyhof, J., Wolter, C., 2006. Habitat use of juvenile fish in the lower Danube and the Danube delta: Implications for ecotone connectivity. Hydrobiologia 571, 51–61. https://doi.org/10.1007/s10750-006-0216-y

Söhngen, B., Koop, J., Knight, S., Rytkönen, J., Beckwith, P., Ferrari, N., Iribarren, J., Keevin, T., Wolter, C., Maynord, S., 2008. Considerations to reduce environmental impacts of vessels (PIANC REPORT No. N° 99), PIANC Report Series. PIANC, Brussels.

Somerfield, P.J., Clarke, K.R., Warwick, R.M., 2008. Simpson Index, in: Fath, B.D. (Ed.), Encyclopedia of Ecology. Academic Press, Oxford, pp. 3252–3255.

Sommerwerk, N., Wolter, C., Freyhof, J., Tockner, K., 2017. Components and drivers of change in European freshwater fish faunas. J. Biogeogr. 44, 1781–1790. https://doi.org/10.1111/jbi.13019

Spellerberg, I.F., 2008. Shannon–Wiener Index, in: Fath, B.D. (Ed.), Encyclopedia of Ecology. Academic Press, Oxford, pp. 3249–3252.

Spurgeon, J.J., Pegg, M.A., Halden, N.M., 2018. Mixed-origins of channel catfish in a large-river tributary. Fisheries Research 198, 195–202. https://doi.org/10.1016/j.fishres.2017.09.001

Staentzel, C., Arnaud, F., Combroux, I., Schmitt, L., Trémolières, M., Grac, C., Piégay, H., Barillier, A., Chardon, V., Beisel, J.-N., 2018. How do instream flow increase and gravel augmentation impact biological communities in large rivers: A case study on the Upper Rhine River. River Research and Applications 34, 153–164. https://doi.org/10.1002/rra.3237

Stoll, S., Breyer, P., Tonkin, J.D., Früh, D., Haase, P., 2016. Scale-dependent effects of river habitat quality on benthic invertebrate communities — Implications for stream restoration practice. Science of The Total Environment 553, 495–503. https://doi.org/10.1016/j.scitotenv.2016.02.126

Strayer, D.L., Findlay, S.E.G., 2010. Ecology of freshwater shore zones. Aquatic Sciences 72, 127–163. https://doi.org/10.1007/s00027-010-0128-9

Trautwein, C., Schinegger, R., Schmutz, S., 2013. Divergent reaction of fish metrics to human pressures in fish assemblage types in Europe. Hydrobiologia 718, 207–220. https://doi.org/10.1007/s10750-013-1616-4

Valova, Z., Janac, M., Svanyga, J., Jurajda, P., 2014. Structure of 0+ juvenile fish assemblages in the modified upper stretch of the River Elbe, Czech Republic. Czech J. Anim. Sci. 59, 35–44.

Van Looy, K., Tonkin, J.D., Floury, M., Leigh, C., Soininen, J., Larsen, S., Heino, J., Poff, N.L., Delong, M., Jähnig, S.C., Datry, T., Bonada, N., Rosebery, J., Jamoneau, A., Ormerod, S.J., Collier, K.J., Wolter, C., in press. The three Rs of river ecosystem resilience: Resources, recruitment, and refugia. River Research and Applications 0. https://doi.org/10.1002/rra.3396

Van Oorschot, M., Kleinhans, M., Buijse, T., Geerling, G., Middelkoop, H., 2018. Combined effects of climate change and dam construction on riverine ecosystems. Ecological Engineering 120, 329–344. https://doi.org/10.1016/j.ecoleng.2018.05.037

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E., 1980. The River Continuum Concept. Can. J. Fish. Aquat. Sci. 37, 130–137. https://doi.org/10.1139/f80-017

Vaughan, I. p., Diamond, M., Gurnell, A. m., Hall, K. a., Jenkins, A., Milner, N. j., Naylor, L. a., Sear, D. a., Woodward, G., Ormerod, S. j., 2009. Integrating ecology with hydromorphology: a priority for river science and management. Aquatic Conserv: Mar. Freshw. Ecosyst. 19, 113–125. https://doi.org/10.1002/aqc.895

Venohr, M., Langhans, S.D., Peters, O., Hölker, F., Arlinghaus, R., Mitchell, L., Wolter, C., 2018. The underestimated dynamics and impacts of water-based recreational activities on freshwater ecosystems. Environ. Rev. 26, 199–213. https://doi.org/10.1139/er-2017-0024

Verhelst, P., Baeyens, R., Reubens, J., Benitez, J.-P., Coeck, J., Goethals, P., Ovidio, M., Vergeynst, J., Moens, T., Mouton, A., 2018. European silver eel (Anguilla anguilla L.) migration behaviour in a highly regulated shipping canal. Fisheries Research 206, 176–184. https://doi.org/10.1016/j.fishres.2018.05.013

Vincent, R., 1971. River electrofishing and fish population estimates. The Progressive Fish-Culturist 33, 163–169. https://doi.org/10.1577/1548-8640(1971)33[163:REAFPE]2.0.CO;2

Vörösmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R., Davies, P.M., 2010. Global threats to human water security and river biodiversity. Nature 467, 555–561. https://doi.org/10.1038/nature09440

Voulvoulis, N., Arpon, K.D., Giakoumis, T., 2017. The EU Water Framework Directive: From great expectations to problems with implementation. Science of The Total Environment 575, 358–366. https://doi.org/10.1016/j.scitotenv.2016.09.228

Vriese, F.T., Semmekrot, S., Raat, A.J.P., 1994. Assessment of spawning and nursery areas in the river Meuse. Water Science and Technology 29, 297–299.

Vukov, D., Ilić, M., Ćuk, M., Radulović, S., Igić, R., Janauer, G.A., 2018. Combined effects of physical environmental conditions and anthropogenic alterations are associated with macrophyte habitat fragmentation in rivers - Study of the Danube in Serbia. Science of The Total Environment 634, 780–790. https://doi.org/10.1016/j.scitotenv.2018.03.367

Weber, A., Lautenbach, S., Wolter, C., 2012. Improvement of aquatic vegetation in urban waterways using protected artificial shallows. Ecological Engineering 42, 160–167. https://doi.org/10.1016/j.ecoleng.2012.01.007

Weber, A., Wolter, C., 2017. Habitat rehabilitation for juvenile fish in urban waterways: A case study from Berlin, Germany. J. Appl. Ichthyol. 33, 136–143. https://doi.org/10.1111/jai.13212

Welcomme, R.L., Winemiller, K.O., Cowx, I.G., 2006. Fish environmental guilds as a tool for assessment of ecological condition of rivers. River Res. Applic. 22, 377–396. https://doi.org/10.1002/rra.914

Wetzel, F.T., Bingham, H.C., Groom, Q., Haase, P., Kõljalg, U., Kuhlmann, M., Martin, C.S., Penev, L., Robertson, T., Saarenmaa, H., Schmeller, D.S., Stoll, S., Tonkin, J.D., Häuser, C.L., 2018. Unlocking biodiversity data: Prioritization and filling the gaps in biodiversity observation data in Europe. Biological Conservation 221, 78–85. https://doi.org/10.1016/j.biocon.2017.12.024

Winemiller, K.O., 1989. Patterns of variation in life history among South American fishes in seasonal environments. Oecologia 81, 225–241. https://doi.org/10.1007/BF00379810

Wolter, C., Arlinghaus, R., 2003. Navigation impacts on freshwater fish assemblages: the ecological relevance of swimming performance. Reviews in Fish Biology and Fisheries 13, 63–89. https://doi.org/10.1023/A:1026350223459

Wolter, C., Arlinghaus, R., Sukhodolov, A., Engelhardt, C., 2004a. A model of navigation-induced currents in inland waterways and implications for juvenile fish displacement. Environmental Management 34, 656–668. https://doi.org/10.1007/s00267-004-0201-z

Wolter, C., Bischoff, A., 2001. Seasonal changes of fish diversity in the main channel of the large lowland River Oder. Regul. Rivers: Res. Mgmt. 17, 595–608. https://doi.org/10.1002/rrr.645

Wolter, C., Bischoff, A., Faller, M., Schomaker, C., Wysujack, K., 2004b. Sampling design and site selection in large rivers, in: Steinberg, C., Calmano, W., Klapper, H., Wilken, R.-D. (Eds.), Handbuch Angewandte Limnologie. Ecomed-Verlag, Landsberg, pp. 38–57.

Wolter, C., Bischoff, A., Wysujack, K., 2003. The use of historical data to characterize fish-faunistic reference conditions for large lowland rivers in northern Germany. Large Rivers 37–51. https://doi.org/10.1127/lr/15/2003/37

Wolter, C., Buijse, A.D., Parasiewicz, P., 2016. Temporal and spatial patterns of fish response to hydromorphological processes. River Res. Applic. 32, 190–201. https://doi.org/10.1002/rra.2980

Wolter, C., Freyhof, J., 2004. Diel distribution patterns of fishes in a temperate large lowland river. Journal of Fish Biology 64, 632–642. https://doi.org/10.1111/j.1095-8649.2004.00327.x

Wolter, C., Röhr, F., 2010. Distribution history of non-native freshwater fish species in Germany: how invasive are they? Journal of Applied Ichthyology 26, 19–27. https://doi.org/10.1111/j.1439-0426.2010.01505.x

Zaggia, L., Lorenzetti, G., Manfé, G., Scarpa, G.M., Molinaroli, E., Parnell, K.E., Rapaglia, J.P., Gionta, M., Soomere, T., 2017. Fast shoreline erosion induced by ship wakes in a coastal lagoon: Field evidence and remote sensing analysis. PLOS ONE 12, e0187210. https://doi.org/10.1371/journal.pone.0187210

Zajicek, P., Radinger, J., Wolter, C., 2018. Disentangling multiple pressures on fish assemblages in large rivers. Science of The Total Environment 627, 1093–1105. https://doi.org/10.1016/j.scitotenv.2018.01.307

Zajicek, P., Wolter, C., 2019. The effects of recreational and commercial navigation on fish assemblages in large rivers. Science of The Total Environment 646, 1304–1314. https://doi.org/10.1016/j.scitotenv.2018.07.403

Zajicek, P., Wolter, C., 2018. The gain of additional sampling methods for the fish-based assessment of large rivers. Fisheries Research 197, 15–24. https://doi.org/10.1016/j.fishres.2017.09.018

Appendix

Chapter one

Supporting information

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

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Tables S1 – S19

Table S 1. Species names and guild classifications according to Scharf et al. (2011), Dußling et al. (2004) and EFI+ Consortium (2009). Hab = habitat guilds (EURY = eurytopic; LIMNO = limnophilic; RH = rheophilic), Repro = reproduction guilds (ARIAD = ariadnophilic; LIPE = litho-pelagophilic; LITH = lithophilic; OSTRA = ostracophilic; PHLI = phyto-lithophilic; PHYT = phytophilic; POLY = polyphilic; PSAM = psammophilic; SPEL = speleophilic), MIG = migratory species (AM = amphidromous; ANA = anadromous; CAT = catadromous; POT = potamodromous), HD = species listed in the Habitat Directive (II, IV, V = listed in annexes 2, 4, 5, respectively), Potamal species are indicated by a [P] in conjunction with the Latin name. Bold font highlights potamal, migratory and Habitat Directive Species

Latin name (EFI+ Consortium 2009)	Common name	Hab	Repro	MIG	HD	FRI	SFRI
Abramis ballerus [P]	Blue bream	RH	PHLI			7.08	0.45
Abramis brama [P]	Common bream	EURY	PHLI			7.00	0.55
Abramis sapa	White-eye bream	RH	LITH			6.75	0.39
Alburnoides bipunctatus	Spirlin	RH	LITH			5.42	0.45
Alburnus alburnus	Bleak	EURY	PHLI			6.58	0.63
Ameiurus nebulosus	Brown bullhead	EURY	SPEL			6.58	0.27
Anguilla anguilla	European eel	EURY	PELA	CAT		6.67	1.70
Aspius aspius	Asp	RH	LITH	POT	II	6.75	0.39
Barbatula barbatula	Stone loach	RH	PSAM			5.25	0.93
Barbus barbus	Barbel	RH	LITH	POT	V	6.08	0.45
Blicca bjoerkna [P]	White bream	EURY	PHYT			7.00	0.55
Carassius carassius	Crucian carp	LIMNO	PHYT			6.92	0.27
Carassius gibelio	Prussian carp	EURY	PHYT			6.67	0.79
Chelon labrosus	Thicklip mullet	LIMNO	PELA	AM		--	--
Chondrostoma nasus	Nase	RH	LITH			5.67	0.61
Cobitis taenia	Northern spined loach	RH	PHYT		II	6.50	0.64
Coregonus lavaretus	Lavaret	RH	LITH	ANA	II	--	--
Coregonus maraena	Maraene	RH	LITH	ANA	II	7.33	0.42
Coregonus oxyrinchus	Houting	RH	LITH	ANA	IV	7.25	0.39
Coregonus peled	Peled	LIMNO	LITH	POT	V	--	--
Cottus gobio	Sculpin	RH	SPEL		II	4.17	1.24
Cottus poecilopus	Siberian sculpin	RH	SPEL			4.42	0.99
Ctenopharyngodon idella	Grass carp	RH	PELA			7.17	0.15
Cyprinus carpio	Carp	EURY	PHYT			7.00	0.36
Dicentrarchus labrax	European seabass	EURY	PELA	AM		7.83	0.15
Esox lucius	Northern pike	EURY	PHYT			6.58	0.99
Gasterosteus aculeatus	Three-spined stickleback	EURY	ARIAD			7.17	1.06
Gobio gobio	Gudgeon	RH	PSAM			5.83	1.24
Gymnocephalus cernuus	Ruffe	EURY	PHLI			7.42	0.45
Hypophthalmichthys nobilis	Bighead carp	RH	LITH			7.08	0.27
Lampetra fluviatilis	River lamprey	RH	LITH	ANA	II, V	5.17	0.52
Lampetra planeri	Brook lamprey	RH	LITH		II	4.58	0.45
Lepomis gibbosus	Pumpkinseed	LIMNO	POLY			6.83	0.33
Leucaspius delineatus	Sunbleak	LIMNO	PHYT			6.83	0.33
Leuciscus cephalus	Chub	RH	LITH	POT		5.83	1.24
Leuciscus idus	Ide	RH	PHLI			6.83	0.52
Leuciscus leuciscus	Common dace	RH	LITH			5.75	0.93
Lota lota	Burbot	RH	LIPE	POT		6.33	1.52
Misgurnus fossilis	European weatherfish	LIMNO	PHYT		II	7.00	0.36
Neogobius gymnotrachelus	Racer goby	EURY	unclear			7.25	0.57
Oncorhynchus mykiss	Rainbow trout	RH	LITH			4.00	0.73
Osmerus eperlanus	European smelt	EURY	LIPE	ANA		7.42	0.45
Perca fluviatilis	European perch	EURY	PHLI			6.92	0.99
Perccottus glenii	Amur sleeper	LIMNO	unclear			6.83	0.33
Petromyzon marinus	Sea lamprey	RH	LITH	ANA	II	5.75	0.39
Phoxinus phoxinus	Eurasian minnow	RH	LITH			4.67	0.79
Platichthys flesus	Flounder	RH	PELA	CAT		7.50	0.45
Proterorhinus marmoratus	Tubenose goby	EURY	SPEL			7.08	0.63
Pseudorasbora parva	Stone moroko	EURY	PHLI			6.58	0.63
Pungitius pungitius	Ninespine stickleback	EURY	ARIAD			7.17	0.52
Rhodeus amarus	European bitterling	LIMNO	OSTRA			6.50	0.27
Romanogobio belingi [P]	Northern whitefin gudgeon	RH	PSAM		II	6.58	0.27
Rutilus rutilus	Roach	EURY	PHLI			6.83	0.88
Sabanejewia aurata	Golden spined loach	RH	PHYT		II	6.00	0.55
Salmo salar	Salmon	RH	LITH	ANA	II, V	5.00	0.55

Table S 1. (continued)

Latin name (EFI+ Consortium 2009)	Common name	Hab	Repro	MIG	HD	FRI	SFRI
Salmo trutta fario	Brown trout	RH	LITH			3.75	0.57
Salmo trutta trutta	Sea trout	RH	LITH	ANA		5.00	0.55
Salvelinus fontinalis	Brook trout	RH	LITH			3.50	0.27
Sander lucioperca [P]	Pike-perch	EURY	PHLI			7.25	0.57
Scardinius erythrophthalmus	Rudd	LIMNO	PHYT			6.92	0.45
Silurus glanis [P]	European catfish	EURY	PHYT			7.00	0.36
Thymallus thymallus	Grayling	RH	LITH		V	4.92	0.45
Tinca tinca	Tench	LIMNO	PHYT			6.92	0.45
Umbra pygmaea	Eastern mudminnow	LIMNO	PHYT			--	--
Vimba vimba	Vimba bream	RH	LITH	POT		6.67	0.79

Table S 2. Number (n) and proportions (%) of all species captured in 849 sampling occasions at 159 sites in five large rivers in total (with all methods combined), only with electrofishing, only with trawling, only with seining and only with drift-netting. Bold font indicates species captured exclusively with the respective gear

Species	n	[%]	Species	n	[%]
Total			Electrofishing		
Total	503593	100.00	**Total**	304155	100.00
Rutilus rutilus	121642	24.15	Rutilus rutilus	89149	29.31
Abramis brama	87727	17.42	Perca fluviatilis	46478	15.28
Perca fluviatilis	52143	10.35	Alburnus alburnus	39199	12.89
Blicca bjoerkna	40463	8.03	Leuciscus idus	21201	6.97
Alburnus alburnus	40373	8.02	Leuciscus cephalus	16823	5.53
Leuciscus idus	22863	4.54	Gobio gobio	14630	4.81
Sander lucioperca	20003	3.97	Anguilla anguilla	13152	4.32
Gobio gobio	17646	3.50	Lota lota	11256	3.70
Leuciscus cephalus	16914	3.36	Blicca bjoerkna	10064	3.31
Anguilla anguilla	15527	3.08	Abramis brama	9475	3.12
Gymnocephalus cernuus	12977	2.58	Leuciscus leuciscus	7007	2.30
Lota lota	11263	2.24	Gymnocephalus cernuus	5025	1.65
Platichthys flesus	10614	2.11	Esox lucius	3331	1.10
Leuciscus leuciscus	7178	1.43	Cobitis taenia	2535	0.83
Esox lucius	3449	0.68	Barbus barbus	2382	0.78
Romanogobio belingi	3339	0.66	Aspius aspius	2192	0.72
Osmerus eperlanus	2682	0.53	**Romanogobio belingi**	1908	0.63
Aspius aspius	2625	0.52	Scardinius erythrophthalmus	1422	0.47
Abramis ballerus	2585	0.51	Platichthys flesus	1116	0.37
Cobitis taenia	2546	0.51	Sander lucioperca	1010	0.33
Barbus barbus	2414	0.48	**Barbatula barbatula**	847	0.28
Scardinius erythrophthalmus	1428	0.28	Chondrostoma nasus	687	0.23
Cottus gobio	855	0.17	Cottus gobio	633	0.21
Barbatula barbatula	847	0.17	Rhodeus amarus	414	0.14
Chondrostoma nasus	703	0.14	Gasterosteus aculeatus	383	0.13
Rhodeus amarus	491	0.10	**Neogobius gymnotrachelus**	336	0.11
Gasterosteus aculeatus	412	0.08	Tinca tinca	244	0.08
Neogobius gymnotrachelus	336	0.07	Silurus glanis	170	0.06
Tinca tinca	247	0.05	Abramis ballerus	138	0.05
Silurus glanis	232	0.05	Cyprinus carpio	131	0.04
Cyprinus carpio	142	0.03	**Lampetra planeri**	105	0.03
Lampetra planeri	105	0.02	**Leucaspius delineatus**	90	0.03
Carassius gibelio	90	0.02	Osmerus eperlanus	89	0.03
Leucaspius delineatus	90	0.02	Carassius gibelio	86	0.03
Coregonus maraena	84	0.02	**Salmo trutta fario**	71	0.02
Salmo trutta fario	71	0.01	**Ameiurus nebulosus**	62	0.02
Proterorhinus marmoratus	63	0.01	Salmo salar	39	0.01
Ameiurus nebulosus	62	0.01	**Misgurnus fossilis**	36	0.01
Lampetra fluviatilis	59	0.01	Pungitius pungitius	36	0.01
Salmo salar	41	0.01	Proterorhinus marmoratus	31	0.01
Pungitius pungitius	38	0.01	**Pseudorasbora parva**	28	0.01
Misgurnus fossilis	36	0.01	**Carassius carassius**	27	0.01
Pseudorasbora parva	28	0.01	**Oncorhynchus mykiss**	17	0.01
Carassius carassius	27	0.01	Lampetra fluviatilis	15	< 0.01
Vimba vimba	23	< 0.01	**Perccottus glenii**	15	< 0.01
Oncorhynchus mykiss	17	< 0.01	**Thymallus thymallus**	13	< 0.01
Perccottus glenii	15	< 0.01	Salmo trutta trutta	10	< 0.01
Thymallus thymallus	13	< 0.01	**Alburnoides bipunctatus**	9	< 0.01
Salmo trutta trutta	11	< 0.01	Chelon labrosus	7	< 0.01
Alburnoides bipunctatus	9	< 0.01	**Lepomis gibbosus**	6	< 0.01
Chelon labrosus	8	< 0.01	Vimba vimba	6	< 0.01
Abramis sapa	7	< 0.01	**Ctenopharyngodon idella**	4	< 0.01
Lepomis gibbosus	6	< 0.01	**Dicentrarchus labrax**	3	< 0.01
Ctenopharyngodon idella	4	< 0.01	**Phoxinus phoxinus**	3	< 0.01
Sabanejewia aurata	4	< 0.01	Petromyzon marinus	2	< 0.01
Dicentrarchus labrax	3	< 0.01	Sabanejewia aurata	2	< 0.01
Petromyzon marinus	3	< 0.01	Abramis sapa	1	< 0.01

Table S 2. (continued)

Species	n	[%]	Species	n	[%]
Total			**Electrofishing**		
Phoxinus phoxinus	3	< 0.01	**Cottus poecilopus**	1	< 0.01
Coregonus lavaretus	1	< 0.01	**Hypophthalmichthys nobilis**	1	< 0.01
Coregonus oxyrinchus	1	< 0.01	**Salvelinus fontinalis**	1	< 0.01
Coregonus peled	1	< 0.01	**Umbra pygmaea**	1	< 0.01
Cottus poecilopus	1	< 0.01			
Hypophthalmichthys nobilis	1	< 0.01			
Salvelinus fontinalis	1	< 0.01			
Umbra pygmaea	1	< 0.01			
Trawling			**Seining**		
Total	177924	100.00	**Total**	21219	100.00
Abramis brama	67412	37.89	Abramis brama	10837	51.07
Rutilus rutilus	29647	16.66	Blicca bjoerkna	4454	20.99
Blicca bjoerkna	25677	14.43	Rutilus rutilus	2834	13.36
Sander lucioperca	18921	10.63	Alburnus alburnus	601	2.83
Platichthys flesus	9498	5.34	**Romanogobio belingi**	449	2.12
Gymnocephalus cernuus	7865	4.42	Leuciscus idus	389	1.83
Perca fluviatilis	5485	3.08	Abramis ballerus	338	1.59
Gobio gobio	2764	1.55	Aspius aspius	314	1.48
Osmerus eperlanus	2593	1.46	Gobio gobio	252	1.19
Anguilla anguilla	2358	1.33	Perca fluviatilis	180	0.85
Abramis ballerus	2108	1.18	Leuciscus leuciscus	162	0.76
Leuciscus idus	1272	0.71	Gymnocephalus cernuus	81	0.38
Romanogobio belingi	982	0.55	Esox lucius	80	0.38
Alburnus alburnus	573	0.32	Rhodeus amarus	77	0.36
Cottus gobio	222	0.12	Sander lucioperca	69	0.33
Aspius aspius	119	0.07	Leuciscus cephalus	61	0.29
Coregonus maraena	84	0.05	Anguilla anguilla	16	0.08
Silurus glanis	62	0.03	Cobitis taenia	9	0.04
Lampetra fluviatilis	44	0.02	Scardinius erythrophthalmus	3	0.01
Esox lucius	38	0.02	Carassius gibelio	2	0.01
Barbus barbus	32	0.02	Cyprinus carpio	2	0.01
Proterorhinus marmoratus	32	0.02	Lota lota	2	0.01
Leuciscus cephalus	30	0.02	Sabanejewia aurata	2	0.01
Gasterosteus aculeatus	29	0.02	Salmo salar	2	0.01
Vimba vimba	17	0.01	Tinca tinca	2	0.01
Chondrostoma nasus	16	0.01	**Coregonus peled**	1	< 0.01
Cyprinus carpio	9	0.01			
Leuciscus leuciscus	9	0.01	**Drift-netting**		
Abramis sapa	6	< 0.01	**Total**	295	100.00
Lota lota	5	< 0.01	Blicca bjoerkna	268	90.85
Scardinius erythrophthalmus	3	< 0.01	Rutilus rutilus	12	4.07
Carassius gibelio	2	< 0.01	Gymnocephalus cernuus	6	2.03
Cobitis taenia	2	< 0.01	Abramis brama	3	1.02
Pungitius pungitius	2	< 0.01	Sander lucioperca	3	1.02
Chelon labrosus	1	< 0.01	Abramis ballerus	1	0.34
Coregonus lavaretus	1	< 0.01	Anguilla anguilla	1	0.34
Coregonus oxyrinchus	1	< 0.01	Leuciscus idus	1	0.34
Petromyzon marinus	1	< 0.01			
Salmo trutta trutta	1	< 0.01			
Tinca tinca	1	< 0.01			

Table S 3. Number (n) and proportions (%) of all species captured in the standardized comparison of electrofishing versus trawling. Bold font indicates species captured exclusively with the respective method

Total			Electrofishing			Trawling		
Species	**n**	**[%]**	**Species**	**n**	**[%]**	**Species**	**n**	**[%]**
Total	249040	100.00	**Total**	74393	100.00	**Total**	174647	100.00
Abramis brama	67254	27.01	Rutilus rutilus	28786	38.69	Abramis brama	66132	37.87
Rutilus rutilus	58097	23.33	Lota lota	9641	12.96	Rutilus rutilus	29311	16.78
Blicca bjoerkna	27441	11.02	Perca fluviatilis	9064	12.18	Blicca bjoerkna	25294	14.48
Sander lucioperca	19089	7.67	Leuciscus idus	6923	9.31	Sander lucioperca	18655	10.68
Perca fluviatilis	14489	5.82	Alburnus alburnus	4783	6.43	Platichthys flesus	8861	5.07
Platichthys flesus	9898	3.97	Anguilla anguilla	2313	3.11	Gymnocephalus cernuus	7852	4.50
Gymnocephalus cernuus	9703	3.90	Blicca bjoerkna	2147	2.89	Perca fluviatilis	5425	3.11
Lota lota	9646	3.87	Gymnocephalus cernuus	1851	2.49	Osmerus eperlanus	2590	1.48
Leuciscus idus	8159	3.28	Cobitis taenia	1490	2.00	Gobio gobio	2544	1.46
Alburnus alburnus	5352	2.15	Abramis brama	1122	1.51	Anguilla anguilla	2338	1.34
Anguilla anguilla	4651	1.87	Platichthys flesus	1037	1.39	Abramis ballerus	2108	1.21
Gobio gobio	2752	1.11	Leuciscus cephalus	1028	1.38	Leuciscus idus	1236	0.71
Osmerus eperlanus	2678	1.08	Romanogobio belingi	869	1.17	Romanogobio belingi	982	0.56
Abramis ballerus	2169	0.87	Esox lucius	848	1.14	Alburnus alburnus	569	0.33
Romanogobio belingi	1851	0.74	Aspius aspius	677	0.91	Cottus gobio	218	0.12
Cobitis taenia	1492	0.60	Sander lucioperca	434	0.58	Aspius aspius	109	0.06
Leuciscus cephalus	1058	0.42	Leuciscus leuciscus	273	0.37	**Coregonus maraena**	84	0.05
Esox lucius	886	0.36	Gobio gobio	208	0.28	Silurus glanis	62	0.04
Aspius aspius	786	0.32	Gasterosteus aculeatus	160	0.22	Lampetra fluviatilis	43	0.02
Leuciscus leuciscus	282	0.11	Scardinius erythrophthalmus	129	0.17	Esox lucius	38	0.02
Cottus gobio	250	0.10	Osmerus eperlanus	88	0.12	Proterorhinus marmoratus	32	0.02
Gasterosteus aculeatus	189	0.08	Cyprinus carpio	77	0.10	Leuciscus cephalus	30	0.02
Scardinius erythrophthalmus	132	0.05	Barbus barbus	74	0.10	Gasterosteus aculeatus	29	0.02
Barbus barbus	102	0.04	Abramis ballerus	61	0.08	Barbus barbus	28	0.02
Cyprinus carpio	86	0.03	**Leucaspius delineatus**	55	0.07	**Vimba vimba**	17	0.01
Coregonus maraena	84	0.03	Chondrostoma nasus	50	0.07	Chondrostoma nasus	16	0.01
Silurus glanis	74	0.03	Tinca tinca	47	0.06	Cyprinus carpio	9	0.01
Chondrostoma nasus	66	0.03	Cottus gobio	32	0.04	Leuciscus leuciscus	9	0.01
Proterorhinus marmoratus	62	0.02	Proterorhinus marmoratus	30	0.04	**Abramis sapa**	6	< 0.01
Leucaspius delineatus	55	0.02	**Barbatula barbatula**	23	0.03	Lota lota	5	< 0.01
Tinca tinca	48	0.02	**Rhodeus amarus**	17	0.02	Scardinius erythrophthalmus	3	< 0.01
Lampetra fluviatilis	46	0.02	**Misgurnus fossilis**	15	0.02	Carassius gibelio	2	< 0.01
Barbatula barbatula	23	0.01	Silurus glanis	12	0.02	Cobitis taenia	2	< 0.01
Rhodeus amarus	17	0.01	Chelon labrosus	7	0.01	Pungitius pungitius	2	< 0.01
Vimba vimba	17	0.01	Pungitius pungitius	6	0.01	Chelon labrosus	1	< 0.01
Misgurnus fossilis	15	0.01	Carassius gibelio	4	0.01	**Coregonus lavaretus**	1	< 0.01
Chelon labrosus	8	< 0.01	**Ctenopharyngodon idella**	3	< 0.01	**Coregonus oxyrinchus**	1	< 0.01
Pungitius pungitius	8	< 0.01	**Dicentrarchus labrax**	3	< 0.01	**Petromyzon marinus**	1	< 0.01
Abramis sapa	6	< 0.01	Lampetra fluviatilis	3	< 0.01	Salmo trutta trutta	1	< 0.01
Carassius gibelio	6	< 0.01	**Carassius carassius**	2	< 0.01	Tinca tinca	1	< 0.01
Ctenopharyngodon idella	3	< 0.01	Salmo trutta trutta	1	< 0.01			
Dicentrarchus labrax	3	< 0.01						
Carassius carassius	2	< 0.01						
Salmo trutta trutta	2	< 0.01						
Coregonus lavaretus	1	< 0.01						
Coregonus oxyrinchus	1	< 0.01						
Petromyzon marinus	1	< 0.01						

Table S 4. Number (n) and proportions (%) of all species captured in the standardized comparison of electrofishing versus seining. Bold font indicates species captured exclusively with the respective method

Total			Electrofishing			Seining		
Species	n	[%]	Species	n	[%]	Species	n	[%]
Total	39389	100.00	**Total**	30238	100.00	**Total**	9151	100.00
Rutilus rutilus	8437	21.42	Rutilus rutilus	6680	22.09	Abramis brama	3986	43.56
Abramis brama	6250	15.87	Leuciscus idus	5672	18.76	Blicca bjoerkna	2508	27.41
Leuciscus idus	5994	15.22	Perca fluviatilis	5546	18.34	Rutilus rutilus	1757	19.20
Perca fluviatilis	5626	14.28	Abramis brama	2264	7.49	Leuciscus idus	322	3.52
Blicca bjoerkna	4518	11.47	Blicca bjoerkna	2010	6.65	Aspius aspius	168	1.84
Alburnus alburnus	1925	4.89	Alburnus alburnus	1810	5.99	Alburnus alburnus	115	1.26
Leuciscus cephalus	1569	3.98	Leuciscus cephalus	1533	5.07	Perca fluviatilis	80	0.87
Gobio gobio	1400	3.55	Gobio gobio	1397	4.62	Gymnocephalus cernuus	61	0.67
Anguilla anguilla	1043	2.65	Anguilla anguilla	1036	3.43	Esox lucius	48	0.52
Aspius aspius	614	1.56	Aspius aspius	446	1.47	Leuciscus cephalus	36	0.39
Esox lucius	455	1.16	Esox lucius	407	1.35	Sander lucioperca	24	0.26
Gymnocephalus cernuus	401	1.02	Gymnocephalus cernuus	340	1.12	Abramis ballerus	17	0.19
Lota lota	311	0.79	Lota lota	310	1.03	Romanogobio belingi	8	0.09
Romanogobio belingi	308	0.79	Romanogobio belingi	300	0.99	Anguilla anguilla	7	0.08
Leuciscus leuciscus	283	0.72	Leuciscus leuciscus	277	0.92	Leuciscus leuciscus	6	0.07
Sander lucioperca	81	0.21	Sander lucioperca	57	0.19	Gobio gobio	3	0.03
Abramis ballerus	52	0.13	**Scardinius erythrophthalmus**	37	0.12	**Salmo salar**	2	0.02
Scardinius erythrophthalmus	37	0.09	Abramis ballerus	35	0.12	Cyprinus carpio	1	0.01
Cobitis taenia	24	0.06	**Cobitis taenia**	24	0.08	Lota lota	1	0.01
Barbus barbus	18	0.05	**Barbus barbus**	18	0.06	Tinca tinca	1	0.01
Carassius carassius	14	0.04	**Carassius carassius**	14	0.05			
Cyprinus carpio	8	0.02	Cyprinus carpio	7	0.02			
Tinca tinca	7	0.02	Tinca tinca	6	0.02			
Gasterosteus aculeatus	3	0.01	**Gasterosteus aculeatus**	3	0.01			
Pungitius pungitius	3	0.01	**Pungitius pungitius**	3	0.01			
Salmo salar	2	0.01	**Barbatula barbatula**	1	< 0.01			
Barbatula barbatula	1	< 0.01	**Carassius gibelio**	1	< 0.01			
Carassius gibelio	1	< 0.01	**Chondrostoma nasus**	1	< 0.01			
Chondrostoma nasus	1	< 0.01	**Hypophthalmichthys nobilis**	1	< 0.01			
Hypophthalmichthys nobilis	1	< 0.01	**Lampetra fluviatilis**	1	< 0.01			
Lampetra fluviatilis	1	< 0.01	**Leucaspius delineatus**	1	< 0.01			
Leucaspius delineatus	1	< 0.01						

Table S 5. Number (n) and proportions (%) of all species captured in the standardized comparison of electrofishing versus drift-netting. Bold font indicates species captured exclusively with the respective method

Total			Electrofishing			Drift-netting		
Species	n	[%]	Species	n	[%]	Species	n	[%]
Total	4192	100.00	**Total**	3897	100.00	**Total**	295	100.00
Rutilus rutilus	1217	29.03	Rutilus rutilus	1205	30.92	Blicca bjoerkna	268	90.85
Leuciscus idus	814	19.42	Leuciscus idus	813	20.86	Rutilus rutilus	12	4.07
Perca fluviatilis	781	18.63	**Perca fluviatilis**	781	20.04	Gymnocephalus cernuus	6	2.03
Blicca bjoerkna	368	8.78	**Gobio gobio**	184	4.72	Abramis brama	3	1.02
Gobio gobio	184	4.39	Anguilla anguilla	156	4.00	Sander lucioperca	3	1.02
Anguilla anguilla	157	3.75	Abramis brama	151	3.87	**Abramis ballerus**	1	0.34
Abramis brama	154	3.67	**Alburnus alburnus**	150	3.85	Anguilla anguilla	1	0.34
Alburnus alburnus	150	3.58	**Aspius aspius**	108	2.77	Leuciscus idus	1	0.34
Aspius aspius	108	2.58	Blicca bjoerkna	100	2.57			
Leuciscus cephalus	97	2.31	**Leuciscus cephalus**	97	2.49			
Lota lota	60	1.43	**Lota lota**	60	1.54			
Romanogobio belingi	28	0.67	**Romanogobio belingi**	28	0.72			
Leuciscus leuciscus	26	0.62	**Leuciscus leuciscus**	26	0.67			
Esox lucius	18	0.43	**Esox lucius**	18	0.46			
Gymnocephalus cernuus	17	0.41	Gymnocephalus cernuus	11	0.28			
Sander lucioperca	7	0.17	**Barbus barbus**	5	0.13			
Barbus barbus	5	0.12	Sander lucioperca	4	0.10			
Abramis ballerus	1	0.02						

Table S 6. Sample sizes (n), means, standard errors (SE) and medians of biodiversity indices and of densities of selected guilds for the preliminary comparison of all sampling gears (E = electrofishing, T = trawling, S = seining and D = drift-netting

Biodiversity indices	n				mean +/- SE				median			
	E	T	S	D	E	T	S	D	E	T	S	D
Species richness	512	297	38	2	13.57 +/- 0.16	9.47 +/- 0.11	9.87 +/- 0.43	6.00 +/- 1.00	13.50	9.00	9.00	6.00
Shannon Index	512	297	38	2	1.65 +/- 0.01	1.29 +/- 0.01	1.17 +/- 0.02	0.41 +/- 0.04	1.72	1.31	1.16	0.41
Evenness	512	297	38	2	0.64 +/- 0.01	0.58 +/- 0.01	0.52 +/- 0.02	0.23 +/- 0.04	0.66	0.59	0.54	0.23
Simpson Index	512	297	38	2	0.71 +/- 0.01	0.61 +/- 0.01	0.56 +/- 0.02	0.16 +/- 0.05	0.75	0.64	0.58	0.16
Fish Region Index	512	297	38	2	6.72 +/- 0.01	7.06 +/- 0.01	6.96 +/- 0.01	7.01 +/- 0.00	6.77	7.05	6.96	7.01
Selected guilds					Density [Ind/100m^2]							
Eurytopic	512	297	38	2	14.77 +/- 0.81	3.34 +/- 0.38	9.21 +/- 3.15	0.13 +/- 0.02	90.00	20.00	30.00	0.13
Rheophilic	510	292	37	1	4.39 +/- 0.26	0.26 +/- 0.02	1.60 +/- 1.24	0.002 +/- --	2.52	0.13	0.21	0.00
Lithophilic	466	122	37	0	1.49 +/- 0.13	0.01 +/- 0.00	0.41 +/- 0.25	--	0.66	0.01	0.08	--
Phytophilic	441	272	38	2	1.31 +/- 0.13	0.24 +/- 0.03	1.93 +/- 0.57	0.12 +/- 0.01	0.38	0.07	0.49	0.12
Psammophilic	307	213	7	0	1.22 +/- 0.15	0.07 +/- 0.01	4.96 +/- 4.94	--	0.33	0.02	0.01	--
Potamal	477	297	38	2	1.38 +/- 0.11	2.06 +/- 0.16	7.23 +/- 2.70	0.12 +/- 0.01	0.57	1.38	2.65	0.12

Table S 7. Results of linear mixed effects models and calculated R² values for biodiversity indices and selected guilds for the preliminary comparison of all sampling gears. Density [Ind/100m²] is the response for guilds (models ETSD06-ETSD11). “Est” = estimated regression parameters, “SE” = standard errors, “df” = degrees of freedom, ”t” = t-values, “p” = p-values, “var” = variance of the intercept of random effects, "imp" indicates the amount of explained variation by the random effect on the total unexplained variation by the fixed effect, “n” = sample sizes per stratum; "mar" = marginal R² of fixed effects, "cond" = conditional R² of fixed and random effects, “diff” = R²mar-R²cond, i.e. R² of only random effects

Model	Response	Fixed effects						Random effects				R²		
		Fixed	Est	SE	df	t	p	Random	var	imp	n	mar	cond	diff
ETSD01	**Species richness**	Intercept	14.25	0.81	8.94	17.70	<0.001	Site:River	2.78	0.17	159	0.11	0.70	0.60
	(not transformed)	MethodT	-2.24	0.23	772.19	-9.75	<0.001	Season:Year	0.20	0.01	47			
		MethodS	-4.73	0.53	823.89	-8.95	<0.001	Year	0.00	0.00	15			
		MethodD	-7.86	1.77	722.99	-4.45	<0.001	River	7.68	0.48	14			
								Residual	5.31	0.33	849			
ETSD02	**Evenness**	Intercept	0.62	0.02	13.83	36.20	<0.001	Site:River	0.00	0.06	159	0.09	0.33	0.24
	(not transformed)	MethodT	-0.04	0.01	768.94	-3.69	<0.001	Season:Year	0.00	0.05	47			
		MethodS	-0.17	0.02	592.23	-7.51	<0.001	Year	0.00	0.00	15			
		MethodD	-0.40	0.08	826.15	-4.80	<0.001	River	0.00	0.15	14			
								Residual	0.01	0.74	849			
ETSD03	**Shannon Index**	Intercept	1.61	0.06	12.18	28.42	<0.001	Site:River	0.01	0.09	159	0.18	0.46	0.28
	(not transformed)	MethodT	-0.22	0.03	814.85	-7.65	<0.001	Season:Year	0.00	0.02	47			
		MethodS	-0.70	0.06	613.01	-11.08	<0.001	Year	0.00	0.00	15			
		MethodD	-1.31	0.23	819.97	-5.80	<0.001	River	0.03	0.23	14			
								Residual	0.09	0.65	849			
ETSD04	**Simpson Index**	Intercept	0.69	0.02	12.71	40.34	<0.001	Site:River	0.00	0.04	159	0.14	0.32	0.18
	(not transformed)	MethodT	-0.06	0.01	696.35	-5.18	<0.001	Season:Year	0.00	0.03	47			
		MethodS	-0.22	0.02	509.80	-8.97	<0.001	Year	0.00	0.00	15			
		MethodD	-0.56	0.09	827.72	-6.13	<0.001	River	0.00	0.14	14			
								Residual	0.02	0.80	849			
ETSD05	**Fish Region Index**	Intercept	6.70	0.04	11.97	175.83	<0.001	Site:River	0.02	0.42	159	0.19	0.83	0.64
	(not transformed)	MethodT	0.21	0.01	725.57	21.11	<0.001	Season:Year	0.00	0.00	47			
		MethodS	0.18	0.02	771.07	7.84	<0.001	Year	0.00	0.01	15			
		MethodD	0.25	0.07	701.38	3.43	0.001	River	0.02	0.36	14			
								Residual	0.01	0.21	849			
ETSD06	**Eurytopic guild**	Intercept	2.52	0.20	15.39	12.97	<0.001	Site:River	0.38	0.27	159	0.42	0.74	0.33
		MethodT	-2.12	0.08	775.40	-26.70	<0.001	Season:Year	0.06	0.04	47			
	(log transformed)	MethodS	-1.06	0.19	836.83	-5.73	<0.001	Year	0.00	0.00	15			
		MethodD	-4.58	0.61	748.57	-7.45	<0.001	River	0.37	0.26	14			
								Residual	0.63	0.44	849			
ETSD07	**Rheophilic guild**	Intercept	0.99	0.27	13.77	3.70	0.002	Site:River	0.49	0.23	159	0.51	0.81	0.30
	(log transformed)	MethodT	-3.09	0.09	753.33	-33.62	<0.001	Season:Year	0.06	0.03	47			
		MethodS	-2.69	0.22	824.20	-12.38	<0.001	Year	0.03	0.01	15			
		MethodD	-7.70	0.96	702.99	-8.05	<0.001	River	0.75	0.35	14			
								Residual	0.84	0.39	840			
ETSD08	**Lithophilic guild**	Intercept	-0.24	0.37	13.10	-0.64	0.536	Site:River	0.56	0.18	150	0.47	0.86	0.39
	(log transformed)	MethodT	-4.11	0.12	533.60	-34.51	<0.001	Season:Year	0.02	0.01	45			
		MethodS	-2.20	0.21	592.10	-10.37	<0.001	Year	0.05	0.02	15			
								River	1.65	0.54	14			
								Residual	0.78	0.26	625			
ETSD09	**Phytophilic guild**	Intercept	-0.54	0.36	15.24	-1.50	0.154	Site:River	0.65	0.19	151	0.11	0.67	0.56
	(log transformed)	MethodT	-1.38	0.13	700.44	-10.99	<0.001	Season:Year	0.04	0.01	45			
	6 outlier excluded	MethodS	-0.29	0.26	725.60	-1.09	0.276	Year	0.11	0.03	15			
		MethodD	-1.46	0.88	652.16	-1.67	0.096	River	1.36	0.39	14			
								Residual	1.30	0.38	747			
ETSD10	**Psammophilic guild**	Intercept	-1.07	0.32	13.50	0.01	0.005	Site:River	0.91	0.27	123	0.24	0.70	0.47
	(log transformed)	MethodT	-1.97	0.19	494.60	-10.38	<0.001	Season:Year	0.16	0.05	44			
	2 outlier excluded	MethodS	-4.00	0.51	415.30	-7.80	<0.001	Year	0.03	0.01	15			
								River	0.95	0.28	14			
								Residual	1.30	0.39	525			
ETSD11	**Potamal guild**		-0.63	0.14	10.71	-4.57	0.001	Site:River	0.84	0.43	156	0.05	0.51	0.46
	(log transformed)		0.55	0.10	734.75	5.28	<0.001	Season:Year	0.01	0.01	47			
			0.71	0.24	800.53	3.00	0.003	Year	0.01	0.01	15			
			-2.26	0.78	682.56	-2.92	0.004	River	0.08	0.04	14			
								Residual	1.01	0.52	814			

Table S 8. Results of Tukey post-hoc tests for pairwise comparisons (Comp) of electrofishing (E), trawling (T), seining (S) and drift-netting (D) based on models ETSD01-ETSD11 (Table S7), "Est" = estimated regression parameters, "SE" = standard errors, "z" = z-values, "p" = p-values

Response	Tukey coefficients				
	Comp	Est	SE	z	p
Species richness	D - E	-7.86	1.77	-4.45	<0.001
(not transformed)	S - E	-4.73	0.53	-8.95	<0.001
	T - E	-2.24	0.23	-9.75	<0.001
	S - D	3.13	1.79	1.75	0.253
	T - D	5.62	1.78	3.16	0.006
	T - S	2.49	0.58	4.32	<0.001
Shannon Index	D - E	-1.31	0.23	-5.80	<0.001
(not transformed)	S - E	-0.70	0.06	-11.08	<0.001
	T - E	-0.22	0.03	-7.65	<0.001
	S - D	0.61	0.23	2.65	0.030
	T - D	1.10	0.23	4.80	<0.001
	T - S	0.49	0.07	6.96	<0.001
Evenness	D - E	-0.40	0.08	-4.80	<0.001
(not transformed)	S - E	-0.17	0.02	-7.51	<0.001
	T - E	-0.04	0.01	-3.69	<0.001
	S - D	0.23	0.08	2.68	0.028
	T - D	0.36	0.08	4.32	<0.001
	T - S	0.13	0.03	5.33	<0.001
Simpson Index	D - E	-0.56	0.09	-6.13	<0.001
(not transformed)	S - E	-0.22	0.02	-8.97	<0.001
	T - E	-0.06	0.01	-5.18	<0.001
	S - D	0.34	0.09	3.65	0.001
	T - D	0.50	0.09	5.46	<0.001
	T - S	0.16	0.03	6.00	<0.001
Fish Region Index	D - E	0.25	0.07	3.43	0.002
(not transformed)	S - E	0.18	0.02	7.84	<0.001
	T - E	0.21	0.01	21.11	<0.001
	S - D	-0.07	0.07	-0.98	0.729
	T - D	-0.05	0.07	-0.63	0.907
	T - S	0.03	0.03	1.02	0.699
Eurytopic guild	D - E	-4.57	0.61	-7.45	<0.001
(log transformed)	S - E	-1.06	0.19	-5.73	<0.001
	T - E	-2.12	0.08	-26.70	<0.001
	S - D	3.51	0.62	5.64	<0.001
	T - D	2.45	0.62	3.96	<0.001
	T - S	-1.06	0.20	-5.27	<0.001
Rheophilic guild	D - E	-7.70	0.96	-8.05	<0.001
(log transformed)	S - E	-2.69	0.22	-12.38	<0.001
	T - E	-3.09	0.09	-33.62	<0.001
	S - D	5.00	0.96	5.19	<0.001
	T - D	4.61	0.96	4.80	<0.001
	T - S	-0.39	0.24	-1.66	0.292
Lithophilic guild	S - E	-2.20	0.21	-10.37	<0.001
(log transformed)	T - E	-4.11	0.12	-34.51	<0.001
	T - S	-1.91	0.24	-7.84	<0.001
Phytophilic guild	D - E	-1.46	0.88	-1.67	0.296
(log transformed)	S - E	-0.29	0.26	-1.09	0.655
	T - E	-1.38	0.13	-10.99	<0.001
	S - D	1.18	0.89	1.32	0.500
	T - D	0.08	0.89	0.09	1.000
	T - S	-1.09	0.29	-3.75	<0.001
Psammophilic guild	S - E	-4.00	0.51	-7.80	<0.001
(log transformed)	T - E	-1.97	0.19	-10.38	<0.001
	T - S	2.02	0.54	3.71	<0.001
Potamal guild	D - E	-2.26	0.78	-2.92	0.013
(log transformed)	S - E	0.71	0.24	3.00	0.011
	T - E	0.55	0.10	5.28	<0.001
	S - D	2.97	0.78	3.80	<0.001
	T - D	2.81	0.78	3.60	0.001
	T - S	-0.16	0.26	-0.61	0.92

Table S 9 Sample sizes (n), means, standard errors (SE) and medians of biodiversity indices and of densities of selected guilds for the standardized comparison of electrofishing (E) vs. trawling (T)

Biodiversity indices	n		mean +/- SE		median	
	E	T	E	T	E	T
Species richness	162	284	12.14 +/- 0.29	9.47 +/- 0.11	11.50	9.00
Shannon Index	162	284	1.49 +/- 0.03	1.29 +/- 0.02	1.55	1.30
Evenness	162	284	0.60 +/- 0.01	0.58 +/- 0.01	0.64	0.59
Simpson Index	162	284	0.66 +/- 0.01	0.61 +/- 0.01	0.70	0.64
Fish Region Index	162	284	6.85 +/- 0.01	7.06 +/- 0.01	6.86	7.05
Selected guilds			Density [Ind/100m^2]			
Eurytopic	162	284	18.29 +/- 1.26	3.44 +/- 0.39	13.65	2.06
Rheophilic	161	279	5.21 +/- 0.40	0.25 +/- 0.02	3.39	13.07
Lithophilic	136	115	0.63 +/- 0.06	0.01 +/- 0.002	0.40	0.01
Phytophilic	133	259	0.95 +/- 0.16	0.24 +/- 0.003	0.32	0.06
Psammophilic	48	202	0.34 +/- 0.09	0.07 +/- 0.01	0.14	0.02
Potamal	143	284	1.18 +/- 0.16	2.11 +/- 0.16	0.63	1.42

Table S 10. Results of linear mixed effects models and calculated R² values for biodiversity indices and selected guilds for the standardized comparison of electrofishing vs. trawling. Density [Ind/100m²] is the response for guilds (models ET06-ET11). "Est" = estimated regression parameters, "SE" = standard errors, "df" = degrees of freedom, "t" = t-values, "p" = p-values, "var" = variance of the intercept of random effects, "imp" indicates the amount of explained variation by the random effect on the total unexplained variation by the fixed effect, "n" = sample sizes per stratum; "mar" = marginal R² of fixed effects, "cond" = conditional R² of fixed and random effects, "diff" = R²mar-R²cond, i.e. R² of only random effects

Model	Response	Fixed effects						Random effects				R^2		
		Fixed	Est	SE	df	t	p	Random	var	imp	n	mar	cond	diff
ET01	**Species richness**	Intercept	11.92	0.64	2.43	18.52	0.001	Season:Year	0.00	0.00	33	0.13	0.41	0.28
	(not transformed)	MethodT	-2.20	0.23	434.76	-9.57	<0.001	Site:River	0.92	0.12	17			
								Year	0.05	0.01	12			
								River	1.52	0.20	5			
								Residual	5.09	0.67	446			
ET02	**Shannon Index**	Intercept	1.49	0.04	22.96	39.69	<0.001	Season:Year	0.01	0.08	33	0.07	0.18	0.11
	(not transformed)	MethodT	-0.20	0.03	425.18	-6.07	<0.001	Site:River	0.00	0.03	17			
								Year	0.00	0.01	12			
								River	0.00	0.00	5			
								Residual	0.10	0.88	446			
ET03	**Evenness**	Intercept	0.62	0.02	45.13	39.32	<0.001	Season:Year	0.00	0.11	33	0.01	0.17	0.16
	(not transformed)	MethodT	-0.03	0.01	426.97	-2.49	0.013	Site:River	0.00	0.06	17			
								Year	0.00	0.00	12			
								River	0.00	0.00	5			
								Residual	0.02	0.83	446			
ET04	**Simpson Index**	Intercept	-0.47	0.03	14.35	-14.49	<0.001	Season:Year	0.01	0.08	33	0.01	0.10	0.09
	(log transformed)	MethodT	-0.06	0.03	425.16	-2.16	0.032	Site:River	0.00	0.00	17			
								Year	0.00	0.01	12			
								River	0.00	0.01	5			
								Residual	0.08	0.90	446			
ET05	**Fish Region Index**	Intercept	6.86	0.03	2.90	233.74	<0.001	Season:Year	0.00	0.06	33	0.37	0.70	0.33
	(not transformed)	MethodT	0.20	0.01	415.80	22.35	<0.001	Site:River	0.01	0.31	17			
								Year	0.00	0.00	12			
								River	0.00	0.13	5			
								Residual	0.01	0.50	446			
ET06	**Eurytopic guild**	Intercept	2.64	0.25	4.15	10.79	<0.001	Season:Year	0.06	0.05	33	0.48	0.72	0.24
	(log transformed)	MethodT	-2.18	0.08	393.04	-26.53	<0.001	Site:River	0.34	0.29	17			
								Year	0.00	0.00	12			
								River	0.15	0.12	5			
								Residual	0.64	0.54	446			
ET07	**Rheophilic guild**	Intercept	0.98	0.25	6.13	3.98	0.007	Season:Year	0.03	0.02	33	0.62	0.75	0.13
	(log transformed)	MethodT	-3.14	0.10	411.55	-31.58	<0.001	Site:River	0.22	0.16	17			
								Year	0.08	0.06	12			
								River	0.14	0.10	5			
								Residual	0.93	0.66	440			
ET08	**Lithophilic guild**	Intercept	3.71	0.14	26.52	26.54	<0.001	Season:Year	0.01	0.00	33	0.78	0.81	0.03
	(log transformed)	MethodT	-4.05	0.13	247.50	-30.66	<0.001	Site:River	0.16	0.14	17			
								Year	0.00	0.00	12			
								River	0.00	0.00	5			
								Residual	0.97	0.85	251			
ET09	**Phytophilic guild**	Intercept	-0.66	0.28	13.23	-2.35	0.035	Season:Year	0.00	0.00	33	0.19	0.56	0.37
	(log transformed)	MethodT	-1.66	0.14	355.88	-12.32	<0.001	Site:River	0.08	0.07	17			
								Year	0.00	0.00	12			
								River	0.00	0.00	5			
								Residual	1.13	0.93	392			
ET10	**Psammophilic guild**	Intercept	-1.69	0.31	10.18	-5.43	<0.001	Season:Year	0.17	0.09	32	0.24	0.53	0.29
	(log transformed)	MethodT	-1.98	0.20	226.43	-9.90	<0.001	Site:River	0.43	0.22	17			
								Year	0.00	0.00	12			
								River	0.12	0.06	5			
								Residual	1.19	0.62	250			
ET11	**Potamal guild**	Intercept	-0.47	0.23	5.32	-2.04	0.093	Season:Year	0.18	0.12	33	0.04	0.49	0.45
	(log transformed)	MethodT	0.53	0.10	363.22	5.41	<0.001	Site:River	0.50	0.32	17			
								Year	0.00	0.00	12			
								River	0.04	0.03	5			
								Residual	0.82	0.54	427			

Table S 11. Sample sizes (n), means, standard errors (SE) and medians of biodiversity indices and of densities of selected guilds for the standardized comparison of electrofishing (E) vs. seining (S)

Biodiversity indices	n		mean +/- SE		median	
	E	S	E	S	E	S
Species richness	56	22	14.55 +/- 0.29	9.95 +/- 0.54	15.00	10.00
Shannon Index	56	22	1.94 +/- 0.02	1.17 +/- 0.06	1.96	1.15
Evenness	56	22	0.73 +/- 0.01	0.52 +/- 0.02	0.74	0.54
Simpson Index	56	22	0.80 +/- 0.01	0.56 +/- 0.03	0.81	0.59
Fish Region Index	56	22	6.78 +/- 0.01	6.96 +/- 0.00	6.78	6.95
Selected guilds			Density [Ind/100m²]			
Eurytopic	56	22	10.35 +/- 1.16	2.65 +/- 0.39	8.02	2.48
Rheophilic	56	21	4.90 +/- 0.60	0.17 +/- 0.02	3.89	0.17
Lithophilic	55	21	1.13 +/- 0.15	0.07 +/- 0.01	0.69	0.06
Phytophilic	54	22	1.20 +/- 0.15	0.66 +/- 0.2	0.89	0.37
Psammophilic	50	5	0.92 +/- 0.14	0.01 +/- 0.01	0.6	0.01
Potamal	55	22	2.33 +/- 0.33	2.11 +/- 0.30	1.55	2.13

Table S 12. Results of linear mixed effects models and calculated R^2 values for biodiversity indices and selected guilds for the standardized comparison of electrofishing vs. seining. Density [Ind/100m²] is the response for guilds (models ES06-ES11). "Est" = estimated regression parameters, "SE" = standard errors, "df" = degrees of freedom, "t" = t-values, "p" = p-values, "var" = variance of the intercept of random effects, "imp" indicates the amount of explained variation by the random effect on the total unexplained variation by the fixed effect "n" = sample sizes per stratum, "mar" = marginal R^2 of fixed effects, "cond" = conditional R^2 of fixed and random effects, "diff" = R^2mar-R^2cond, i.e. R^2 of only random effects

Model	Response	Fixed effects						Random effects				R^2		
		Fixed	Est	SE	df	t	p	Random	var	imp	n	mar	cond	diff
ES01	**Species richness**	Intercept	14.25	0.61	4.37	23.42	<0.001	Season:Year	0.00	0.00	21	0.43	0.56	0.13
	(not transformed)	MethodS	-4.53	0.54	73.97	-8.41	<0.001	Year	0.36	0.06	8			
								Site	0.93	0.17	4			
								Residual	4.26	0.77	78			
ES02	**Shannon Index**	Intercept	1.91	0.07	4.23	27.09	<0.001	Season:Year	0.00	0.00	21	0.69	0.80	0.11
	(not transformed)	MethodS	-0.75	0.05	72.79	-15.58	<0.001	Year	0.01	0.11	8			
								Site	0.01	0.26	4			
								Residual	0.03	0.63	78			
ES03	**Evenness**	Intercept	0.72	0.02	3.33	29.73	<0.001	Season:Year	0.00	0.00	21	0.58	0.72	0.14
	(not transformed)	MethodS	-0.20	0.02	71.38	-12.25	<0.001	Year	0.00	0.00	8			
								Site	0.00	0.33	4			
								Residual	0.00	0.67	78			
ES04	**Simpson Index**	Intercept	-0.25	0.05	3.60	-5.38	0.008	Season:Year	0.00	0.00	21	0.56	0.69	0.13
	(log transformed)	MethodS	-0.39	0.03	73.73	-11.36	<0.001	Year	0.00	0.04	8			
								Site	0.01	0.28	4			
								Residual	0.02	0.68	78			
ES05	**Fish Region Index**	Intercept	6.80	0.03	7.34	216.31	<0.001	Season:Year	0.00	0.00	21	0.44	0.77	0.33
	(not transformed)	MethodS	0.20	0.02	62.81	11.28	<0.001	Year	0.01	0.50	8			
	2 outlier excluded							Site	0.00	0.10	4			
								Residual	0.00	0.40	76			
ES06	**Eurytopic guild**	Intercept	2.03	0.21	4.59	9.80	<0.001	Season:Year	0.11	0.17	21	0.40	0.62	0.22
	(log transformed)	MethodS	-1.43	0.17	64.91	-8.37	<0.001	Year	0.03	0.04	8			
								Site	0.10	0.15	4			
								Residual	0.40	0.63	78			
ES07	**Rheophilic guild**	Intercept	0.98	0.27	7.90	3.58	0.007	Season:Year	0.33	0.34	21	0.73	0.92	0.19
	(log transformed)	MethodS	-3.59	0.15	55.49	-24.06	<0.001	Year	0.32	0.33	8			
								Site	0.04	0.04	4			
								Residual	0.28	0.29	77			
ES08	**Lithophilic guild**	Intercept	-0.47	0.25	7.13	-1.87	0.103	Season:Year	0.03	0.04	21	0.63	0.82	0.19
	(log transformed)	MethodS	-2.67	0.18	65.29	-15.14	<0.001	Year	0.38	0.45	8			
								Site	0.02	0.02	4			
								Residual	0.42	0.49	76			
ES09	**Phytophilic guild**	Intercept	-0.41	0.25	6.31	-1.63	0.152	Season:Year	0.00	0.00	21	0.05	0.19	0.14
	(log transformed)	MethodS	-0.61	0.29	72.48	-2.12	0.038	Year	0.16	0.11	8			
								Site	0.06	0.04	4			
								Residual	1.23	0.85	76			
ES10	**Psammophilic guild**	Intercept	-0.82	0.49	4.39	-1.67	0.164	Season:Year	0.84	0.36	20	0.45	0.82	0.37
	(log transformed)	MethodS	-4.74	0.47	36.21	-10.03	<0.001	Year	0.03	0.01	8			
								Site	0.68	0.30	4			
								Residual	0.76	0.33	55			
ES11	**Potamal guild**	Intercept	0.64	0.2	5.99	3.67	0.01	Season:Year	0.01	0.01	21	0.00	0.20	0.20
	(log transformed)	MethodS	0.01	0.2	64.1	0.03	0.98	Year	0.14	0.19	8			
	6 outlier excluded							Site	0.00	0.00	4			
								Residual	0.57	0.80	71			

Table S 13. Sample sizes (n), means, standard errors (SE) and medians of biodiversity indices and of densities of selected guilds for the standardized comparison of electrofishing (E) vs. drift-netting (D)

Biodiversity indices	n		mean +/- SE		median	
	E	D	E	D	E	D
Species richness	8	2	13.5 +/- 0.60	6.00 +/- 1.00	13.00	6.00
Shannon Index	8	2	1.86 +/- 0.06	0.41 +/- 0.10	1.84	0.41
Evenness	8	2	0.72 +/- 0.02	0.23 +/- 0.04	0.70	0.23
Simpson Index	8	2	0.79 +/- 0.01	0.16 +/- 0.05	0.78	0.16
Fish Region Index	8	2	6.77 +/- 0.02	7.01 +/- 0.00	6.76	7.01
Selected guilds			Density [Ind/100m^2]			
Eurytopic	8	2	21.02 +/- 5.33	0.13 +/- 0.02	20.82	0.13
Rheophilic	8	1	10.57 +/- 2.88	0.002 +/- --	6.07	0.002
Lithophilic	8	0	1.87 +/- 0.67	--	104.17	--
Phytophilic	8	2	0.83 +/- 0.42	0.12 +/- 0.01	0.39	0.12
Psammophilic	8	0	1.73 +/- 0.47	--	1.18	--
Potamal	7	2	2.47 +/- 1.47	0.12 +/- 0.01	1.38	0.12

Table S 14. Sample sizes (n), means, standard errors (SE) and medians of densities [Ind/100m²] of common species for the standardized comparison of electrofishing (E) vs. trawling (T)

Species	n		mean +/- SE		median	
	E	T	E	T	E	T
Abramis brama	124	284	0.59 +/- 0.09	1.53 +/- 0.15	0.26	0.79
Gymnocephalus cernuus	112	251	0.83 +/- 0.13	0.21 +/- 0.04	0.34	0.04
Leuciscus idus	158	144	2.87 +/- 0.28	0.05 +/- 0.02	1.68	0.01
Perca fluviatilis	159	200	2.96 +/- 0.27	0.21 +/- 0.1	1.85	0.03
Rutilus rutilus	161	277	11.39 +/- 1.07	0.89 +/- 0.27	6.65	0.16

Table S 15. Results of linear mixed effects models and calculated R^2 values for densities of common species for the standardized comparison of electrofishing vs. trawling. Log transformed density [Ind/100m²] is the response in each model. "Est" = estimated regression parameters, "SE" = standard errors, "df" = degrees of freedom, "t" = t-values, "p" = p-values, "var" = variance of the intercept of random effects, "imp" indicates the amount of explained variation by the random effect on the total unexplained variation by the fixed effect, "n" = sample sizes per stratum; "mar" = marginal R^2 of fixed effects, "cond" = conditional R^2 of fixed and random effects, "diff" = R^2mar-R^2cond, i.e. R^2 of only random effects

Model	Response	Fixed effects						Random effects				R^2		
		Fixed	Est	SE	df	t	p	Random	var	imp	n	mar	cond	diff
ET12	**Abramis brama**	Intercept	-1.25	0.26	22.50	-4.88	<0.001	Season:Year	0.13	0.07	32	0.05	0.55	0.50
	(log transfomed)	Method T	0.65	0.11	379.42	6.02	<0.001	Site:River	0.86	0.46	17			
	Density [Ind/100m2]							Year	0.00	0.00	12			
								River	0.00	0.00	5			
								Residual	0.88	0.47	408			
ET13	**Gymnocephalus cernuus**	Intercept	-0.83	0.51	4.13	-1.62	0.178	Season:Year	0.08	0.02	32	0.26	0.64	0.38
	(log transfomed)	Method T	-2.30	0.15	343.41	-14.96	<0.001	Site:River	0.54	0.17	17			
	Density [Ind/100m2]							Year	0.02	0.01	12			
								River	1.00	0.31	5			
								Residual	1.58	0.49	363			
ET14	**Leuciscus idus**	Intercept	0.25	0.25	4.26	0.97	0.382	Season:Year	0.14	0.07	33	0.74	0.80	0.06
	(log transfomed)	Method T	-4.58	0.15	284.07	-31.14	<0.001	Site:River	0.13	0.07	17			
	Density [Ind/100m2]							Year	0.00	0.00	12			
								River	0.19	0.10	5			
								Residual	1.42	0.76	302			
ET15	**Perca fluviatilis**	Intercept	0.54	0.30	5.57	1.78	0.129	Season:Year	0.06	0.03	33	0.69	0.79	0.10
	(log transfomed)	Method T	-4.49	0.14	332.81	-32.21	<0.001	Site:River	0.33	0.15	17			
	Density [Ind/100m2]							Year	0.10	0.04	12			
								River	0.23	0.10	5			
								Residual	1.48	0.68	359			
ET16	**Rutilus rutilus**	Intercept	1.85	0.47	3.18	3.96	0.026	Season:Year	0.15	0.05	33	0.53	0.76	0.23
	(log transfomed)	Method T	-3.95	0.13	363.96	-29.45	<0.001	Site:River	0.64	0.20	17			
	Density [Ind/100m2]							Year	0.00	0.00	12			
								River	0.76	0.24	5			
								Residual	1.68	0.52	438			

Table S 16. Sample sizes (n), means, standard errors (SE) and medians of densities [Ind/100m²] of common species for the standardized comparison of electrofishing (E) vs. seining (S)

Species	n		mean +/- SE		median	
	E	S	E	S	E	S
Abramis brama	52	22	1.33 +/- 0.27	1.46 +/- 0.22	0.51	1.23
Gymnocephalus cernuus	35	11	0.2 +/- 0.08	0.03 +/- 0.01	0.07	0.01
Leuciscus idus	56	21	2.75 +/- 0.42	0.09 +/- 0.02	1.9	0.06
Perca fluviatilis	56	15	2.7 +/- 0.43	0.03 +/- 0.01	1.65	0.02
Rutilus rutilus	56	22	3.69 +/- 0.6	0.46 +/- 0.13	1.84	0.21

Table S 17. Results of linear mixed effects models and calculated R^2 values for densities of common species for the standardized comparison of electrofishing vs. seining. Log transformed density [Ind/100m^2] is the response in each model. “Est” = estimated regression parameters, “SE” = standard errors, “df” = degrees of freedom, ”t” = t-values, “p” = p-values, “var” = variance of the intercept of random effects, "imp" indicates the amount of explained variation by the random effect on the total unexplained variation by the fixed effect, “n” = sample sizes per stratum; "mar" = marginal R^2 of fixed effects, "cond" = conditional R^2 of fixed and random effects, “diff” = R^2mar-R^2cond, i.e. R^2 of only random effects

Model	Response	Fixed effects						Random effects				R^2		
		Fixed	Est	SE	df	t	p	Random	var	imp	n	mar	cond	diff
ES12	**Abramis brama**	Intercept	-0.42	0.39	6.75	-1.08	0.316	Season:Year	0.00	0.00	21	0.12	0.53	2.15
	(log transfomed)	Method S	1.17	0.29	67.28	4.08	<0.001	Year	0.99	0.46	8			
	Density [Ind/100m2]							Site	0.00	0.00	4			
								Residual	1.16	0.54	74			
ES13	**Gymnocephalus cernuus**	Intercept	-2.71	0.24	5.88	-11.25	<0.001	Season:Year	0.20	0.12	17	0.16	0.28	1.60
	(log transfomed)	Method S	-1.27	0.43	40.87	-2.98	0.005	Year	0.04	0.02	7			
	Density [Ind/100m2]							Site	0.00	0.00	4			
								Residual	1.36	0.85	46			
ES14	**Leuciscus idus**	Intercept	0.09	0.37	7.49	0.25	0.813	Season:Year	0.68	0.35	21	0.61	0.85	1.93
	(log transfomed)	Method S	-3.89	0.25	56.27	-15.77	<0.001	Year	0.30	0.15	8			
	Density [Ind/100m2]							Site	0.19	0.10	4			
								Residual	0.76	0.39	77			
ES15	**Perca fluviatilis**	Intercept	0.26	0.34	6.99	0.76	0.474	Season:Year	0.33	0.21	21	0.70	0.85	1.55
	(log transfomed)	Method S	-4.63	0.28	51.60	-16.51	<0.001	Year	0.24	0.16	8			
	Density [Ind/100m2]							Site	0.20	0.13	4			
								Residual	0.78	0.50	71			
ES16	**Rutilus rutilus**	Intercept	0.42	0.35	6.74	1.20	0.270	Season:Year	0.30	0.17	21	0.42	0.68	1.78
	(log transfomed)	Method S	-2.51	0.27	62.85	-9.28	<0.001	Year	0.34	0.19	8			
	Density [Ind/100m2]							Site	0.15	0.08	4			
								Residual	0.99	0.56	78			

Table S 18. Sample sizes (n = number of measured fish), means, standard errors (SE) and medians of total lengths [mm] of common species for the standardized comparison of electrofishing (E) vs. trawling (T)

Species	n		mean +/- SE		median	
	E	T	E	T	E	T
Abramis brama	778	60384	194 +/- 7	219 +/- 1	85	125
Gymnocephalus cernuus	859	7674	85 +/- 1	86+/- 0	83	83
Leuciscus idus	4740	969	130 +/- 1	193 +/- 4	105	125
Perca fluviatilis	4496	5325	109 +/- 1	114 +/- 1	95	105
Rutilus rutilus	19044	28546	88 +/- 0	136 +/- 0	85	105

Table S 19. Results of linear mixed effects models and calculated R^2 values for total lengths of common species for the standardized comparison of electrofishing vs. trawling. Log transformed total length [mm] is the response in each model. “Est” = estimated regression parameters, “SE” = standard errors, “df” = degrees of freedom, ”t” = t-values, “p” = p-values, “var” = variance of the intercept of random effects, "imp" indicates the amount of explained variation by the random effect on the total unexplained variation by the fixed effect, “n” = sample sizes per stratum; "mar" = marginal R^2 of fixed effects, "cond" = conditional R^2 of fixed and random effects, “diff” = R^2mar-R^2cond, i.e. R^2 of only random effects

Model	Response	Fixed effects						Random effects				R^2		
		Fixed	Est	SE	df	t	p	Random	var	imp	n	mar	cond	diff
ET17	**Abramis brama**	Intercept	5.05	0.10	6.66	52.34	<0.001	Sampling	0.01	0.05	355	0.00	0.49	0.49
	(log transfomed)	Method T	0.39	0.06	384.87	6.70	<0.001	Season:Year	0.00	0.00	20			
	Length [mm]							Site:River	0.02	0.15	16			
								Year	0.01	0.05	10			
								River	0.00	0.00	4			
								Residual	0.10	0.72	61162			
ET18	**Gymnocephalus cernuus**	Intercept	4.47	0.03	4.49	173.31	<0.001	Sampling	0.01	0.15	314	0.00	0.38	0.38
	(log transfomed)	Method T	0.02	0.01	239.94	1.40	0.164	Season:Year	0.00	0.06	20			
	Length [mm]							Site:River	0.01	0.18	16			
								Year	0.00	0.00	10			
								River	0.00	0.00	4			
								Residual	0.02	0.62	8533			
ET19	**Leuciscus idus**	Intercept	4.92	0.07	5.81	66.39	<0.001	Sampling	0.06	0.23	247	0.14	0.55	0.41
	(log transfomed)	Method T	0.53	0.04	238.69	12.72	<0.001	Season:Year	0.02	0.10	20			
	Length [mm]							Site:River	0.03	0.12	16			
								Year	0.00	0.00	10			
								River	0.01	0.00	4			
								Residual	0.12	0.52	5709			
ET20	**Perca fluviatilis**	Intercept	4.67	0.05	25.35	97.68	<0.001	Sampling	0.07	0.48	314	0.11	0.68	0.57
	(log transfomed)	Method T	0.26	0.03	244.86	7.73	<0.001	Season:Year	0.00	0.02	20			
	Length [mm]							Site:River	0.01	0.10	16			
								Year	0.01	0.04	10			
								River	0.00	0.00	4			
								Residual	0.05	0.36	9821			
ET21	**Rutilus rutilus**	Intercept	4.50	0.05	7.93	83.41	<0.001	Sampling	0.07	0.42	383	0.41	0.76	0.35
	(log transfomed)	Method T	0.71	0.03	343.60	22.95	<0.001	Season:Year	0.01	0.07	20			
	Length [mm]							Site:River	0.02	0.10	16			
								Year	0.00	0.00	10			
								River	0.00	0.00	4			
								Residual	0.07	0.40	47590			

Chapter two

Appendix

Disentangling multiple pressures on fish assemblages in large rivers

Petr Zajicek, Johannes Radinger & Christian Wolter

Tables A.1 – A.3

Figure A.1

Table A.1 Captured fish species and their affiliation to ecological guilds and to the Fish Region Index. Hab = habitat guilds (EURY = eurytopic; LIMNO = limnophilic; RH = rheophilic), Repro = reproduction guilds (ARIAD = ariadnophilic; LIPE = litho-pelagophilic; LITH = lithophilic; OSTRA = ostracophilic; PHLI = phyto-lithophilic; PHYT = phytophilic; POLY = polyphilic; PSAM = psammophilic; SPEL = speleophilic), FRI = Fish Region Index, SFRI = Variance of the Fish Region Index. Classifications follow Scharf et al. (2011), Dußling et al. (2004b) and EFI+ Consortium (2009).

Latin name	Common name	Hab	Repro	FRI	SFRI
Abramis ballerus	Blue bream	RH	PHLI	7.08	0.45
Abramis brama	Common bream	EURY	PHLI	7.00	0.55
Alburnus alburnus	Bleak	EURY	PHLI	6.58	0.63
Ameiurus nebulosus	Brown bullhead	EURY	SPEL	6.58	0.27
Anguilla anguilla	European eel	EURY	PELA	6.67	1.70
Aspius aspius	Asp	RH	LITH	6.75	0.39
Barbatula barbatula	Stone loach	RH	PSAM	5.25	0.93
Barbus barbus	Barbel	RH	LITH	6.08	0.45
Blicca bjoerkna	White bream	EURY	PHYT	7.00	0.55
Carassius carassius	Crucian carp	LIMNO	PHYT	6.92	0.27
Carassius gibelio	Prussian carp	EURY	PHYT	6.67	0.79
Chelon labrosus	Thicklip mullet	LIMNO	PELA	--	--
Chondrostoma nasus	Nase	RH	LITH	5.67	0.61
Cobitis taenia	Northern spined loach	RH	PHYT	6.50	0.64
Cottus gobio	Sculpin	RH	SPEL	4.17	1.24
Ctenopharyngodon idella	Grass carp	RH	PELA	7.17	0.15
Cyprinus carpio	Carp	EURY	PHYT	7.00	0.36
Dicentrarchus labrax	European seabass	EURY	PELA	7.83	0.15
Esox lucius	Northern pike	EURY	PHYT	6.58	0.99
Gasterosteus aculeatus	Three-spined stickleback	EURY	ARIAD	7.17	1.06
Gobio gobio	Gudgeon	RH	PSAM	5.83	1.24
Gymnocephalus cernuus	Ruffe	EURY	PHLI	7.42	0.45
Hypophthalmichthys molitrix	Silver Carp	EURY	PELA	--	--
Hypophthalmichthys nobilis	Bighead carp	RH	LITH	7.08	0.27
Lampetra fluviatilis	River lamprey	RH	LITH	5.17	0.52
Lampetra planeri	Brook lamprey	RH	LITH	4.58	0.45
Lepomis gibbosus	Pumpkinseed	LIMNO	POLY	6.83	0.33
Leucaspius delineatus	Sunbleak	LIMNO	PHYT	6.83	0.33
Leuciscus cephalus	Chub	RH	LITH	5.83	1.24
Leuciscus idus	Ide	RH	PHLI	6.83	0.52
Leuciscus leuciscus	Common dace	RH	LITH	5.75	0.93
Lota lota	Burbot	RH	LIPE	6.33	1.52
Misgurnus fossilis	European weatherfish	LIMNO	PHYT	7.00	0.36
Oncorhynchus mykiss	Rainbow trout	RH	LITH	4.00	0.73
Osmerus eperlanus	European smelt	EURY	LIPE	7.42	0.45
Perca fluviatilis	European perch	EURY	PHLI	6.92	0.99
Petromyzon marinus	Sea lamprey	RH	LITH	5.75	0.39
Phoxinus phoxinus	Eurasian minnow	RH	LITH	4.67	0.79
Platichthys flesus	Flounder	RH	PELA	7.50	0.45
Proterorhinus marmoratus	Tubenose goby	EURY	SPEL	7.08	0.63
Pseudorasbora parva	Stone moroko	EURY	PHLI	6.58	0.63
Pungitius pungitius	Ninespine stickleback	EURY	ARIAD	7.17	0.52
Rhodeus amarus	European bitterling	LIMNO	OSTRA	6.50	0.27
Romanogobio belingi	Northern whitefin gudgeon	RH	PSAM	6.58	0.27
Rutilus rutilus	Roach	EURY	PHLI	6.83	0.88
Salmo salar	Salmon	RH	LITH	5.00	0.55
Salmo trutta fario	Brown trout	RH	LITH	3.75	0.57
Salmo trutta trutta	Sea trout	RH	LITH	5.00	0.55
Sander lucioperca	Pike-perch	EURY	PHLI	7.25	0.57
Scardinius erythrophthalmus	Rudd	LIMNO	PHYT	6.92	0.45
Silurus glanis	European catfish	EURY	PHYT	7.00	0.36
Thymallus thymallus	Grayling	RH	LITH	4.92	0.45
Tinca tinca	Tench	LIMNO	PHYT	6.92	0.45
Vimba vimba	Vimba bream	RH	LITH	6.67	0.79

Table A.2 Catch statistics for 250 samplings at 76 sampling sites in 8 European large rivers. "Total catch" refers to the number (n) of fish and their frequency in the overall catch; "Samplings" refers to the amount (n) and frequency (%) of samplings in which the given species was captured; "Sites" refers to the amount (n) and frequency (%) of sites at which the given species was captured; "Rivers" refers to the amount (n) and frequency (%) of rivers in which the given species was captured.

Species	Total catch		Samplings		Sites		Rivers	
	n	[%]	n	[%]	n	[%]	n	[%]
Rutilus rutilus	38523	25.86	249	99.60	76	100	8	100
Alburnus alburnus	21345	14.33	199	79.60	70	92.1	8	100
Perca fluviatilis	19180	12.88	247	98.80	76	100	8	100
Leuciscus idus	12872	8.64	236	94.40	68	89.5	8	100
Gobio gobio	9797	6.58	144	57.60	56	73.7	8	100
Leuciscus cephalus	8794	5.90	173	69.20	62	81.6	8	100
Anguilla anguilla	6221	4.18	207	82.80	62	81.6	8	100
Abramis brama	5073	3.41	215	86.00	69	90.8	8	100
Lota lota	4910	3.30	71	28.40	33	43.4	6	75
Leuciscus leuciscus	4784	3.21	132	52.80	57	75	7	87.5
Blicca bjoerkna	3713	2.49	130	52.00	51	67.1	8	100
Gymnocephalus cernuus	2352	1.58	153	61.20	58	76.3	8	100
Esox lucius	1570	1.05	177	70.80	59	77.6	8	100
Romanogobio belingi	1723	1.15	75	30	31	40.8	4	50
Aspius aspius	1458	0.98	185	74.00	62	81.6	8	100
Barbus barbus	1233	0.83	96	38.40	49	64.5	6	75
Platichthys flesus	1063	0.71	75	30.00	14	18.4	3	37.5
Sander lucioperca	711	0.48	153	61.20	48	63.2	7	87.5
Barbatula barbatula	636	0.43	29	11.60	17	22.4	4	50
Scardinius erythrophthalmus	489	0.33	79	31.60	40	52.6	7	87.5
Cobitis taenia	427	0.29	41	16.40	29	38.2	7	87.5
Carassius gibelio	271	0.18	21	8.40	17	22.4	5	62.5
Cottus gobio	268	0.18	33	13.20	15	19.7	5	62.5
Ameiurus nebulosus	256	0.17	28	11.20	11	14.5	1	12.5
Chondrostoma nasus	240	0.16	38	15.20	22	29	4	50
Gasterosteus aculeatus	212	0.14	55	22.00	21	27.6	7	87.5
Rhodeus amarus	210	0.14	25	10.00	20	26.3	5	62.5
Silurus glanis	113	0.08	40	16.00	21	27.6	4	50
Cyprinus carpio	92	0.06	44	17.60	19	25	6	75
Tinca tinca	85	0.06	37	14.80	23	30.3	7	87.5
Lampetra planeri	74	0.05	4	1.60	4	5.26	1	12.5
Leucaspius delineatus	64	0.04	9	3.60	7	9.21	5	62.5
Proterorhinus marmoratus	27	0.02	6	2.40	3	3.95	2	25
Abramis ballerus	26	0.02	10	4.00	9	11.8	2	25
Salmo trutta fario	25	0.02	12	4.80	7	9.21	3	37.5
Pseudorasbora parva	24	0.02	8	3.20	6	7.89	2	25
Salmo salar	21	0.01	15	6.00	8	10.5	2	25
Carassius carassius	14	0.01	7	2.80	5	6.58	1	12.5
Thymallus thymallus	14	0.01	5	2.00	2	2.63	1	12.5
Pungitius pungitius	10	0.01	4	1.60	4	5.26	3	37.5
Chelon labrosus	7	< 0.01	2	0.80	2	2.63	1	12.5
Lampetra fluviatilis	7	< 0.01	6	2.40	6	7.89	3	37.5
Ctenopharyngodon idella	5	< 0.01	4	1.60	3	3.95	2	25
Misgurnus fossilis	4	< 0.01	2	0.80	2	2.63	2	25
Vimba vimba	4	< 0.01	4	1.60	3	3.95	2	25
Dicentrarchus labrax	3	< 0.01	3	1.20	2	2.63	2	25
Lepomis gibbosus	3	< 0.01	1	0.40	1	1.32	1	12.5
Osmerus eperlanus	3	< 0.01	3	1.20	2	2.63	2	25
Petromyzon marinus	2	< 0.01	1	0.40	1	1.32	1	12.5
Salmo trutta trutta	2	< 0.01	2	0.80	2	2.63	2	25
Hypophthalmichthys molitrix	1	< 0.01	1	0.40	1	1.32	1	12.5
Hypophthalmichthys nobilis	1	< 0.01	1	0.40	1	1.32	1	12.5
Oncorhynchus mykiss	1	< 0.01	1	0.40	1	1.32	1	12.5
Phoxinus phoxinus	1	< 0.01	1	0.40	1	1.32	1	12.5

Table A.3 Composition of the studied guilds as determined in 250 samplings at 76 sampling sites in 8 European large rivers. Total catch (TC) refers to the frequency of fish of the respective species in the overall catch.

Eurytopic guild	TC [%]	Rheophilic guild	TC [%]	Lithophilic guild	TC [%]	Phytophilic guild	TC [%]	Psammophilic guild	TC [%]
Abramis brama	3.41	Abramis ballerus	0.02	Aspius aspius	0.98	Blicca bjoerkna	2.49	Barbatula barbatula	0.43
Alburnus alburnus	14.33	Aspius aspius	0.98	Barbus barbus	0.83	Carassius carassius	0.01	Gobio albipinnatus	0.1
Ameiurus nebulosus	0.17	Barbatula barbatula	0.43	Chondrostoma nasus	0.16	Carassius gibelio	0.18	Romanogobio belingi	1.15
Anguilla anguilla	4.18	Barbus barbus	0.83	Hypophthalmichthys nobilis	< 0.01	Cobitis taenia	0.29	**TOTAL:**	**1.68**
Blicca bjoerkna	2.49	Chondrostoma nasus	0.16	Lampetra fluviatilis	< 0.01	Cyprinus carpio	0.06		
Carassius gibelio	0.18	Cobitis taenia	0.29	Lampetra planeri	0.05	Esox lucius	1.05		
Cyprinus carpio	0.06	Cottus gobio	0.18	Leuciscus cephalus	5.9	Leucaspius delineatus	0.04		
Dicentrarchus labrax	< 0.01	Ctenopharyngodon idella	< 0.01	Leuciscus leuciscus	3.21	Misgurnus fossilis	< 0.01		
Esox lucius	1.05	Gobio albipinnatus	0.1	Oncorhynchus mykiss	< 0.01	Scardinius erythrophthalmus	0.33		
Gasterosteus aculeatus	0.14	Gobio gobio	6.58	Petromyzon marinus	< 0.01	Silurus glanis	0.08		
Gymnocephalus cernuus	1.58	Hypophthalmichthys nobilis	< 0.01	Phoxinus phoxinus	< 0.01	Tinca tinca	0.06		
Hypophthalmichthys molitrix	< 0.01	Lampetra fluviatilis	< 0.01	Salmo salar	0.01	**TOTAL:**	**4.59**		
Osmerus eperlanus	< 0.01	Lampetra planeri	0.05	Salmo trutta fario	0.02				
Perca fluviatilis	12.88	Leuciscus cephalus	5.9	Salmo trutta trutta	< 0.01				
Proterorhinus marmoratus	0.02	Leuciscus idus	8.64	Thymallus thymallus	0.01				
Pseudorasbora parva	0.02	Leuciscus leuciscus	3.21	Vimba vimba	< 0.01				
Pungitius pungitius	0.01	Lota lota	3.3	**TOTAL:**	**11.17**				
Rutilus rutilus	25.86	Oncorhynchus mykiss	< 0.01						
Sander lucioperca	0.48	Petromyzon marinus	< 0.01						
Silurus glanis	0.08	Phoxinus phoxinus	< 0.01						
TOTAL:	**66.94**	Platichthys flesus	0.71						
		Romanogobio belingi	1.05						
		Salmo salar	0.01						
		Salmo trutta fario	0.02						
		Salmo trutta trutta	< 0.01						
		Thymallus thymallus	0.01						
		Vimba vimba	< 0.01						
		TOTAL:	**32.47**						

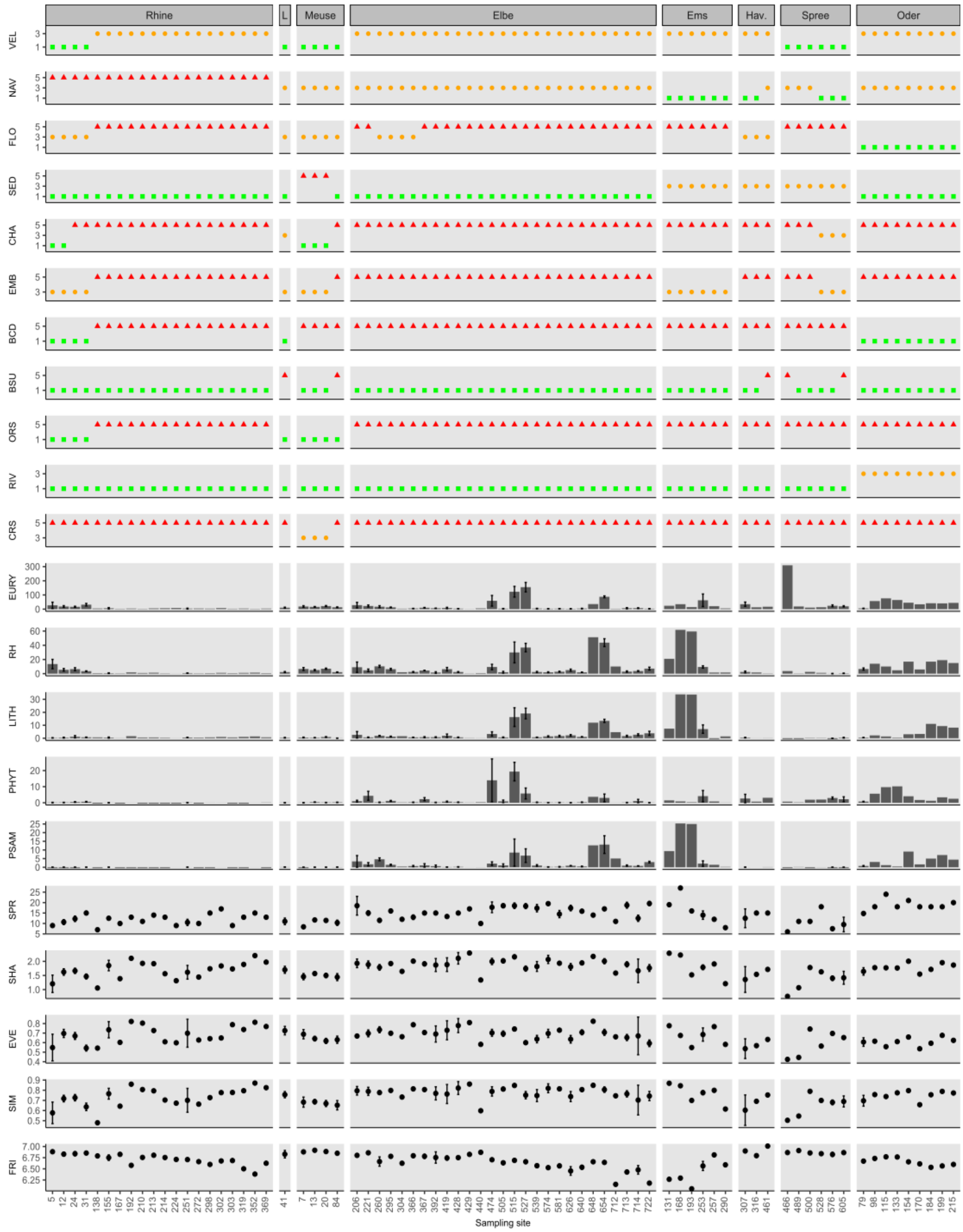

Figure A.1 Overview of pressures and fish population metrics (FPM) per sampling sites within rivers. L = river Lek; Hav. = river Havel. PRESSURES: VEL = velocity increase; NAV = navigation intensity; FLO = loss of floodplains; SED = sedimentation; CHA = channelization; EMB = embankment; BCD = barriers catchment down; BSU = barriers segment up; ORS = organic siltation; RIV = riparian vegetation; CRS = cross-section. Alteration of the natural state increases from one to five [different symbols and colors are used for better visualization: 1 = square (green) = low or no modification; 3 = circle (orange) = intermediate modification; 5 = triangle (red) = high modification], for more details on pressures see compare Table 1 in the paper; DENSITIES OF FISH IN SELECTED GUILDS: EURY = eurytopic, RH = rheophilic, LITH = lithophilic, PHYT = phytophilic, PSAM = psammophilic; BIODIVERSITY METRICS: SPR = species richness, SHA = Shannon Index, EVE = Evenness, SIM = Simpson diversity Index, FRI = Fish Region Index. Pressure classes are shown for all pressures and means and +/- standard errors are shown for each FPM. The x-axis labels show the distance of each sampling site to the Ocean in kilometers. Note: This figure has been originally provided in A3 format and downscaled here to A4. For better readability, readers are kindly referred to the original online version (https://doi.org/10.1016/j.scitotenv.2018.01.307)

Chapter three

Appendix

The effects of recreational and commercial navigation on fish assemblages in large rivers

Petr Zajicek and Christian Wolter

Tables A.1 – A.3

Figures A.1 – A.4

Table A.4 Catch statistics for 396 samplings at 88 sampling sites in six European large rivers. "Total catch" refers to the number (n) of fish and their relative abundance in the overall catch; "Samplings" refers to the amount (n) and frequency (%) of samplings in which the given species was captured; "Sites" refers to the amount (n) and frequency (%) of sites at which the given species was captured; "Rivers" refers to the amount (n) and presence (%) of rivers in which the given species was captured

Latin name	Common name	Total catch		Samplings		Sites		Rivers	
		n	[%]	n	[%]	n	[%]	n	[%]
Rutilus rutilus	Roach	65950	28.72	391	98.74	87	98.86	6	100
Perca fluviatilis	Perch	36185	15.76	382	96.46	85	96.59	6	100
Alburnus alburnus	Bleak	25539	11.12	326	82.32	81	92.05	6	100
Leuciscus idus	Ide	18485	8.05	351	88.64	83	94.32	6	100
Leuciscus cephalus	Chub	11915	5.19	298	75.25	70	79.55	6	100
Lota lota	Burbot	10866	4.73	138	34.85	46	52.27	4	66.67
Gobio gobio	Gudgeon	10718	4.67	236	59.60	67	76.14	6	100
Anguilla anguilla	Eel	10533	4.59	341	86.11	74	84.09	6	100
Abramis brama	Common bream	8263	3.60	336	84.85	82	93.18	6	100
Blicca bjoerkna	White bream	7762	3.38	221	55.81	67	76.14	6	100
Leuciscus leuciscus	Common dace	5141	2.24	198	50.00	59	67.05	5	83.33
Gymnocephalus cernuus	Ruffe	3531	1.54	242	61.11	70	79.55	6	100
Esox lucius	Pike	2246	0.98	246	62.12	67	76.14	6	100
Barbus barbus	Barbel	2134	0.93	170	42.93	55	62.5	5	83.33
Aspius aspius	Asp	1900	0.83	265	66.92	78	88.64	6	100
Romanogobio belingi	Common river gudgeon	1864	0.81	87	21.97	29	32.95	3	50
Cobitis taenia	Spined loach	1829	0.80	64	16.16	28	31.82	4	66.67
Platichthys flesus	Flounder	908	0.40	74	18.69	18	20.45	3	50
Sander lucioperca	Pike-perch	868	0.38	217	54.80	65	73.86	6	100
Scardinius erythrophthalmus	Rudd	764	0.33	104	26.26	46	52.27	6	100
Chondrostoma nasus	Nase	678	0.30	88	22.22	32	36.36	4	66.67
Barbatula barbatula	Stone loach	247	0.11	46	11.62	18	20.45	4	66.67
Gasterosteus aculeatus	Three-spined stickleback	210	0.09	72	18.18	23	26.14	6	100
Rhodeus amarus	Bitterling	142	0.06	29	7.32	21	23.86	6	100
Abramis ballerus	Blue bream	132	0.06	21	5.30	10	11.36	2	33.33
Cottus gobio	Sculpin	129	0.06	42	10.61	15	17.05	4	66.67
Silurus glanis	Catfish	112	0.05	53	13.38	30	34.09	5	83.33
Cyprinus carpio	Carp	100	0.04	53	13.38	23	26.14	6	100
Tinca tinca	Tench	78	0.03	41	10.35	23	26.14	5	83.33
Leucaspius delineatus	Sunbleak	72	0.03	13	3.28	8	9.09	4	66.67
Ameiurus nebulosus	Brown bullhead	62	0.03	21	5.30	8	9.09	1	16.67
Carassius gibelio	Prussian carp	59	0.03	23	5.81	18	20.45	5	83.33
Salmo trutta fario	Brown trout	54	0.02	31	7.83	15	17.05	3	50
Salmo salar	Salmon	39	0.02	22	5.56	13	14.77	3	50
Carassius carassius	Crucian carp	20	0.01	13	3.28	7	7.95	2	33.33
Misgurnus fossilis	Weatherfish	19	0.01	7	1.77	3	3.41	2	33.33
Oncorhynchus mykiss	Rainbow trout	17	0.01	5	1.26	4	4.55	2	33.33
Thymallus thymallus	Grayling	13	0.01	5	1.26	2	2.27	1	16.67
Proterorhinus marmoratus	Tubenose goby	12	0.01	7	1.77	4	4.55	3	50
Lampetra fluviatilis	River lamprey	11	0.00	9	2.27	8	9.09	3	50
Salmo trutta trutta	Sea trout	10	0	10	2.53	7	7.95	3	50
Pseudorasbora parva	Stone moroko	8	0	8	2.02	6	6.82	2	33.33
Chelon labrosus	Thicklip mullet	7	0	2	0.51	2	2.27	1	16.67
Pungitius pungitius	Ninespine stickleback	7	0	5	1.26	5	5.68	3	50
Ctenopharyngodon idella	Grass carp	4	0	3	0.76	2	2.27	2	33.33
Lepomis gibbosus	Pumpkinseed	4	0	2	0.51	2	2.27	1	16.67
Vimba vimba	Vimba bream	4	0	4	1.01	3	3.41	2	33.33
Osmerus eperlanus	Smelt	3	0	3	0.76	2	2.27	2	33.33
Phoxinus phoxinus	Minnow	3	0	3	0.76	3	3.41	2	33.33
Dicentrarchus labrax	Seabass	2	0	2	0.51	1	1.14	1	16.67
Petromyzon marinus	Sea lamprey	2	0	1	0.25	1	1.14	1	16.67
Sabanejewia aurata	Golden spined loach	2	0	2	0.51	1	1.14	1	16.67
Hypophthalmichthys nobilis	Bighead carp	1	0	1	0.25	1	1.14	1	16.67
Salvelinus fontinalis	Brook trout	1	0	1	0.25	1	1.14	1	16.67
Umbra pygmaea	Mudminnow	1	0	1	0.25	1	1.14	1	16.67

Table A.5 Composition of the studied guilds as determined in 396 samplings at 88 sampling sites in six European large rivers. Total catch (TC) refers to the relative abundance of fish of the respective species in the overall catch

Eurytopic guild	TC [%]	Rheophilic guild	TC [%]	Lithophilic guild	TC [%]	Phytophilic guild	TC [%]	Psammophilic guild	TC [%]
Abramis brama	3.6	Abramis ballerus	0.06	Aspius aspius	0.83	Blicca bjoerkna	3.38	Barbatula barbatula	0.11
Alburnus alburnus	11.12	Aspius aspius	0.83	Barbus barbus	0.93	Carassius carassius	0.01	Romanogobio belingi	0.81
Ameiurus nebulosus	0.03	Barbatula barbatula	0.11	Chondrostoma nasus	0.3	Carassius gibelio	0.03	Gobio gobio	4.67
Anguilla anguilla	4.59	Barbus barbus	0.93	Hypophthalmichthys nobilis	< 0.01	Cobitis taenia	0.8	**TOTAL:**	**5.59**
Blicca bjoerkna	3.38	Chondrostoma nasus	0.3	Lampetra fluviatilis	< 0.01	Cyprinus carpio	0.04		
Carassius gibelio	0.03	Cobitis taenia	0.8	Leuciscus cephalus	5.19	Esox lucius	0.98		
Cyprinus carpio	0.04	Cottus gobio	0.06	Leuciscus leuciscus	2.24	Leucaspius delineatus	0.03		
Dicentrarchus labrax	< 0.01	Ctenopharyngodon idella	< 0.01	Oncorhynchus mykiss	0.01	Misgurnus fossilis	0.01		
Esox lucius	0.98	Gobio gobio	4.67	Petromyzon marinus	< 0.01	Sabanejewia aurata	< 0.01		
Gasterosteus aculeatus	0.09	Hypophthalmichthys nobilis	< 0.01	Phoxinus phoxinus	< 0.01	Scardinius erythrophthalmus	0.33		
Gymnocephalus cernuus	1.54	Lampetra fluviatilis	< 0.01	Salmo salar	0.02	Silurus glanis	0.05		
Osmerus eperlanus	< 0.01	Leuciscus cephalus	5.19	Salmo trutta fario	0.02	Tinca tinca	0.03		
Perca fluviatilis	15.76	Leuciscus idus	8.05	Salmo trutta trutta	< 0.01	Umbra pygmaea	< 0.01		
Proterorhinus marmoratus	0.01	Leuciscus leuciscus	2.24	Salvelinus fontinalis	< 0.01	**TOTAL:**	**5.69**		
Pseudorasbora parva	< 0.01	Lota lota	4.73	Thymallus thymallus	0.01				
Pungitius pungitius	< 0.01	Oncorhynchus mykiss	0.01	Vimba vimba	< 0.01				
Rutilus rutilus	28.72	Petromyzon marinus	< 0.01	**TOTAL:**	**9.55**				
Sander lucioperca	0.38	Phoxinus phoxinus	< 0.01						
Silurus glanis	0.05	Platichthys flesus	0.4						
TOTAL:	**70.32**	Romanogobio belingi	0.81						
		Sabanejewia aurata	< 0.01						
		Salmo salar	0.02						
		Salmo trutta fario	0.02						
		Salmo trutta trutta	< 0.01						
		Salvelinus fontinalis	< 0.01						
		Thymallus thymallus	0.01						
		Vimba vimba	< 0.01						
		TOTAL:	**29.24**						

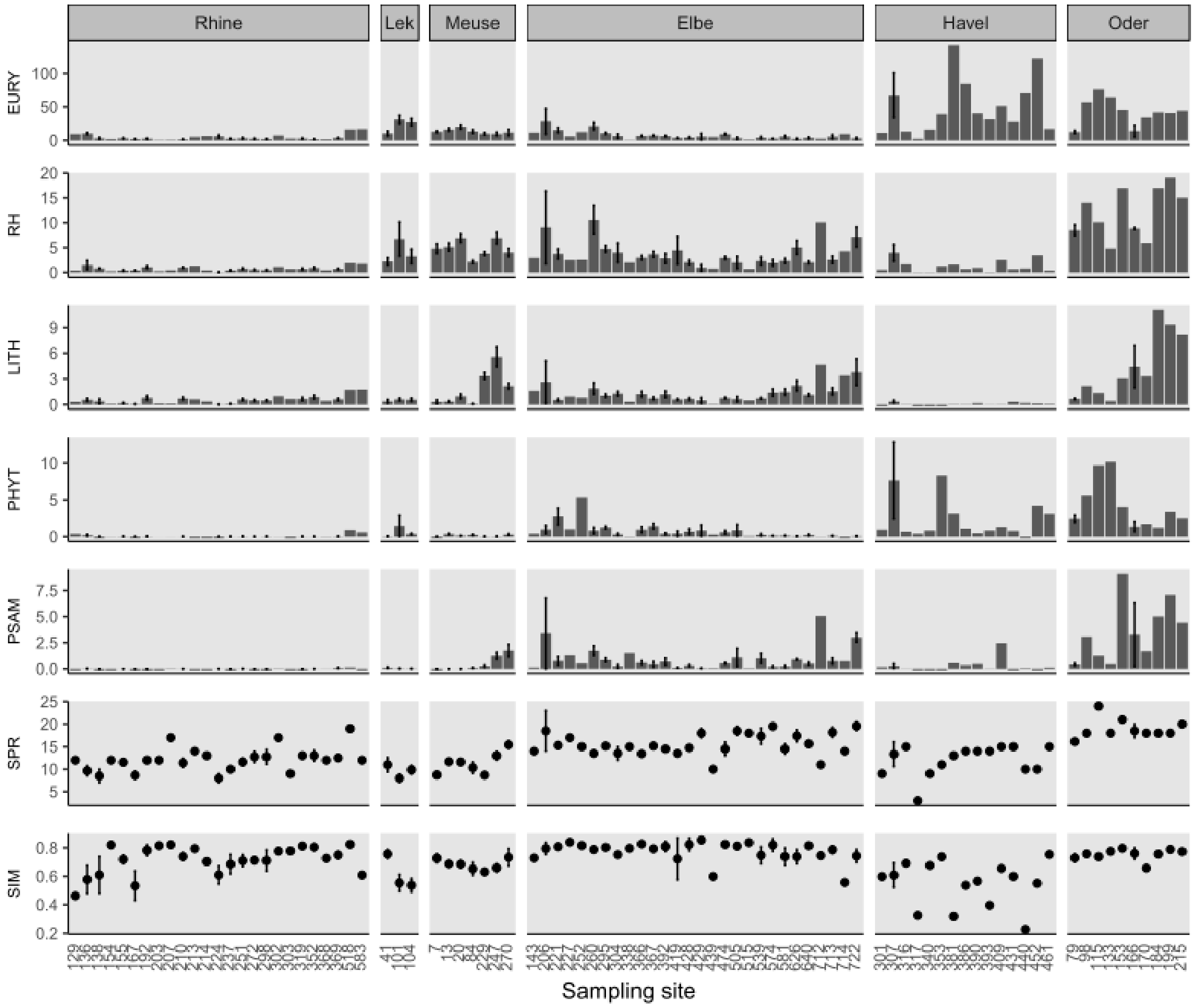

Figure A.2 Site-specific estimates of fish population metrics. Densities of fish in guilds (Individuals per 100 m²): EURY = eurytops, RH = rheophils, LITH = lithophils, PHYT = phytophils, PSAM = psammophils; BIODIVERSITY METRICS: SPR = species richness, SIM = Simpson Diversity Index. Means +/- standard errors are shown. The x-axis labels show the distance of each sampling site to the Ocean in kilometers. Note: This figure has been originally provided in A3 format and downscaled here to A4. For better readability, readers are kindly referred to the original online version (https://doi.org/10.1016/j.scitotenv.2018.07.403)

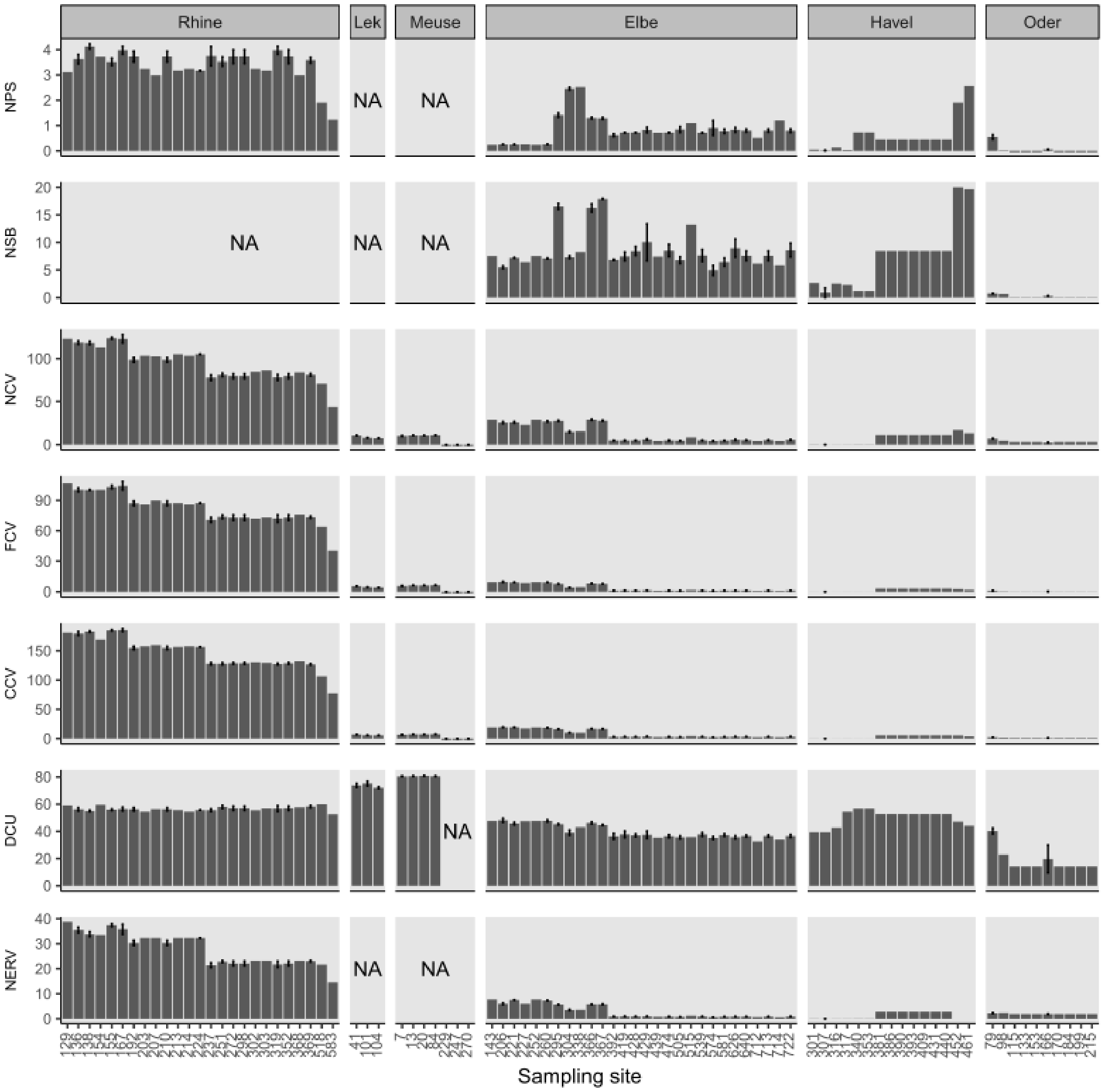

Figure A.3 Site-specific estimates of navigation metrics. NSB = Number of sport boats; NPS = Number of passenger ships; NCV = Number of cargo vessels; FCV = Freight of cargo vessels; CCV = Carrying capacity of cargo vessels; NERV = Number of empty running cargo vessels; DCU = Degree of capacity utilization. Means +/- standard errors are shown. The x-axis labels show the distance of each sampling site to the Ocean in kilometers. Note: This figure has been originally provided in A3 format and downscaled here to A4. For better readability, readers are kindly referred to the original online version (https://doi.org/10.1016/j.scitotenv.2018.07.403)

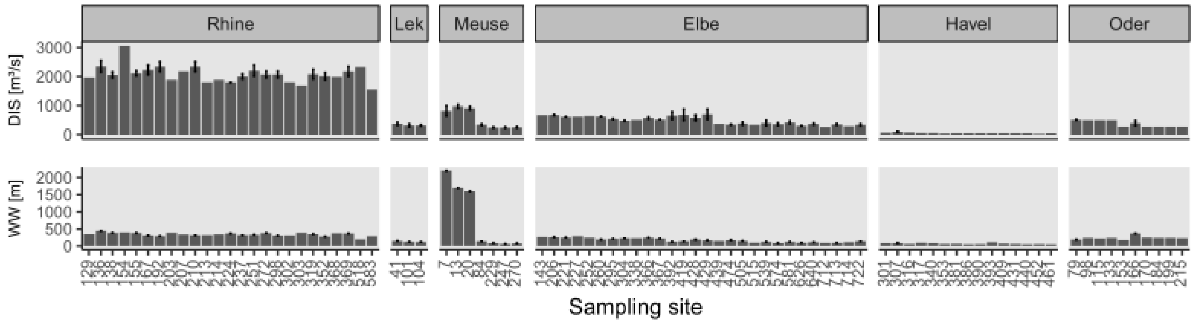

Figure A.4 Site-specific estimates of discharge (DIS) and wetted width (WW). The x-axis labels show the distance of each sampling site to the Ocean in kilometers. Note: This figure has been originally provided in A3 format and downscaled here to A4. For better readability, readers are kindly referred to the original online version (https://doi.org/10.1016/j.scitotenv.2018.07.403)

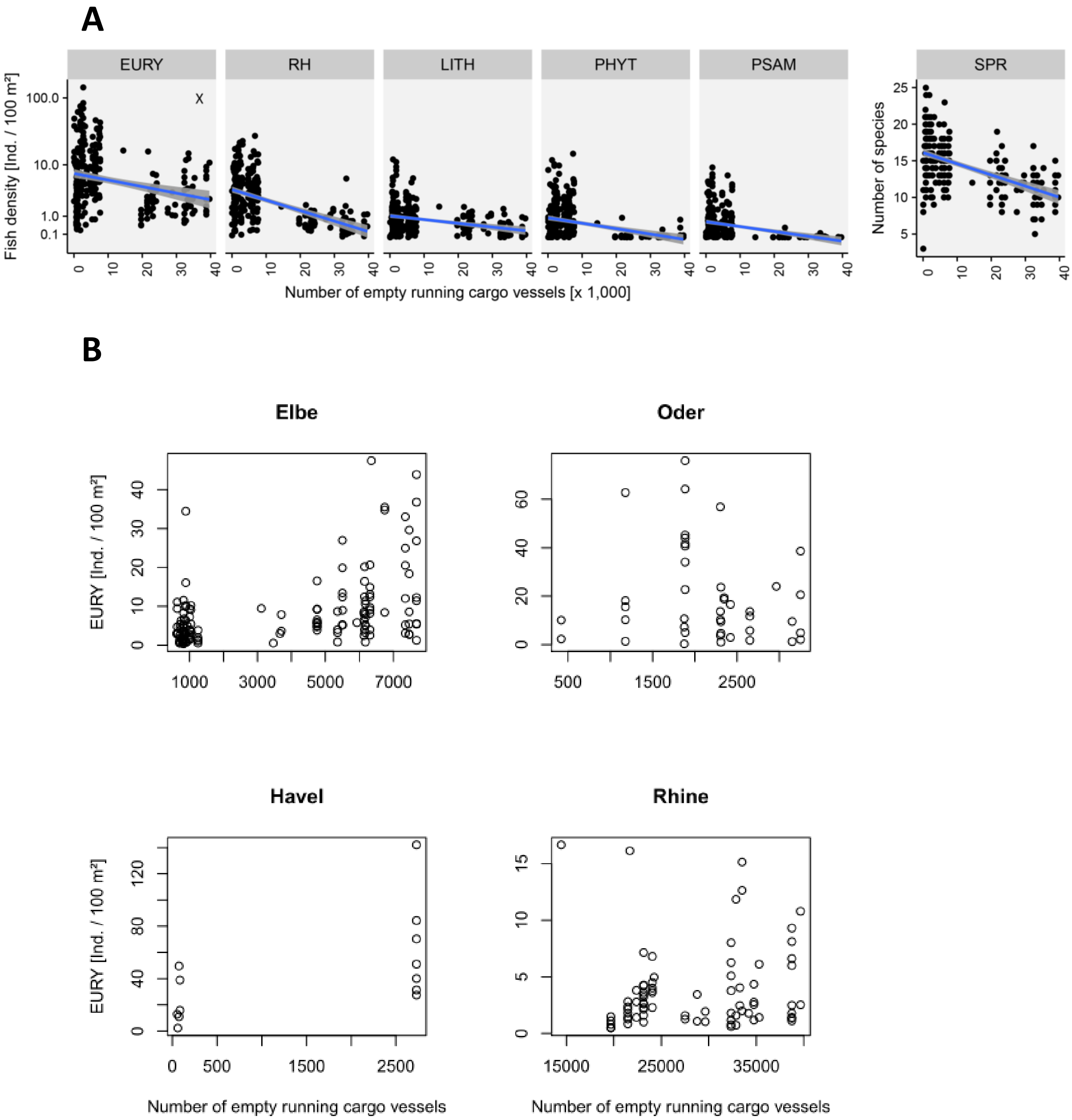

Figure A.5

A: Response of fish population metrics (EURY = eurytopic guild, RH = rheophilic guild, LITH = lithophilic guild, PHYT = phytophilic guild, PSAM = psammophilic guild; SPR = species richness) to the number of empty running cargo vessels. This figure refers to ds2 and includes the rivers Havel, Oder, Elbe and Rhine. Raw data are shown and a linear smoother line (blue) with standard errors (grey) is included for visualization. „X" denotes significant ($p < 0.05$) effects; Note: number of empty running cargo vessels are significantly inversely correlated to densities of eurytopic fish which is the result of accounting for random effects in a mixed-effects model; the inverse correlation is masked in this figure due to very low densities of eurytopic fish in the river Rhine compared to the other three rivers included; however, within each of the rivers included, a positive correlation becomes visible as is shown in part B of this Figure. Y-axes [Ind. = Individuals] representing guild densities are log-scaled; PHYT and PSAM were not assessed statistically whereas the Simpson Index is not shown as there was no significant [$p > 0.05$] relation to navigation metrics, also not by trend [$p > 0.1$])

B: Response of fish density in the eurytopic guild (EURY) within the rivers included in Fig. A.4 A. Note: all axes are differently scaled, in particular: river Rhine has much lower densities of eurytopic fish than the remaining rivers. Each river indicates an inverse correlation of the number of empty running cargo vessels with density of eurytopic fish, as is validated by a mixed-effects model accounting for the random river effect. Note: This figure has been originally provided in A3 format and downscaled here to A4. For better readability, readers are kindly referred to the original online version (https://doi.org/10.1016/j.scitotenv.2018.07.403)

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Declaration of authorship / Selbstständigkeitserklärung

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I hereby declare that I completed the doctoral thesis independently based on the stated resources and aids. I have not applied for a doctoral degree elsewhere and do not have a corresponding doctoral degree. I have not submitted the doctoral thesis, or parts of it, to another academic institution and the thesis has not been accepted or rejected. I declare that I have acknowledged the Doctoral Degree Regulations which underlie the procedure of the Faculty of Life Sciences of Humboldt-Universität zu Berlin, as amended on 5 th March 2015. Furthermore, I declare that no collaboration with commercial doctoral degree supervisors took place, and that the principles of Humboldt-Universität zu Berlin for ensuring good academic practice were abided by.

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