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

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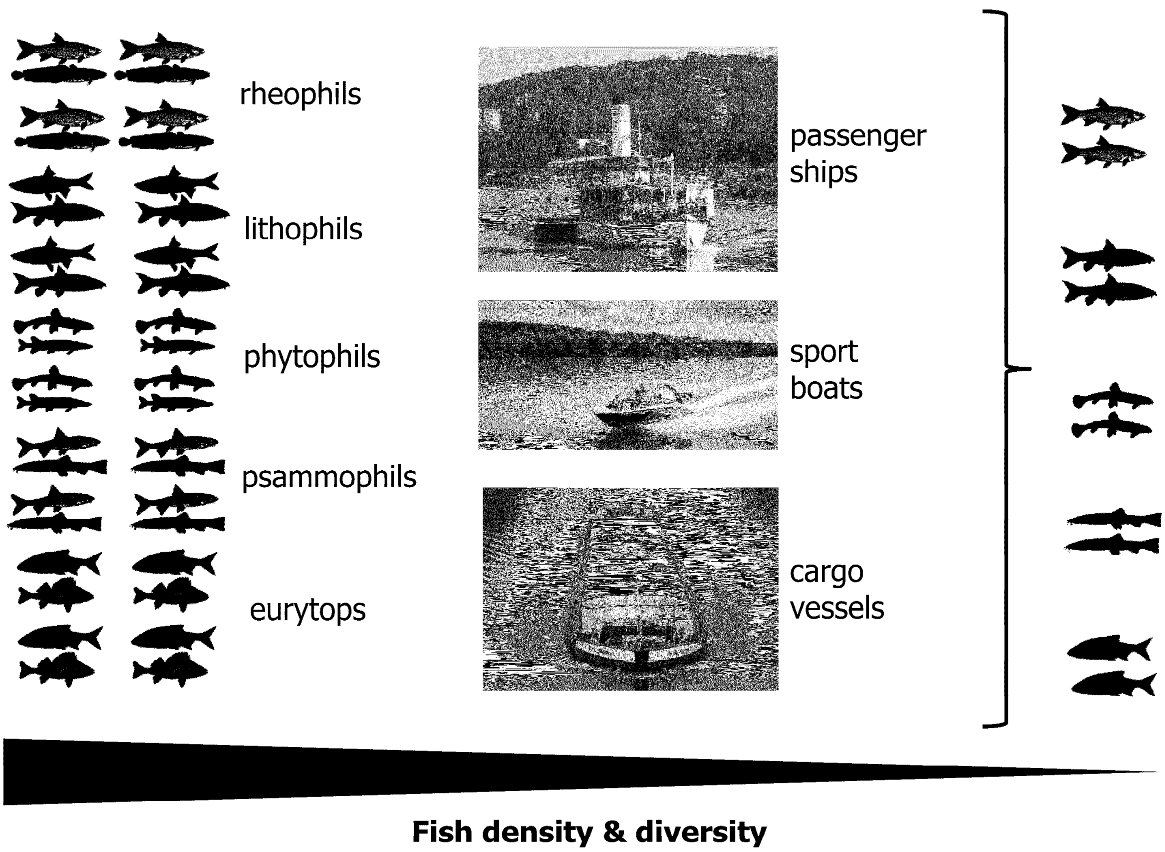
Keywords

Inland navigation; waterways; ship traffic; fish-based assessment; river conservation; river rehabilitation

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:



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 sensitive FPM 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.

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., 2016, 2014) 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., 2012b; 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 m², respectively. Consequently, selection of fish samples followed recommendations for representative assessments of running waters (e.g., Belletti et al., 2015; Dußling et al., 2004a; 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 m²) 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 less than 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 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 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, 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, 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 m^2, 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).

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

Number (NCV), freight (FCV) and carrying capacity of cargo vessels (CCV)

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.

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 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), also when using ds1.

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).

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 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 pressures 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., 2016, 2012; 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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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

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			

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		

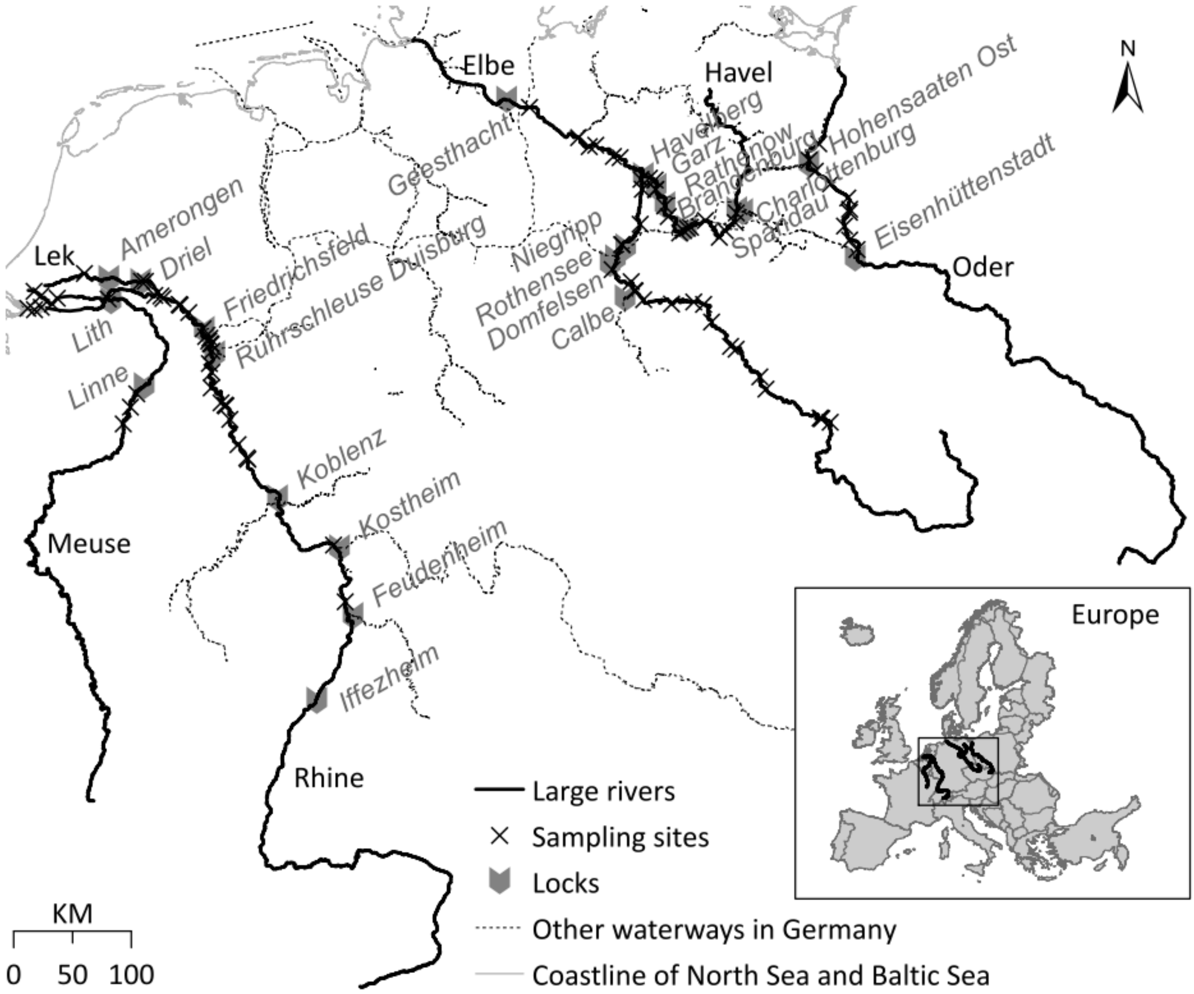

Fig. 1. Location of sampling sites and ship locks. Flow direction of all rivers is North; river Havel flows into river Elbe; river Rhine splits into rivers Lek and Waal in the Netherlands, the latter is the main branch and therefore referred to as river Rhine. Sampling sites in the river Meuse located 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

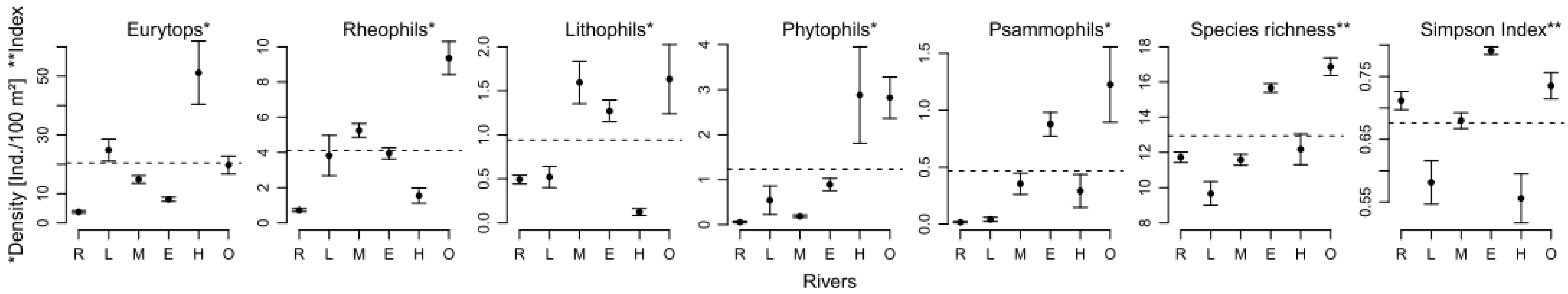

Fig. 2. River-specific estimates of fish population metrics (FPM). R = Rhine (number of samplings: 145); L = Lek (27); M = Meuse (89); E = Elbe (145); H = Havel (17); O = Oder (42). Means ± standard errors are shown, dashed lines indicate the averages of within-river sample-means. Note: y-axes [Ind.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

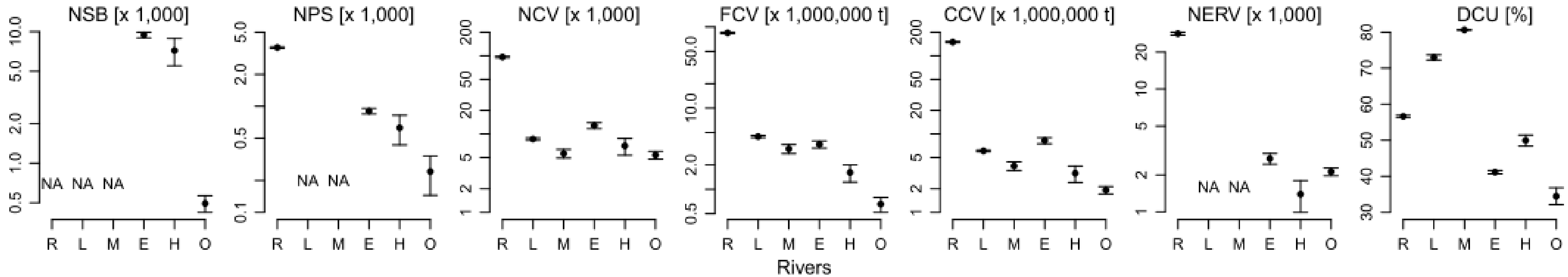

Fig. 3. River-specific estimates of navigation metrics. NSB = Number of sport boats; NPS = Number of passenger ships; NCV = Number of cargo vessels; FCV = Freight of cargo vessels; CCV = Carrying capacity of cargo vessels; NERV = Number of empty running cargo vessels; DCU = Degree of capacity utilization. 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.

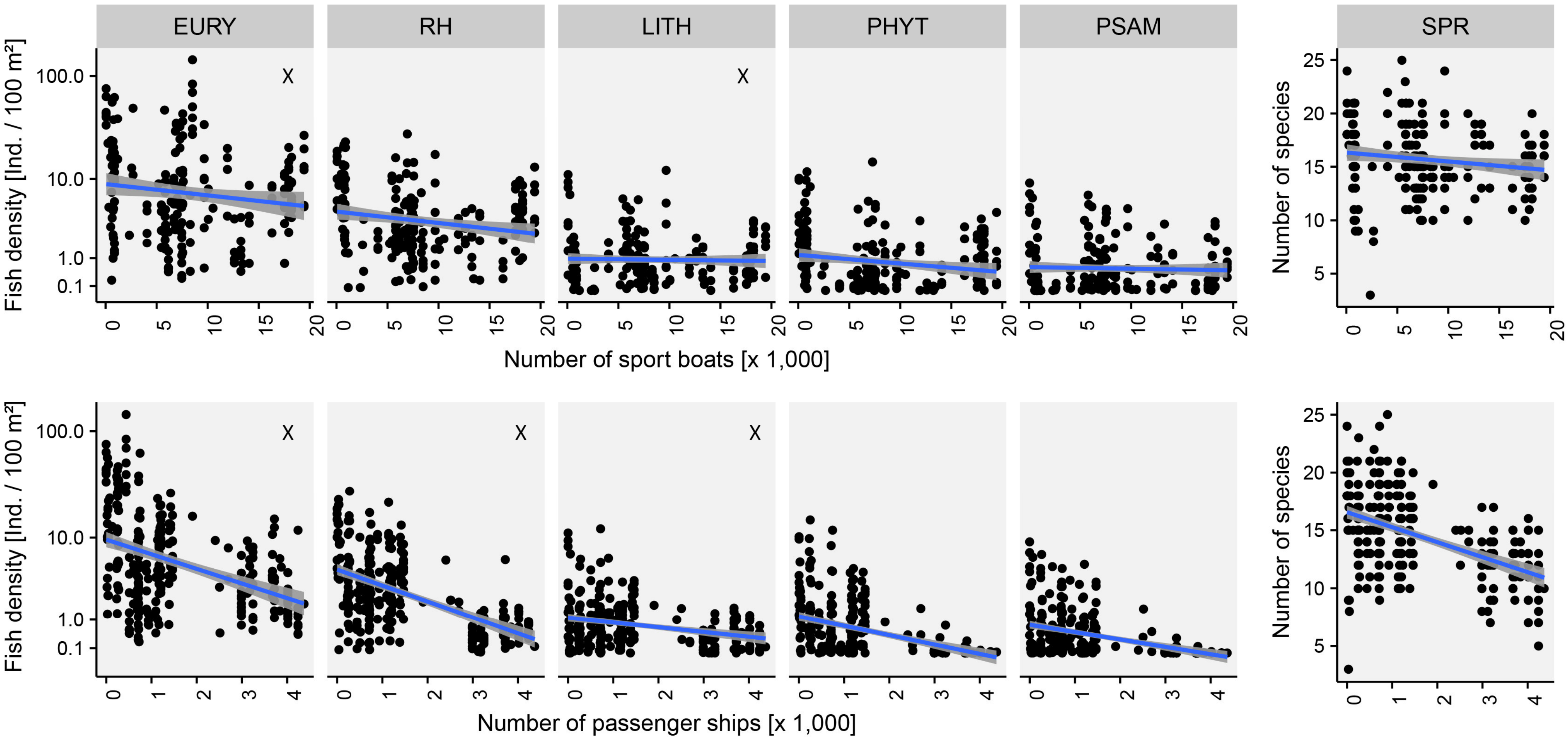

Fig. 4 Response of fish population metrics (EURY = eurytopic guild, RH = rheophilic guild, LITH = lithophilic guild, PHYT = phytophilic guild, PSAM = psammophilic guild; SPR = species richness) to recreational navigation (number of sport boats refers to ds1 and includes rivers Elbe, Havel and Oder; number 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 [$p > 0.1$])

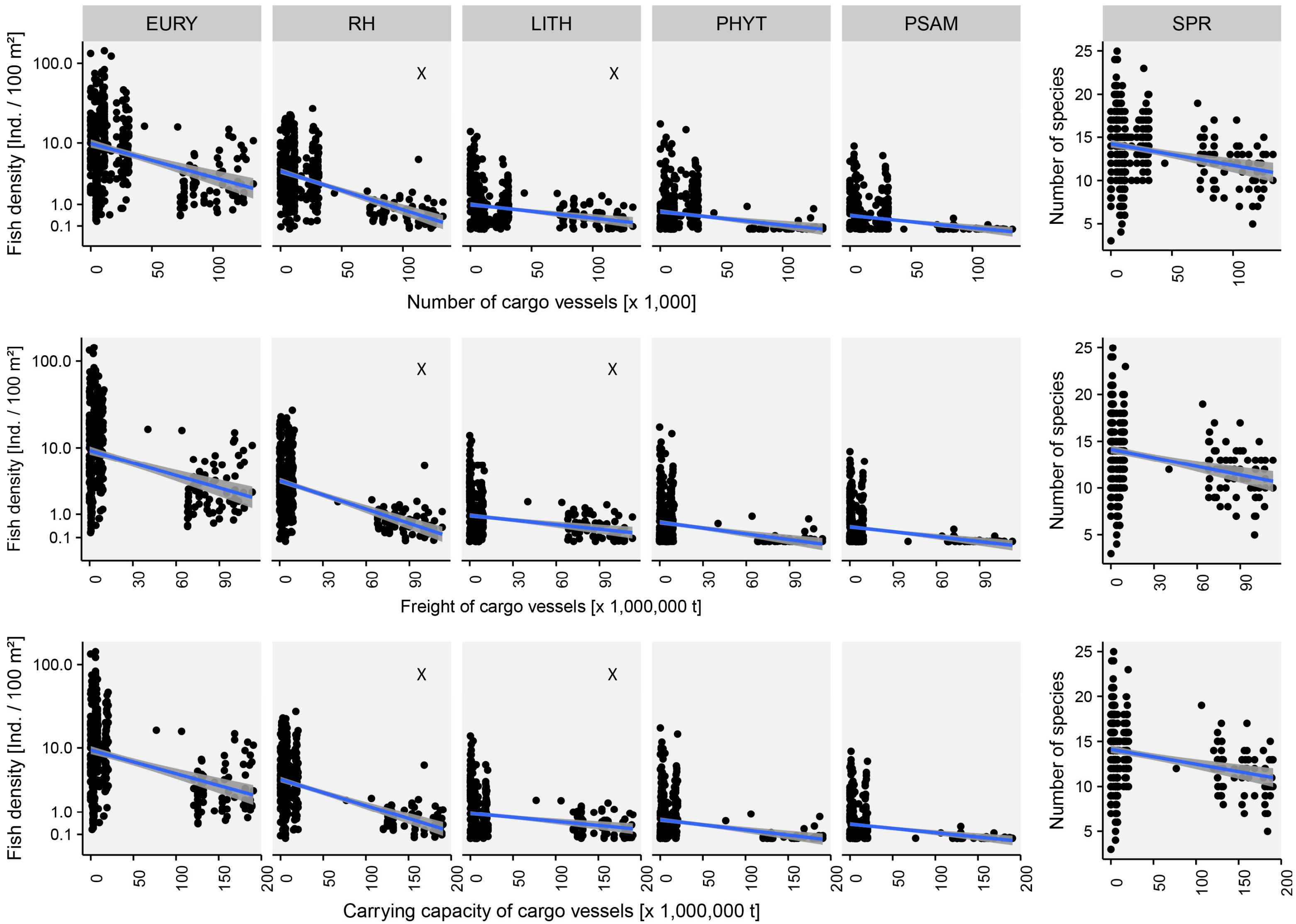

Fig. 5 Response of fish population metrics (EURY = eurytopic guild, RH = rheophilic guild, LITH = lithophilic guild, PHYT = phytophilic guild, PSAM = psammophilic guild; SPR = species richness) to commercial navigation (referring to ds4, the full dataset comprising all sampling sites in all six rivers [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 [$p > 0.1$])

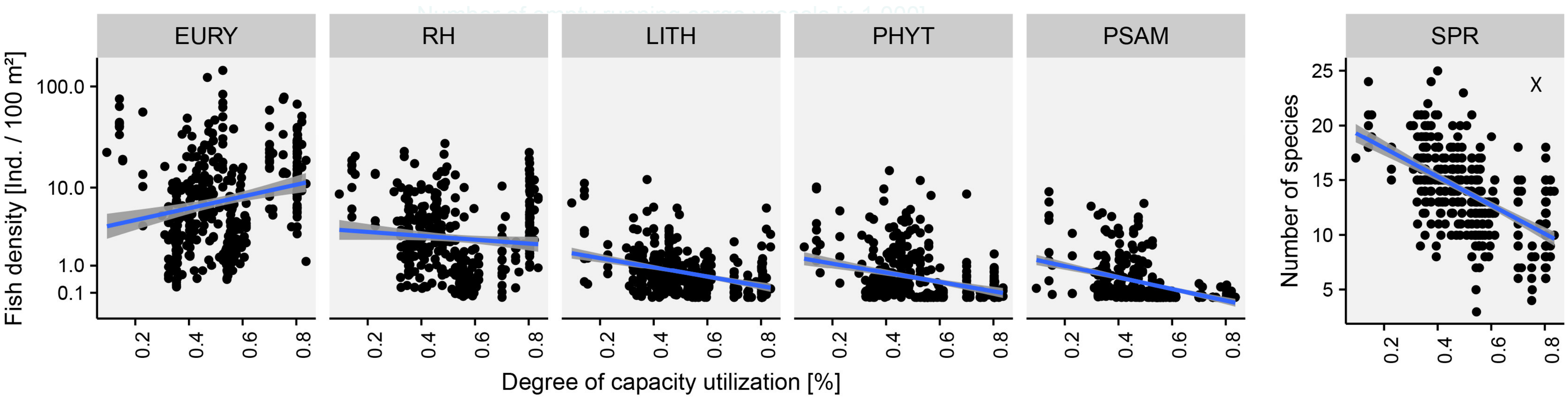

Fig. 6 Response of fish population metrics (EURY = eurytopic guild, RH = rheophilic guild, LITH = lithophilic guild, PHYT = phytophilic guild, PSAM = psammophilic guild; SPR = species richness) to the degree of capacity utilization of loaded cargo vessels. This figure refers to ds3 and includes the rivers 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 [$p > 0.1$])