# Fish species sensitivity classification for environmental impact assessment, conservation and restoration planning

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## HIGHLIGHTS

- Resilience traits of 168 European freshwater lampreys and fishes were analyzed.
- A classification system of fishes' sensitivity against mortality was developed.
- Rheophils and lithophils are more sensitive than limnophils and phytophils.
- The system informs both impact assessment and rehabilitation planning.

## GRAPHICAL ABSTRACT
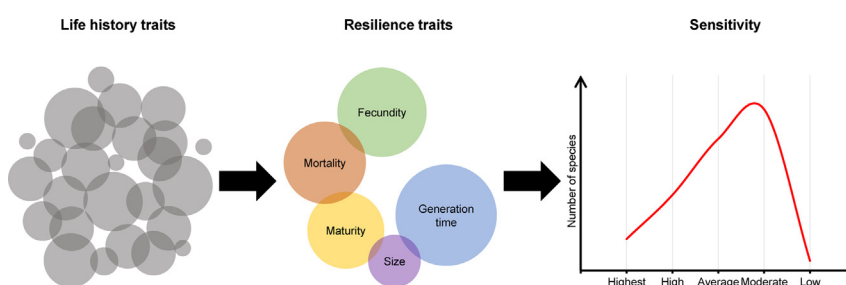


## ARTICLE INFO

## ABSTRACT

Species conservation, river rehabilitation, stock enhancement, environmental impact assessment and related planning tools require indicators to identify significant impacts but also mitigation success. Since river systems are shaped by disturbances from floods and droughts, typical riverine fish species should have evolved life history traits providing resilience against such disturbances. This study compiled and analyzed resilience traits of European lampreys and fish species to derive a novel sensitivity classification of species to mortality. We assembled life history traits like maximum length, migration type, mortality, fecundity, age at maturity, and generation time of 168 species and created a novel method to weigh and integrate all traits to generate a final sensitivity score from one (low sensitivity) to three (high sensitivity) for each species. Large-bodied, diadromous, rheophilic and lithophilic species such as sturgeons, sea trout, and Atlantic salmon usually appeared to have high sensitivity to additional adult fish mortality, whereas small-bodied, limnophilic and phytophilic species with fast generation cycles were of low sensitivity. The final scoring and classification of 168 European lampreys and fish species according to their sensitivity can be easily regionalized by selecting the most sensitive candidates according to the local species pool. This sensitivity classification has major implications for advancing impact assessment, allowing better targeting of species for conservation measures, benchmarking progress during rehabilitation and enhancing the objective evaluation of the success of restoration projects.

## 1. Introduction

Globally, we are experiencing higher species extinction rates than ever before (Barnosky et al., 2011). Of all ecosystems, freshwaters are among the most threatened in the world (Dudgeon et al., 2006) and metrics of freshwater biodiversity are changing

at a more severe pace than in most affected terrestrial ecosystems (Sala et al., 2000). Several anthropogenic activities like overharvesting, introduction of non-native species, pollution, habitat destruction and human-induced climate change have been identified as key components to species declines (Abramovitz, 1996, Gurevitch and Padilla, 2004, Xenopoulos et al., 2005, Dudgeon et al., 2006). There has been considerable research effort devoted to identifying the species most prone to extinction. The resulting criteria (IUCN, 2012) have classified species according to different threat categories (IUCN, 2018). Numerous Red Data books at various spatial scales (ranging from regional to global) correspond in the main finding that species at high risk are more likely to go extinct while co-occurring but not threatened ones may prevail. Consequently, there is considerable variation among sympatric species in their resilience against anthropogenic disturbances. Resilience is principally mediated by resistance against and recovery from a disturbance (Holling, 1973); however, we expect highly resistant species to have a lower recovery potential and vice versa. For example, small-bodied fish species often experience higher natural mortality rates corresponding to low resistance, which is balanced by early maturation and high fecundity to support quick recovery. In contrast, large-bodied species experience lower natural mortality corresponding to high resistance, but it takes the affected population longer to recover once the stressor is relieved, e.g. because of a long generation time (Myers and Worm, 2005). The opposite of resilience against disturbances is the sensitivity of a species against mortality, with most sensitive species being the least resilient ones.

Several different life history traits are likely to contribute to a species' resilience respective sensitivity and this study focuses on a number of functional traits in freshwater fish species. For one, because freshwater fish species are the most diverse vertebrate group (Nelson, 2006) and freshwater biodiversity is experiencing significant declines (Dudgeon, 2010), but also, because especially river systems provide excellent opportunity to study resilience (Fuller et al., 2019, Van Looy et al., 2019). Rivers are disturbance dominated systems, with floods and droughts and the associated flow patterns, shear forces, variation in connectivity and varying habitat suitability as significant stressors. According to Reice et al. (1990) naturally disturbed ecosystems often have the highest recovery rates. Fish species that evolved in such systems may be expected to have evolved certain life history traits to cope with less predictable and harsh environmental conditions (Lytle and Poff, 2004). These very same traits might therefore buffer them against human induced disturbances. As such, exploring such "sensitivity traits" can help to inform conservationists and water managers on population bottlenecks, thresholds and successful mitigation practices to better curtail biodiversity loss in freshwaters.

Researchers often determine the species-specific response to disturbances causing mortality (the degree of resistance) or recovery by analyzing their autecological attributes and life histories (e.g., Frisk et al., 2001; King and McFarlane, 2003; Magalhaes et al., 2003; Winemiller, 2005; Olden et al., 2007; Brose et al., 2017; Hutchings and Kuparinen, 2017; Jaric et al., 2018). Identifying traits that increase the individual potential to withstand stressors and analyzing how the species-specific suites of life history traits link to their recovery can help predict how a particular mortality factor acts upon the population as a whole. Life-history traits are likely to play a particularly pivotal role in determining species' responses to anthropogenic activities and are thus frequently used in impact analyses (e.g. Kopf et al., 2017; Rochet et al., 2000; Sharpe and Hendry, 2009). An increasingly popular way to utilize life history data is in individual-based population models. These models are used to quantify the population response to environmental stressors, be they anthropogenic or natural. Models of that type often are highly resolved and may yield very accurate results

but almost exclusively target well-studied flagship or keystone species (Paine, 1969; Simberloff, 1998), such as sturgeons (Jarić and Gessner, 2013), salmon (Nickelson and Lawson, 1998; Rivot et al., 2004), northern pike (Arlinghaus et al., 2009) and other species with comparable availability of biological data (Lorenzen and Enberg, 2002). In contrast, for the majority of species, biological and autecological data are too scarce and too heterogeneous for extensive application of population viability models (e.g. Frimpong and Angermeier, 2009; Teletchea et al., 2009; Schmidt-Kloiber and Hering, 2015). The need for reliable means of predicting likely responses of freshwater systems to severe anthropogenic stressors, however, is as pressing as ever (Tonkin et al., 2019).

Therefore, this study's main objective was to overcome this knowledge gap by using earlier concepts of functional categorization of species based on coarser trait data (e.g. Winemiller, 2005), to derive a classification of fish species according to their sensitivity to adult fish mortality. Conceptually, we base our approach on the life history theory described in MacArthur and Wilson (2001) as two distinct life history strategies: K and r strategists invest either in somatic growth, thus increasing individual resistance or in reproductive performance, resulting in quick recovery from population decline. We hypothesize that fishes will show predictable resilience patterns based on the unique, species-specific suite of r and K life history features: Species that have expressed strong resistance traits like high longevity, large size and a low natural mortality will resist a disturbance longer than those that are prioritizing traits associated with high recovery rates like high fecundity, short generation cycles and high natural mortality. However, once a particular threshold is crossed, we suspect species of higher resistance to take considerably longer to recover. In our analysis, we therefore equate high resistance with high sensitivity to additional mortality caused by anthropogenic disturbances. We reviewed and analyzed various traits of lamprey and fish species in European fresh waters, in particular life history traits that provide resistance against and recovery from mortality (e.g. Hutchings et al., 2012; Van Looy et al., 2019). We scored and processed those traits identified as most informative and generated a final species-specific score that indicates a species' overall sensitivity against mortality resulting from its specific combination of resistance and recovery traits.

In that final sensitivity classification, all species were ranked relative to each other in their sensitivity to mortality. The main advantages of our system are that it includes many more species than available population viability analyses and it can even be specifically applied to distinct mortality factors. The sensitivity classification supports both the selection of target species for river rehabilitation and the prediction of rehabilitation success. As such it might be used by water managers in river rehabilitation planning to identify and prioritize restoration measures. The classification system also serves species conservation by providing a set of highly sensitive candidates serving as target or flagship species.

## 2. Material & methods

### 2.1. Life history traits

The following life history traits were identified to determine the sensitivity of a species to mortality (see Table 1 for a summary):

1. Maximum total length ($L_{max}$) in cm.

Large bodied species usually rank higher in food webs (Reid and Miller, 1989), face lower predation risk, disperse further (Radinger and Wolter, 2014), utilize larger home ranges (Minns, 1995) and thus, experience a comparatively low natural mortality as adults.

**Table 1**
Life history traits and metrics compiled and analyzed in this study.

| No. | Variable | Description | Unit | Usage |
|---|---|---|---|---|
| 1 | $L_{max}$ | Maximum total length | cm | Sensitivity trait 1 |
| 2 | $M$ | Migration type | Categorical | Sensitivity trait 2 |
| 3 | $t_m$ | Age at maturity | Years | Sensitivity trait 3 |
| 4 | $M_m$ | Mortality at maturity | %/year | Sensitivity trait 4 |
| 5 | $F_m$ | Fecundity at maturity | Eggs/female | Sensitivity trait 5 |
| 6 | $O_{min}$ | Minimum generation time | | Sensitivity trait 6a |
| 7 | $O_{max}$ | Maximum generation time | | Sensitivity trait 6b |
| 8 | $S_{min}$ | Minimum survival rate | % survival/year | Calculate $O_{min}$ |
| 9 | $S_{max}$ | Maximum survival rate | % survival/year | Calculate $O_{max}$ |
| 10 | $L_\infty$ | Asymptotic length | cm | VBGP, calculate $M_m$ |
| 11 | $K$ | Growth rate | 1/year | VBGP, calculate $M_m$ |
| 12 | $t_0$ | Age at length 0 | Years | VBGP, calculate $M_m$ |
| 13 | $L_m$ | Length at maturity | cm | Calculate $W_m$, $M_m$ |
| 14 | $W_m$ | Weight at maturity | g, gram | Calculate $F_m$ |
| 15 | $F_r$ | Relative fecundity | Eggs/gram body weight | Calculate $F_m$ |

Variables 1–7 were directly included into the final sensitivity scoring; variables 8 and 9 were used in Eq. (7) and (8); variables 10–12 appear in Eq. (1), 2, 3, 4, 5, 12, 13 and 14; variables 13 and 14 were used in Eq. (1), 4, 6, 7, 8, 10, 12, 13 and 14, variable 15 was used in Eq. (6). VBGP = Von Bertalanffy Growth Parameter.

This in turn makes the largest species most sensitive to anthropogenic factors increasing additional mortality (McCann and Shuter, 1997; Frisk et al., 2001; Winemiller, 2005). For this trait, we considered the maximum ever reported length for each species.

2. The migration type ($M$) of a species as either diadromous, potamodromous, resident and large-bodied or resident and small-bodied.

Diadromous fishes depend on migrations between marine and freshwater habitats. They are considered the first most sensitive due to this highly specialized lifestyle (McDowall, 1999; Britton and Pegg, 2011). Potamodromous fish essentially migrate in freshwaters and were thus considered second sensitive.

3. Age at first maturity ($t_m$) in years.

The time at which an individual becomes mature strongly influences its reproductive potential. A young age at first maturity enables fast adaption to changing environments due to a high population turnover and thus leads to a higher recovery rate (Frisk et al., 2001; Winemiller, 2005). Consequently, we ranked species with increasing age at first maturity as more sensitive. Due to sex differences in this trait only age at first maturity of females was considered, which takes longer in most species. In case of several reported values the median was used.

4. Mortality at maturity ($M_m$).

$$M_m = \left(\frac{L_m}{L_\infty}\right)^{-1.5*K} \qquad (1)$$

$$l_t = L_\infty(1 - e^{-K(t-t_0)}) \qquad (2)$$

The recovery rate of a fish population increases with increasing $M_m$ (Hutchings and Kuparinen, 2017). We therefore included this powerful indicator for resilience in our analysis and assumed a decreasing sensitivity of species with increasing $M_m$. We computed $M_m$ following the approach of Hutchings and Kuparinen (2017) shown in Eq. (1). This equation contains the species' length at maturity ($L_m$), their asymptotic length ($L_\infty$, the theoretically possible length if they grew indefinitely) and their growth rate ($K$), expressed as 1/year, at which they approach $L_\infty$. $L_\infty$ and $K$ are components of the von Bertalanffy Growth Function (1938), shown in Eq. (2). Here, $l_t$ is the length of a fish at time ($t$), and $t_0$ is the

species' hypothetical age at length zero, which is an artificial parameter. Since these parameters vary widely even between populations, we only considered values calculated as follows:

- $L_\infty$ was derived from $L_{max}$ using the empirical relationship shown in Eq. (3) established by Froese and Binohlan (2000).
- $K$ and $t_0$ were calculated using a converted version of the Von Bertalanffy growth function by Von Bertalanffy (1938) in a stepwise procedure suggested by Froese and Binohlan (2003): In Eq. (4), $t_0$ was initially set to zero and the resulting $K$ was inserted in Eq. (5) (Pauly, 1979). This new $t_0$, in turn, was inserted in Eq. (4) to obtain an updated estimate for $K$. The updated $K$ was then used in the reiteration of Eq. (5) to obtain a new $t_0$. This process was repeated until the calculated values for $K$ remained stable. We explored the plausibility of all three Von Bertalanffy growth parameters by comparing them with literature values.

$$L_\infty = 10^{0.04+9.98*log_{10}L_{max}} \qquad (3)$$

$$K = -ln\frac{1 - \frac{L_m}{L_\infty}}{t_m - t_0} \qquad (4)$$

$$t_0 = -1 * 10^{-0.39-0.28*log_{10}L_\infty - 1.04*log_{10}K} \qquad (5)$$

5. Fecundity ($F_m$).

$$F_m = F_r * W_m \qquad (6)$$

The reproductive potential of an organism is a critical fitness factor and component of most life-history models (e.g. Winemiller and Rose, 1992; McCann and Shuter, 1997). The total fecundity of a fish, however, is highly variable and changes with factors like individual state of nutrition (Lambert and Dutil, 2000, Rätz and Lloret, 2003), stress level (Schreck et al., 2001) and body size. We therefore estimated $F_m$ by multiplying the less variable relative fecundity ($F_r$, the number of eggs per gram of total fish weight) by the females' weight at first maturity ($W_m$), as shown in Eq. (6). The Allis shad Alosa alosa, for example, has a relative fecundity of 200 eggs per gram body weight. Its weight at maturity is roughly 3800 g, which results in a total of 760,000 eggs at its time of maturity. When studies directly reported values for $F_m$ for a species without the need to approximate them, we added those to the data pool, too. We ranked species with a higher reproductive potential less sensitive.

6. Minimum and maximum generation time $O$.

$$O_{min} = \frac{(S_{min} * F_m)}{t_m} \qquad (7)$$

$$O_{max} = \frac{(S_{max} * F_m)}{t_m} \qquad (8)$$

This metric was generated using Eq. (7) and (8) and accounts for the reproductive potential $F_m$ of a species, its age at first maturity $t_m$ and the juvenile survival rate $S$, which, according to most studies, is extremely low. However, parental care was shown to increase offspring survival. Despite a variety of parental care-strategies (e.g. nest building and guarding) with potentially differing net effects on offspring survival, we could only consider parental care as a binary trait (yes or no) in our analysis. Based on several empirical results, e.g. by Lang (1987), Mooij et al., (1996), Chaumot et al. (2006), Thiel and Magath (2011), Jarić and Gessner (2013), the annual juvenile survival rates were set at 0.1–2% in case of no or unknown parental care and 0.5–2% with parental care. Both upper ($S_{max}$) and lower ($S_{min}$) survival rates were used for calculating the maximum ($O_{max}$) and minimum ($O_{min}$) generation time. Table 1 summarizes the traits and metrics that we used in this study.

### 2.2. Data compilation

We searched the literature using Web of Science, Google and Google Scholar as well as more specified repositories like Fishbase (Froese, 2017) or the Freshwater Information Platform (www.freshwaterinformationplatform.eu). By using uniform search strings for each piece of life history information and species of interest we ensured a systematic workflow. A typical search string used in Google and Google Scholar was of the structure:

"allintitle: Genus OR specific name OR genus + specific name biology OR life history".

To maximize the number of species in our analysis, we included not only peer-reviewed literature and text book data, but also grey literature, project reports, personal communications and online content, for example hosted by angling associations following observations by Smialek et al. (2019).

To overcome the constraints of missing data, we either drew analogies from better studied species of the same genus or family or we employed empirical regressions to obtain plausible estimates, as follows:

- We estimated missing data for $L_{max}$ by adding 15% and 10% to reported standard and fork lengths, respectively, according to Beckman (1948), Özaydin and Taskavak (2006) and others.
- We estimated missing data for $t_{max}$ by using $t_m$ in a re-arranged equation (9) by Froese and Binohlan (2000). If $t_m$ was not reported for a species either, we estimated $t_{max}$ by drawing analogies from closely related species of the same genus or family.
- We approximated missing weight-at-age data by extrapolating existing weight-at-age series or by converting existing length-at-age series using species-specific length-weight regressions. These were usually reported as shown in Eq. (10), following Ricker (1975).

$$t_{max} = 10^{0.55+0.96*log_{10}t_m} \qquad (9)$$

$$W = a * L^b \rightarrow log_{10}(W) = log_{10}(a) + b * log_{10}(L) \qquad (10)$$

- In Eq. (10), $W$ and $L$ denominate the total weight and length of a fish; $a$ and $b$ are coefficients, of which $b$ is comparable across similarly shaped individuals but typically varies widely across species, populations and sexes. When the sex of the sample population was provided, we used length-weight regressions for females only.

- We estimated missing data on total and relative fecundity using available fecundity-at-age or fecundity-at-length regressions and length-weight regressions. In case of no data, analogies from closely related species were used.

### 2.3. Generating trait-specific sensitivity groups

The resulting, initial data base contained observations and estimates for the traits $L_{max}$ $t_{max}$, $L_m$, $t_m$, $M_m$, $F_m$, $F_r$, length-weight regressions, $O_{min}$, $O_{max}$, and the three von Bertalanffy growth parameters $L_\infty$, $K$, $t_0$ for each of 120 lamprey and fish species.

We determined sensitivity groups trait-specifically: For each trait, we divided the species-specific observations into five classes of equal size using 20-percentiles, from highest (5) to lowest (1) sensitivity. Finally, we assigned all species to one of five sensitivity classes for each life history trait.

### 2.4. Generating the species-specific sensitivity score

We used weighted averaging to combine the trait-specific sensitivity scores to a species-specific sensitivity class as follows:

- Scores of $M_m$, $t_m$, $F_m$ and $L_{max}$ each were weighted by a factor of 1.
- The migration type of the species was scored 1-fold when it was resident, 3-fold when it was potamodromous and 5-fold when it was diadromous, respectively.
- Scores of $O_{min}$ and $O_{max}$ each were weighted by a factor of 0.5 to account only once for the trait "generation time".

We summed the weighted scores and divided them by the number of traits. This yielded the final species-specific sensitivity score rounded to integer that is inversely related to species' resilience (Supplement Table S1).

### 2.5. Validating the classification score

Because of the very heterogeneous empirical data and a substantial need for surrogate estimates, we evaluated the potential effect of data handling on the sensitivity classification of species. To do this, we generated a second database for the identical set of species with all estimates of $L_m$, $t_m$, $M_m$, $F_m$, $O_{min}$ and $O_{max}$ solely calculated for female specimens based on $L_{max}$ and $t_{max}$ using the empirical relationships shown in Eq. (11), Eq. (12), Eq. (13) and Eq. (14), established by Froese and Binohlan (2000).

$$t_m = 10^{1.05*log_{10}t_{max}-0.58} \qquad (11)$$

$$L_{m(all)} = 10^{0.9*log_{10}L_\infty-0.08} \qquad (12)$$

$$L_{m(males)} = 10^{0.89*log_{10}L_\infty-0.10} \qquad (13)$$

$$L_{m(females)} = 10^{0.95*log_{10}L_\infty-0.12} \qquad (14)$$

We validated the calculated estimates of all variables by conducting Pearson product-moment correlation analyses between them and their observed counterparts. We also re-calculated trait-specific sensitivity groups and species' sensitivity scores as described above. After having done that, we conducted another correlation analysis between the two species' sensitivity classifications resulting from both the second "calculated" and the first "observed" database using Spearman-rank correlations and Gwet's (2014) AC coefficient of agreement across all group memberships of the species.

The agreement of the species-specific scoring between the two datasets was high (Fig. 1 and Supplement Figure S1). Only seven species (5.8%) each deviated>0.5 on their sensitivity score. A total

of 90 species (75%) were assigned the same final sensitivity class, and 16 (~13.3%) and 14 (~11.7%) species scored one class less and one class more sensitive in the "calculated" than the "observed" data set. The number of species per class between the two data sets differed to some extent, with the highest numerical deviation in the moderate sensitivity class and the lowest in the high sensitivity class. This phenomenon was strongly influenced by the number of species per class and disappeared when we weighted the deviation index according to the total number of species per group (see Table 2). We statistically compared life history traits as well as the final classification based on "calculated" and "observed" data. The correlation between the calculated and observed variables age, length and fecundity at maturity as well as the minimum and maximum generation time was high with correlation coefficients of $\rho = 0.76$ (p < 0.0001) for age, $\rho = 0.91$ (p < 0.0001) for length and $\rho = 0.74$ (p < 0.0001) for fecundity at maturity, $\rho = 0.91$ (p < 0.0001) for minimum and $\rho = 0.85$ (p < 0.0001) for maximum generation time. The final sensitivity scores were highly significantly correlated (Spearman's Rho 0.84, p < 0.0001) as well. Gwet's (2014) AC coefficient scored 0.86 at a confidence level of 95% (Supplement Figure S2). Because of these results we added another 48 species to the database for which only reported data on $L_{max}$, $t_{max}$, $F_r$, length-weight regressions and the Von Bertalanffy growth parameters could be obtained. After calculating the missing trait values, we re-ran the sensitivity analysis with a total of 168 species. Because $L_{max}$ and $t_m$ were usually reported as integers or common fractions, the derived variables contained many identical values resulting in some percentile splits through a cluster of identical values. Whenever that happened, we shifted the threshold manually to the next biggest data gap either above or beneath the cluster to ensure the correspondence within groups. The analysis produced a total number of 168 species classified according to their sensitivity to additional mortality in adult females. Table 3 provides details on the classification values and thresholds.

Data analysis was done using R (R Core Team 2018), v. 3.5.1, packages "rel", v. 1.3.1., "ggpubr", v. 0.2.2.

## 3. Results

We developed a classification of 168 European freshwater lamprey and fish species based on their sensitivity to adult female fish mortality. Table 4 summarizes the relative data availability per trait, using common metrics of exploratory statistics. Of the 168 species, 32 (~19%), 80 (~48%) and 56 (~33%) were assigned to the "high", "moderate", and "low" sensitivity class, respectively (Supplement Table S3). All species of the Acipenseridae, the closely related non-native Mississippi paddlefish *Polyodon spathula* and the European eel *Anguilla anguilla* were represented in the high sensitivity class. The majority of salmonid species appeared highly sensitive as well except grayling *Thymallus thymallus*, which was assigned to the moderate sensitivity class. Of the Centrarchidae, the smallmouth bass *Micropterus dolomieu* was assigned to the high, while the largemough bass *M. salmoides* and the pumpkinseed *Lepomis gibbosus* to the moderate sensitivity class. Assigned only to the moderate sensitivity class were species of the families Centrarchidae, Cottidae, Ictaluridae, Mugilidae, Xenocyprididae as well as the single species of the Loricariidae, Nemacheilidae, Odontobutidae, Osmeridae, Pleuronectidae, Siluridae, Syngnathidae and Tincidae. Spread out across all sensitivity classes were the three families Petromyzontidae, Cyprinidae and Leuciscidae, with the sea lamprey *Petromyzon marinus* European, Italian, Iberian and Andalusian barbel *Barbus barbus, B. plebejus, B. bocagei* and *B. scla-*

**Table 2**
Agreement in species numbers between the "observed" and the "calculated" data set.

| Sensitivity | High | Moderate | Low | |
|---|---|---|---|---|
| Observed | 23 | 65 | 32 | |
| Calculated | 26 | 57 | 37 | |
| Difference | 3 | 8 | 5 | |
| **Deviation** | **0.06** | **0.07** | **0.07** | x̄=0.07 |

The deviation index was calculated by dividing the numerical difference between the group sizes by the sum of the two groups. Values close to zero indicate very high, values close to 1 very low correspondence between group sizes.
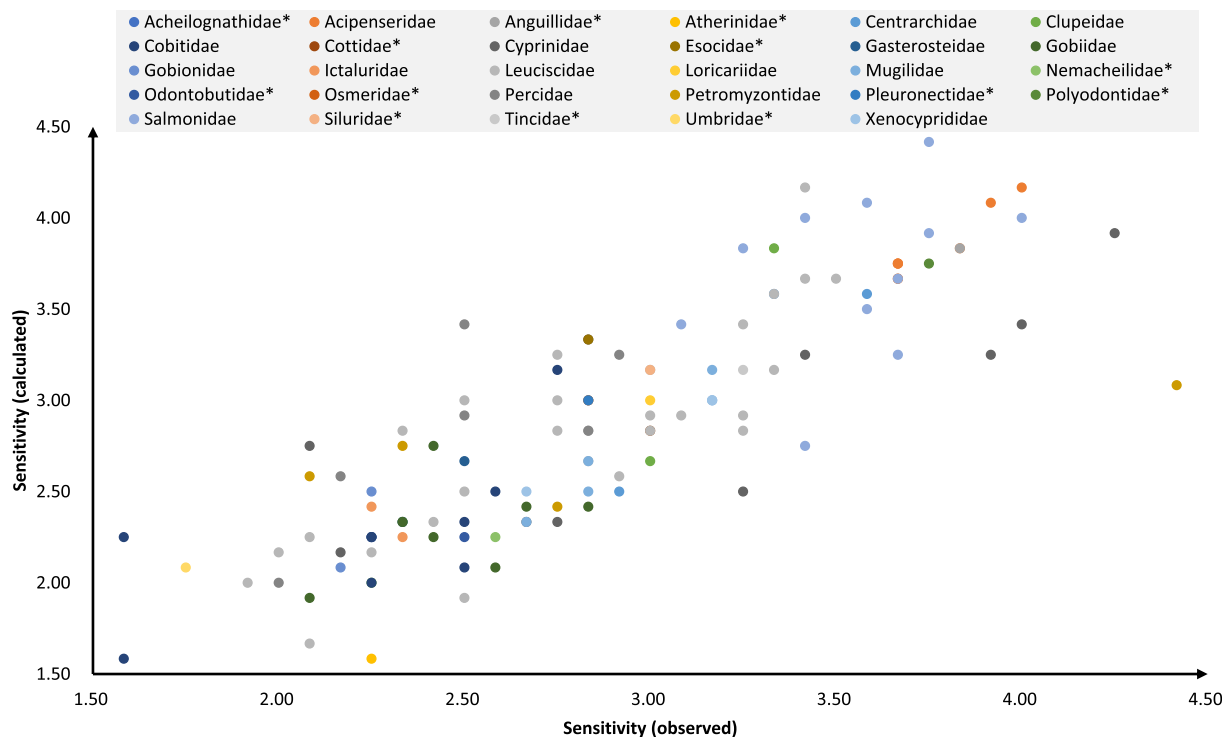


**Fig. 1.** Overall agreement (Rho = 0.84) between the two sensitivity scores of the "calculated" and "observed" data set. Points indicate single species, colours their family membership. Asterisks in the legend indicate families with only one species. N = 120 species of 29 families.

*teri*, blue bream *Ballerus ballerus*, ide *Leuciscus idus*, nase *Chondrostoma nasus*, roach *Rutilus heckelii* and Danube bleak *Alburnus chalcoides* scoring high and *Achondrostoma salmantinum*, *Squalius torgalensis*, *Iberochondrostoma lusitanicum* (Leuciscidae) scoring low. The Clupeidae are located in the lower range of the sensitivity scale with *Alosa alosa* and *A. immaculata* scoring moderate and *A. tanaica* and *Clupeonella cultriventris* low. Only in the low sensitivity class appeared four species of the Acheilognathidae, Atherinidae, Poeciliidae and Umbridae (Fig. 2 and Supplement Table S3).

Spawning guilds were distinguished into lithophilic/litho-pelagophilic, phytophilic/phyto-lithophilic, and "others". Others con-

tained ariadnophilic, ostracophilic, pelagophilic, polyphilic, psammophilic, speleophilic, and viviparous species and appeared most often in the moderate sensitivity class. Lithophils were the most dominant guild in the highest sensitivity class, while phytophils/phyto-lithophils were proportionally most abundant in the low sensitivity class (Fig. 3). Species were additionally classified into rheophilic, limnophilic (including marine/estuary-dwellers) and eurytopic guilds. Rheophilic species were most abundant in the high, limnophilic in the low sensitivity class, respectively. Eurytopic species were most abundant in the moderate sensitivity class (Fig. 4).

**Table 3**

Traits and metrics with their lowest and highest value and percentile thresholds used in the extended data set containing 168 species.

| Sensitivity class | $L_{max}$ (cm) | $M_m$ (%) | $t_m$ (years) | $F_m$ (eggs/female) | $O_{min}$ (Offspring/female/year) | $O_{max}$ (Offspring/female/year) |
|---|---|---|---|---|---|---|
| Highest | >88.6–800 | <27.2–4.9 | >4.5–17.5 (>4–17.5) | <574.3–14.1 | <0.6–0.01 | <7–0.17 |
| High | >46.6–88.6 | <39.6–27.2 | >3.5–4.5 (>3.27–4) | <1805.7–574.3 | <1.3–0.6 | <15.5–7 |
| Moderate | >25–46.6 | <51–39.6 | >2.5–3.5 (>2.35–3.27) | <5237–1805.7 | <3.4–1.3 | <32.37–15.5 |
| Low | >15–25 | <65.4–51 | >2–2.5 (>2.04–2.35) | <74733.6–5237 | <16.1–3.4 | <232.9–32.37 |
| Lowest | 5–15 (5–14.8) | 89.8–65.4 | 0.35–2 (0.35–2.04) | 985628.5–74733.6 | 1232–16.1 | 4928.1–212.9 |

$L_{max}$ = maximum body length, $M_m$ = mortality at maturity, $t_m$ = age at maturity, $F_m$ = fecundity at maturity, $O_{min}$ and $O_{max}$ = number of minimum and maximum offspring surviving the larval stage per female and year. Underlined values in parentheses are the adjusted thresholds at the next biggest data gap below or above the original percentile threshold when it cut through a cluster of identical values.

**Table 4**

Raw data availability per trait for each of the 168 species analyzed.

| | Life history traits | | | | | |
|---|---|---|---|---|---|---|
| **Data availability** | $t_{max}$ | $L_{max}$ | $t_m$ | $L_m$ | LWR | $F_r$ |
| Total number of "observed" data points | 156 | 168 | 572 | 383 | 249 | 435 |
| Number of species with missing information | 12 | 0 | 5 | 15 | 24 | 37 |
| Calculated substitutes used | 9 | 0 | 5 | 15 | 0 | 0 |
| Substitute analogies used | 3 | 0 | 0 | 0 | 24 | 37 |

$t_{max}$ = maximum lifespan, $L_{max}$ = maximum body length, $t_m$ = age at maturity, $L_m$ = length at maturity, LWR = length-weight-regressions, $F_r$ = relative fecundity. For $t_{max}$ and $L_{max}$ only the biggest single observation was considered. Some of the LWR data are means of multiple entries of length-weight tables on Fishbase. The actual number of observations for species with a 'Fishbase' reference can therefore be higher.
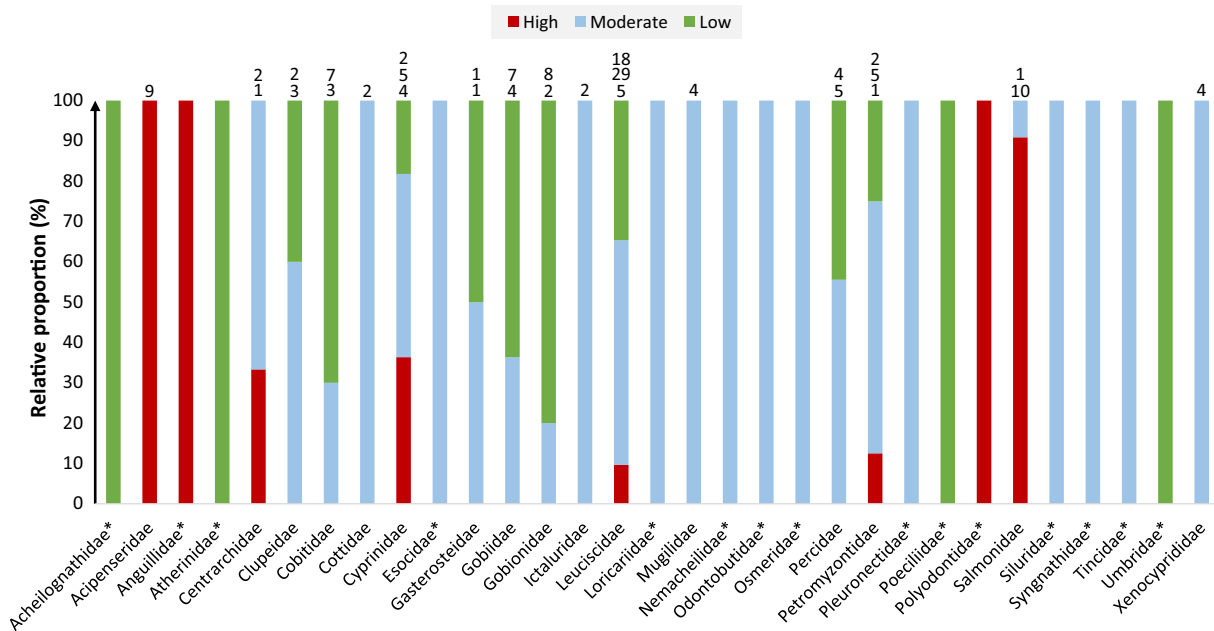


**Fig. 2.** Distribution of species within families and across the sensitivity classes High, Moderate and Low. Numbers above bars indicate the number of species per sensitivity class and family, asterisks behind the family name mark families with only once species. N = 168 species of 31 families.

## 4. Discussion

### 4.1. Species classification

We developed a novel scoring scheme that combines various life history traits determining resistance and recovery potential of a species into a single, species-specific sensitivity score of both native and established non-native European freshwater fish species. This sensitivity score reflects the species' susceptibility to mortality of adults in a population. Our scheme has the great advantage that all available, even very heterogeneous data of reasonable quality could be used and various combinations of resistance and recovery traits considered. Because all single traits were scored separately, the resulting data could be statistically treated depending on their distribution and heterogeneity and the species rank-ordered relative to each other for each specific trait. This approach allowed us to include also lower quality trait estimates as long as the relation between species (e.g. lower or higher number of eggs) remained relatively constant. It is the first of its kind incorporating a large number of freshwater fish species from all across Europe. Because our approach does not require extensive knowledge about population parameters, we were able to include many species that could not be considered in previous population risk assessments. By statistically confirming the very high agreement between the trait variables age, length and fecundity at maturity as well as the final classification scores of 120 species based on "observed" and "calculated" life history traits, we could extend our species pool even further and estimate the sensitivity for 168 species in total. The sensitivity classification offers a versatile tool that is easy to apply for a range of stakeholders and supports the selection of target species for river rehabilitation, stock enhancement and prediction of species-specific responses to disturbances. It also serves conservation actions by providing a set of highly sensitive candidates serving as umbrella species for migratory, habitat and spawning guilds.

Longevity, large size, long generation time, large size and late age at maturity as well as diadromous migration were all considered life history traits that increase the sensitivity to human induced mortality. Therefore, it is no surprise that the high sensitivity class is dominated by large-bodied migratory species: sturgeons, salmonids, the sea lamprey, eel and some riverine cyprinids like nase *Chondrostoma nasus*, Danube bleak *Alburnus chalcoides,* ide *Leuciscus idus, Rutilus heckelii* and common barbel *Barbus barbus.* This corresponds well with the long-lasting, slowly progressing programs to reintroduce Atlantic salmon *Salmo salar* (Zahn et al., 2017; IKSR, 2018; NASCO, 2018) and sturgeons (Gessner et al., 2014; Friedrich et al., 2018) in Europe, the ongoing decline of the European eel stock (ICES, 2018) and the low improvement of river fishes in European waters (EEA, 2018). But the sensitivity classification is not primarily driven by single dominant traits like body size, as indicated by the result for the wels *Silurus glanis. S. glanis* is classified as of moderate sensitivity, but at the same time is very large, matures late and has a very low natural mortality. These traits alone could render it highly resistant and hence, sensitive to anthropogenic disturbance but are offset by a high fecundity, parental care and comparably high recruitment rates. Due to its low demands toward flow regime and spawning substrate (it is eurytopic and phytophilic), it dwells in a broad range of habitats, up to a point where it is even considered invasive in parts of Europe (Copp et al., 2009).

Higher sensitivity scores also have a higher relative proportion of lithophilic species (Fig. 3). This agrees very well with recent assessments of the mostly moderate and poorer ecological quality of European rivers (EEA, 2018). Lithophilic species have rather specific requirements for spawning habitat conditions (e.g. the composition of spawning gravel, water depth, temperature and current velocity), which makes them very susceptible to hydromorphological alterations and degradations. Because early life stages constitute the major bottleneck for population growth (Kamler, 2012), such disturbances have critical consequences on the reproductive success of lithophilic species (Sear, 1995; Fergus, 1997; Acornley and Sear, 1999; Soulsby et al., 2001). Consequently, it is not surprising that most European gravel spawners are considered endangered (Jungwirth et al., 2003). The high sensitivity class also includes the highest relative proportion of rheophilic species (Fig. 4) and this, too, matches observations of declines of specialist guilds (Aarts et al., 2004). However, it has to be noted that species of the rheophilic and lithophilic guild are also repre-
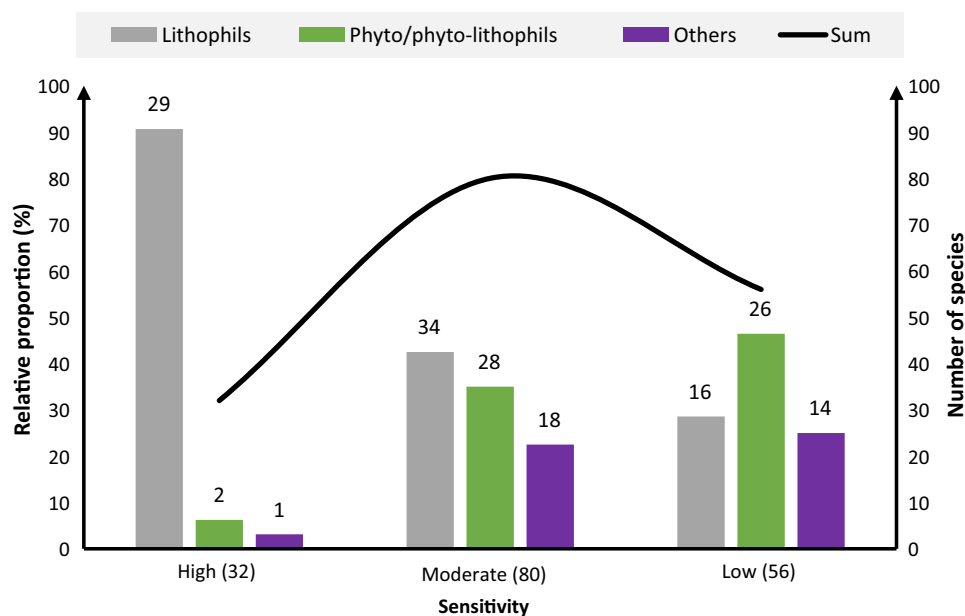


**Fig. 3.** Relative proportion of selected spawning guilds of 168 species within the 3 sensitivity classes High (N = 32), Moderate (N = 80) and Low (N = 56). "Others" include ariadnophils, ostracophils, pelagophils, polyphils, psammophils, speleophils and vivipars. Respective species numbers per sensitivity class and spawning guild are shown above bars. The black line and the numbers in parentheses indicate the total number of species per sensitivity class.
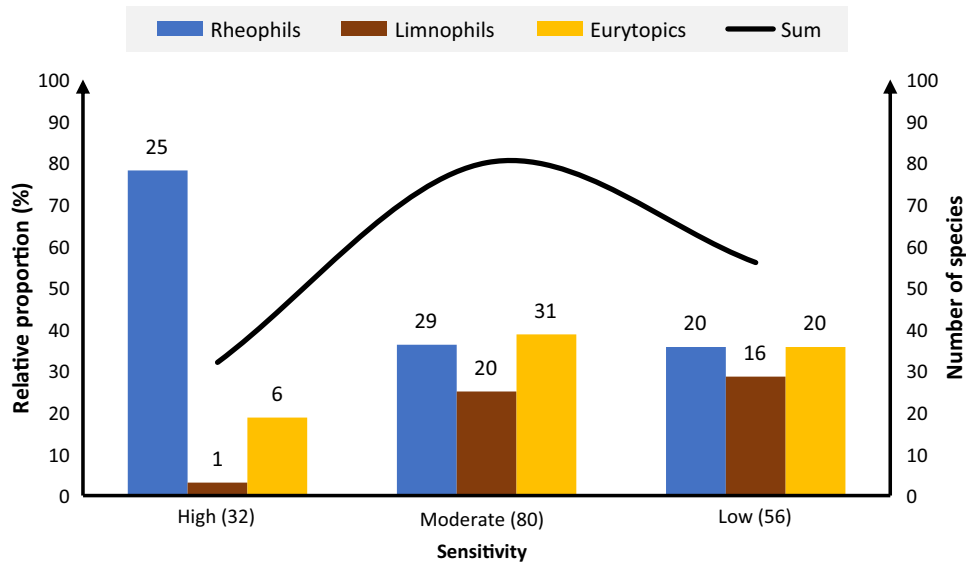
**Fig. 4.** Relative proportion of main habitat preference guilds of 168 species within the 3 sensitivity classes High (N = 32), Moderate (N = 80) and Low (N = 56). Respective species numbers per sensitvity class and habitat guilds are shown above bars. The black line and the numbers in parentheses indicate the total number of species per sensitivity class.

sented in the moderate and low sensitivity class (Figs. 3 & 4). This indicates a broad variety of recovery potential among species of the same habitat guild, and has implications for river rehabilitation planning and benchmarking.

In the moderate and low sensitivity class the relative proportion of rheophilic and lithophilic species decreases while the proportion of limnophils, phytophils and most importantly, eurytops increases. The dominance of these guilds on the lower end of the sensitivity scale is highly plausible as well. It has been repeatedly shown, e.g. by Jurajda (1995), Aarts et al. (2004), Wolter (2010), Scharf et al. (2011), that eurytopic species rather benefit from degraded conditions. Accordingly, roach *Rutilus rutilus* and perch *Perca fluviatilis* (both only moderately sensitive) are even considered indicator species for water quality impairment (Oberdorff and Hughes, 1992) and habitat degradation (Wolter and Vilcinskas, 1997), respectively. Species in the lower sensitivity classes mostly express a trait combination of small size and short life expectation, rapid growth, early maturation and high mortality rates, which results in high population turnover and occasionally very high recruitment facilitating fast recovery (Lande, 1993; Roff, 1993; Hutchings, 2000; Lytle and Poff, 2004). As a consequence, we expect these species to be less resistant, but due to the high recovery potential less sensitive against anthropogenic disturbances.

A significant result is the presence of 1 and 20 limnophilic and 6 and 31 eurytopic species in the high and moderate sensitivity class respectively. Among them are the whitefish *Coregonus maraena*, several barbel species and the Adriatic sturgeon *Acipenser naccarii*. This suggests that the ecological guild approach can sometimes be insufficient to predict the biotic response of species to e.g. habitat improvement, when it does not consider their intrinsic recovery potential at the same time. This was also confirmed by Aarts et al., 2004, and calls for different means of assessing specific population behavior, especially of data-poor species, in response to anthropogenic activities.

### 4.2. Application

The species sensitivity classification developed here provides a tool for conservation and restoration planning and also benchmarking that goes beyond habitat preferences and guild member-

ship of species. Combining resistance and recovery traits within a single scoring system allows for differentiating within habitat guilds between species of high resistance and low recovery potential and vice versa, which is relevant in predicting species' response to degradation and rehabilitation. For example, within the lithophilic, i.e. gravel spawning fishes, species of low sensitivity and high recovery potential are expected to respond faster to the provision of spawning gravel, a common river rehabilitation measure, compared to highly sensitive species. Correspondingly, highly sensitive species should be primarily protected and in focus of conservation actions, while species of low sensitivity could be easier enhanced by rehabilitation measures. By providing guild-specific spawning and habitat conditions water managers would not only aid to conserve highly sensitive species but also greatly accelerate the recovery of less-sensitive species that are expected to recover much faster than the highly sensitive ones after a disturbance-induced population collapse.

The sensitivity classification offers a versatile tool that is easy to apply for a range of stakeholders and supports the selection of target species for river rehabilitation, stock enhancement and prediction of species-specific responses to disturbances. Substantial enhancement of a population of a highly sensitive species would definitively indicate rehabilitation success. In the same sense, the most sensitive species might be selected as target species to implement the most comprehensive rehabilitation measures. The system also supports conservation actions by making use of these highly sensitive candidates serving as umbrella species for habitat protection and enhancement. The success of using umbrella- or keystone species in conservation programs has been demonstrated several times (Lambeck, 1997; Roberge and Angelstam, 2004). Conversely, if prevalent umbrella- or keystone species disappear in an affected water body, the classification system makes it easier to predict which species will follow. Regardless of its application, the detailed scoring and extensive species coverage facilitate success evaluation on a highly resolved, temporal scale. If the reference community assembly is known the sensitivity score can also be part of a "snapshot metric" to evaluate the conservation value of a certain water body at a given time. To that end, the metric may include abundance, species number and a processed specific sensitivity score of a sample, similar to other diversity metrics, described by e.g. Peet (1974), or to the Fish Region Index (Dußling et al.,

2005). The use of this metric would even enable an objective comparison of two or more independent water bodies whose reference communities differ in species richness if a coefficient correcting for species numbers is included.

Further, our system allows for easy regionalization of its diagnostic capabilities by choosing the most sensitive species from the classification that occurs in the regional species pool. Because of that, the application of the sensitivity classification is not limited to a specific biogeographic region, catchment or country within Europe, which sets it apart from other common fish-based approaches surrounding freshwater assessment policies.

We therefore argue that using the sensitivity score developed here in synergy with habitat guilds more comprehensively captures the response pattern of riverine fish communities to degradation, rehabilitation and conservation of river systems.

This new method provides an opportunity to overcome common problems occurring in restoration and rehabilitation tasks everywhere:

- Due to a lack of knowledge of the species' life history, very little is known about their intrinsic resistance or recovery capacity; something that we can resolve by combining resistance and recovery traits to a single score.
- A lack of means to evaluate the success of rehabilitation measures can be overcome, even across many different biogeographic regions, by using increasingly sensitive species as benchmarks.
- Prioritizing conservation and rehabilitation measures can be streamlined by offsetting ecological guilds and conservation concerns with the sensitivity score presented here.

## 5. Limitations

Many physico-chemical pressures like eutrophication or depleted water quality appear as press or ramp disturbance, i.e. they just increase and stagnate in amplitude and may remain in that state for an extended period of time, during which recovery cannot occur (Lake, 2006). Even though our system provides a baseline indication on how severe a species would react to a ramp disturbance (we expect species of the highest sensitivity to withstand greater magnitudes) our system is not suited to identify the exact nature of the disturbance. Furthermore, species might respond to disturbances by adaptation, which was not considered here. For example, cyprinids of the genus *Carassius* and the bitterling *Rhodeus amarus*, have evolved extraordinary resistance against anoxic conditions lasting for weeks (Nilsson and Östlund-Nilsson, 2008). Consequently, the sensitivity score does not constitute a universally valid scale that indicates a population's unconditional performance but should be considered in a site- and situation-specific context to provide the most comprehensive and meaningful information. Therefore, discrepancies cannot be excluded between the sensitivity classification of a species here and its conservation status according to the Habitats Directive (92/43/EEC) or the European Red Data Book (Freyhof and Brooks, 2011).

## 6. Conclusions

Our approach is based on the analysis and compilation of resilience traits and provides a species-specific ranking score of sensitivity to mortality of adults from a population. The classification is intended as a diagnostic tool for rehabilitation planning and identifies particularly sensitive species to streamline conservation efforts and less sensitive ones to benchmark restoration success. The results agree well with other research and can be used across

biogeographic regions in all of Europe and independent of the precise nature of the disturbance.

## Declaration of Competing Interest

The authors declare that there is no conflict of interest regarding the publication of this article.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2019.135173.

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