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Negative influence of a threatened species on ecological status classification: A case study of the influence of European eel within the Swedish fish index VIX

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ABSTRACT

Biological indicators are important quality elements for classification of ecological status of water bodies according to the European Water Framework Directive. Multimetric indices are commonly regarded as robust and reliable indicators of human impact and are often used as quality elements. In fish-based indices, species are often grouped into guilds based on general tolerance to common anthropogenic pressures, with higher proportion of tolerant species being indicative of degraded systems. Within the Swedish electrofishing index VIX, the critically endangered European eel *Anguilla anguilla* (L.) is classified as a tolerant indicator species, and it therefore has a negative effect on classified ecological status. The scientific literature, however, suggests that eels are not generally tolerant and they benefit from similar environmental conditions as many insensitive species. VIX has been criticized for being too sensitive to the presence of eel in catch data, leading to low status classifications when eels are caught in the monitoring surveys. In a case study using manipulations of historical electrofishing data, we assessed the influence of eel presence and abundance on the ecological status classification as determined by VIX. We demonstrate that reduction of eels in survey data have positive effects on the classified status, in many cases substantial effects. An increase of eels in the data had the reverse effect. Mere presence of eel had a strong negative effect, which is problematic if the aim is to increase the endangered eel population. Given the Swedish classification system where the quality element indicating the worst status is decisive, the classified ecological status of Swedish rivers can theoretically be improved by management actions disfavouring eel, unless the results from VIX are carefully evaluated by experts. Along the same lines, measures implemented with an aim to increase the endangered eel population will lead to a decrease in assessed ecological status of Swedish rivers. Our conclusion is that the usage of VIX within Swedish water management is problematic and needs revision. From a broader perspective, the classification of species as generally tolerant need to be approached with great caution when developing new indices for assessing ecological status and integrity.

1. Introduction

Monitoring of relevant biological quality elements is a keystone principle for the classification of ecological status of rivers within the European Union (EU), following the Water Framework Directive (Directive 2000/60/EC; 'WFD') (European Commission, 2000). Within each of the directive's six-year assessment cycles, ecological status of surface water bodies is assessed on a five-tiered scale (hereafter abbreviated as 'Poor', 'Bad', 'Moderate', 'Good', 'High'). When classifications do not reach 'Good' status, management action to identify and rectify problems should be initiated, and worsening of the status from one assessment cycle to the next is not accepted (European Commission, 2000). Through this process, the WFD aims to promote protection and restoration of aquatic ecosystems. The WFD was introduced into Swedish law in 2004, within The Swedish Environmental Code (Miljöbalken, 5 kap.; The Swedish Parliament, 2004a) and regulations 2004:660 and 2017:868 (The Swedish Parliament, 2004b, 2017).

Classification of ecological status according to the most recent Swedish ordinance (Swedish Agency for Marine and Water Management, 2019) follows a specific procedure. First, each individual biological-, physicochemical- and hydromorphological quality element ('BQE', 'PQE', and 'HQE', respectively) is evaluated with respect to its

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uncertainty and plausibility. Thereafter, the biological quality elements are prioritized and weighed together. When the BQE indicate 'High' or 'Good' status, the PQE must also be weighed together and, based on these, the classification can be downgraded to either 'Moderate' or 'Good'. If the status classification is still 'High', the HQE must also be weighed together and the status can be downgraded to 'Good' status. When weighing quality elements, the one signaling the worst status is decisive. Hence, if a BQE indicates an erroneously low status level, this could be transferred to the final status classification, if the error is not identified during the first evaluation step of the process, with subsequent rejection of the BQE in question. For this reason, it is important to know if some types of data render a BQE implausible in a systematic way.

Fish composition, abundance and age structure belong to the BQEs suitable for classification of ecological status within EU waterbody monitoring programs (European Commission, 2000), and it is recommended as a sensitive key element for operational monitoring for habitat and morphological changes (European Commission, 2003). Each EU member state determines the precise sub-element or parameters to be used within their monitoring assessment (European Commission, 2003). Indices composed of multiple parameters indicative of alterations, in relation to historical reference conditions, are often used for such assessment and, hence, for the classification of ecological status (Birk et al., 2012). Within the EU, the BQE used for evaluating ecological status of rivers should be comparable and are therefore intercalibrated among countries, with respect to status classification boundaries (e.g., European Commission, 2018).

The Swedish fish-based index VIX ('VattendragsIndeX'; Beier et al., 2007) is a multimetric index based on standardized wading-electrofishing surveys in rivers. It combines six component parameters describing the fish fauna: 1. *density of Atlantic salmon and brown trout*; 2. *proportion tolerant individuals*; 3. *proportion lithophilic individuals*; 4. *proportion tolerant species*; 5. *proportion intolerant species*; and 6. *proportion reproducing native salmonid species* (species classified as 'tolerant', 'intolerant', and 'lithophilic' are listed in Supplement 1: Table S1). Reference values for fish community composition are derived from multiple regression models using catch- and environmental data from a set of river sites by expert judgement classified as having 'Good' or 'High' ecological status. The magnitude of the deviation from these predicted reference values is used to calculate an Ecological Quality Ratio (EQR) with values ranging between 0 and 1, which is supposed to represent the ecological status of the surveyed site (method summarized in Supplement 1: Box S1; also see Beier et al., 2007). VIX has been successfully intercalibrated with other indices within the 'Nordic' Geographic Intercalibration Group (Finland, Ireland, Sweden, Northern Ireland, and Scotland; European Commission, 2018), and is currently-one of the main analytical methods used to classify ecological status of rivers in Sweden (Swedish Agency for Marine and Water Management, 2018, 2019).

Species that are generally tolerant to common anthropogenic impacts are often assigned indicatory values within fish-based indices for assessment of ecological integrity and status (Karr et al., 1981; Breine et al., 2004; Pont et al., 2006). Tolerant species are expected to increase in relative abundance, as compared to less tolerant species, as the ecosystem function deteriorates (Karr, 1981; Pont et al., 2006; Noble et al., 2007); a consequence of stronger negative impacts on intolerant species, and possibly an increase or immigration of tolerant species when competition is relaxed.

This study specifically concerns the European eel *Anguilla anguilla*, which is currently assessed as critically endangered (CR) in the global IUCN assessment (Pike et al., 2020), in the regional HELCOM assessment (HELCOM, 2013), and in the national Swedish assessment (SLU Artdatabanken, 2020). Overall, the recruitment of European eel is very low across its natural distribution range, as compared to historical records (ICES, 2021). Under obligation from the EU Eel Regulation (Council of the European Union, 2007; Dekker, 2016), Sweden has implemented the Swedish Eel Management Plan to establish measures for the recovery of the eel stock (Dekker et al., 2021). The eel is used as a tolerant indicator species in VIX (Beier et al., 2007), in accordance with several other European fish indices (e.g., Belpaire et al., 2000; Pont et al., 2006; Vehanen et al., 2010), but not all (e.g. Oberdorff et al., 2002; Mihov, 2010). Adult eels are indeed relatively tolerant to several types of poor environmental conditions. As omnivores capable of long-term starvation (Boëtius and Boëtius, 1985; Olivereau and Olivereau, 1997), they can sustain life in a wide range of aquatic habitats (Segurado et al., 2011). They also have a high tolerance to low oxygen conditions (van Ginneken et al., 2001) and are not particularly sensitive to acidification (Almer et al., 1974). Abundance of younger stages, however, generally decreases with acidification, due to a combination of juvenile sensitivity and avoidance behaviour (Ask et al., 1971; Fjellheim et al., 1985; Degerman et al., 1986; Forsberg, 1986). Hence, liming of acidified rivers (i.e. addition of calcium compounds to increase pH) can lead to increases in eel abundance (Larsen et al., 2015). Furthermore, eel abundance tend to decrease with decreasing amount of coarse substrate in rivers, a pattern also seen in some generally intolerant species (e.g. brown trout *Salmo trutta*), and such reduced habitat complexity is often indicative of human-impact and lowered ecological integrity (Degerman et al., 2019; Donadi et al., 2019; Soukup et al., 2022). Eels are also susceptible to several chemical pollutants, from the subcellular- to the population level, with good evidence for strong negative impacts at several life stages (Geeraerts and Belpaire, 2010; Belpaire et al., 2019). Disrupted river connectivity in the form of artificial migration barriers is another environmental problem which affects eel abundance negatively (Lasne et al., 2008; Tamario et al., 2019). Broad analyses of the tolerance of eel show that it varies substantially, from moderately low to high, depending on which assessment criteria are used (Segurado et al., 2011). Another analysis shows that eels are tolerant to water quality alterations, but only moderately tolerant to habitat structure alterations and intolerant to pH-, temperature- and macrophyte alterations (Maceda-Veiga and De Sostoa, 2011). The long and complex catadromous life-cycle makes eels particularly difficult to use for ecological assessment of rivers, since they can also be affected by impacts, known and unknown, in the marine environment (Podda et al., 2021). In sum, it is reasonably clear that the eel is not generally tolerant to anthropogenic pressures and labelling species as "tolerant" is misleading if it is only valid under certain conditions and life stages.

Concerns about eel influencing VIX (and hence the Swedish ecological status assessment of rivers) in an unwarranted negative way have been raised repeatedly (e.g., Degerman et al., 2012; Blomqvist, 2017). Observations suggest that some water bodies are assessed to have less than 'Good' ecological status in years with high eel abundance, whereas they pass the threshold for 'Good' status in other years (County Board of Halland, 2019). The issue of VIX's sensitivity to eel is also acknowledged in the assessment guidelines from the Swedish Agency for Marine and Water Management (2018), but no formal analyses have addressed the generality of this claim. If minor changes in the abundance, or mere presence, of eel can shift the classified ecological status from 'Good' to any status level less than 'Good', then a re-evaluation of whether or not eel is an appropriate indicator of negative human impact is warranted. Such results may lead to management measures which unintentionally disfavours eel presence in the ecosystem, a scenario which is clearly undesirable in consideration to the regulations stated in the Swedish Eel Management Plan. Moreover, management measures specifically aimed at increasing eel abundance could, all else being equal, lead to lowered ecological status (i.e., as classified by VIX) in river water bodies where the measures are successful, which is clearly undesirable from the perspective of the WFD and the Swedish Environmental Code.

In this paper, we exemplify the influence of eel presence and abundance in survey data used for classification of ecological status in Swedish rivers. We use *in silico* modifications of historical electrofishing data and show the effects these modifications have on status classification using VIX. The aim of the paper is to assess whether there is a need to revise the usage of VIX, despite it being an internationally intercalibrated index.

2. Material and methods

2.1. Data information

All analyses were based on electrofishing data registered in the Swedish Electrofishing RegiSter ('SERS'; SERS, 2020); which, at the time of the analyses, contained 71,790 electrofishing records (with 43,690 being quantitative, i.e., based on the multi-pass removal method; Bohlin et al., 1989). Electrofishing data in this database are collected following the European and Swedish standard (CEN, 2003; Bergquist et al., 2014). Eels are today predominantly caught in lowland river sections relatively close to the coast, where upstream migration routes are accessible (Fig. 1A). Hence, in Swedish electrofishing monitoring data, the catadromous European eel primarily associates within the general diadromous fish assemblage in present-day Swedish fish biogeography, in particular together with Atlantic salmon *Salmo salar* (Degerman and Sers, 1992). The historical natural distribution of eel also included many inland waters (Lundberg, 1899), but the present-day natural distribution is largely limited by human-constructed migration barriers (Tamario et al., 2019; Halvorsen et al., 2020). Eel occurrence in many inland waters is currently maintained by compensatory stocking of young eel, typically through translocation from other European countries (Dekker et al., 2021). Eel translocation aimed at stock enhancement or introduction has been part of Swedish fisheries management for more than a century (originally with eels sourced from Swedish rivers) (Brundin, 1939), but has progressively been directed towards an aim of stock maintenance in water systems that the species cannot reach due to connectivity issues.

In total, 33,934 quantitative electrofishing samples from the period 1959–2019 were included for analysis, representing all quantitative samples from what we here call the "eel region" of Sweden (Fig. 1A-C). The eel region is a heuristic geographical delimitation, used solely for the purpose of the present study, constituting the areas south of a diagonal line interpolated between the northern-most occurrences of eel in SERS data in the western (WGS84 dec: 60.660403, 12.703074) and eastern (WGS84 dec: 63.217761, 17.586257) part of the country, and extrapolated in its tangent direction (Fig. 1A). This region fits reasonably well with the main known historical distribution (including the areas draining into Lake Vänern, which eel could reach for certain first in the 1800's, according to Lilljeborg, 1891), but it excludes the northern-most part of the distribution range (Lundberg, 1899; Kullander et al., 2012). It also fits well with occurrence records in the Global Biodiversity Information Facility (GBIF) database, where only a few sites north of our defined borderline are recorded (GBIF, 2020; Supplement 1: Fig. S1). Data were organized, modified (as described below), and visualised using *tidyverse* packages (Wickham et al., 2019) in R (R Core team, 2020).

2.2. Influence of changing eel density on status classification derived from VIX

Simulating changes in the estimated fish density in otherwise empirical data can be a useful approach when investigating sensitivity of indices (Trebitz et al., 2003). Here, we followed this approach by modifying data on estimated eel density from real-world electrofishing datasets, providing alternative-scenario data with respect to eel catches while still retaining all other natural characteristics of the data.

First, the effect of having less eel in the electrofishing catch (the likely scenario if the eel population continues to decrease) was investigated by decreasing the estimated density with 0.1, 1 or 2 individuals • 100 m^{-2} (or until values of 0 were obtained). In addition, data was modified to remove all eels from the catches. For these data modifications, we only used quantitative electrofishing data from sites where eels were present in the original catch. Second, the effect of having more eels in the catch (which would be a likely scenario if the European eel management plan is successful) was investigated by increasing the estimated eel density with 0.1, 1, 2, 5 or 10 individuals • 100 m^{-2}. Here,

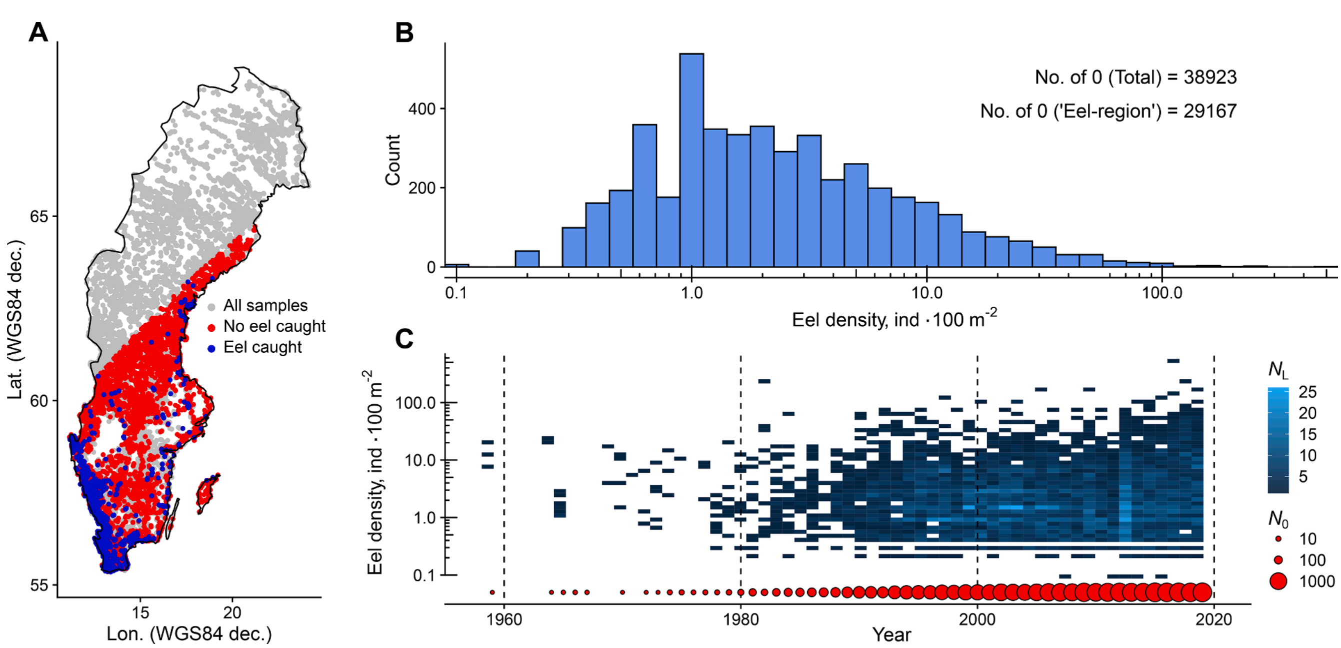

Fig. 1. Description of data from the Swedish Electrofishing Register (SERS) used in the analyses. A) Visualization and selection of data. Grey points show all electrofishing sites in Sweden, red points show all sites within the generalized 'eel-region' (corresponding to the main distribution area of eel), and blue points show sites where eel have been recorded from electrofishing surveys. B) Histogram of estimated densities of eel for the sampled sites, with number of sites with 0-values reported for the whole country (No. of 0 Total) and for the 'eel-region' (No. of 0 eel region). High densities are due to large numbers of young eels. C) Eel-densities observed over time covered in SERS; number of sites with eel is visualized by the colour scale (N_L) and number of sites with 0-values (N_0) are reported as closed red circles at the bottom of the graph. Note that number of electrofishing samples have increased over time; data presented in C) does not represent population trends. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

we used two data subsets: i) including only sites with eel in the original catches, and ii) including only sites where no eels were present in the original catch (Fig. 1A,C). In a final modification, the eel's status as tolerant was omitted from the formula to calculate a modified VIX (i.e., considering eel as a neutral species within the index). While this procedure is not strictly statistically sound, since eels were included as tolerant in the original reference data set from which VIX is derived (Beier et al., 2007), it retains all eel individuals in the data, so that they can still be part of the denominator when calculating proportions based on total number of species or individuals. The 'EQR' derived from this modification should not be considered to be true VIX EQR, instead the modification can be seen a potential tool, within an expert judgment procedure, to investigate the effect of eels in relation to the original EQR.

After modifications, EQR based on VIX were calculated (Beier et al., 2007; see formulas in Supplement 1: Box S1, Tables S3-S4). For each modification, the changes in status assignments were compared graphically against the original data. We limit the main analyses to graphical representations of the results because the aim is to provide an overall view of the influence of eel on VIX. We do not aim to provide any kind of quantitative evidence of probable misclassification of ecological status in Sweden; this remains unknown at this stage. Some electrofishing sites are represented multiple times in the data set, but since catches and environmental conditions at a given site are virtually never identical, we still treat these as independent examples of real-world electrofishing results, for the purpose of this particular analysis. It should, however, be noted that some geographical areas are over- or underrepresented in this analysis (Fig. 1A).

2.3. *Influence of eel on the status assessment for the second cycle of the Water Framework Directive*

To investigate the projected effect of eel occurrence on the previous (second) 6-year cycle of the Water Framework Directive (2016–2021), we extracted all data from the "eel-region" for the years 2016 to 2019. Data from each river, for all the years within this time-frame, were compiled to mean VIX values (hence, effects for a given site in a river may be higher or lower), one based on original data (VIX_{orig}) and one after removing all eels from the catch data ($VIX_{no.eel}$). The difference, $VIX_{no.eel}$ - VIX_{orig}, was used as the response variable in the analyses.

Analyses were based on graphical assessment and parameter estimates from a linear model including the terms 'eel density' (log_{10}-transformed mean number of eels • 100 m^{-2}), 'eel presence' (proportion of surveys with eel in the catch), and 'number of surveys' (log_{10}-transformed number of surveys in the river) as independent variables. We first ran a full global model including all three independent variables, with all interactions. This model was reduced based on comparing AIC (Akaike Information Criterion) for all possible subordinate models, using the dredge() function in the MuMIn package for R (Bartoń, 2020). Among the models with $\Delta AIC < 2$ from the top-ranked model, we chose the one including the most terms, to avoid usage of a too simplified model. The model eventually used for parameter estimation (the second-ranked model; see Results) included the main effects of eel presence (proportion of surveys) and log_{10}(eel density). A residuals vs fits plot indicated a good fit with respect to normality, but unequal error variance where variance decreased with increasing fitted values. A Q-Q plot indicated a heavy-tailed (leptokurtic), but symmetric distribution. The model was retained for parameter estimation, with a caveat that statistical assumptions are not entirely fulfilled.

3. Results

3.1. *Influence of changing eel density on status classification derived from VIX*

Reducing the electrofishing catches of eel generally increased the VIX values, even at very low reductions (0.1 individual • 100 m^{-2}), leading to improved assigned ecological status in many cases (Fig. 2). At a reduction of one eel per 100 m^2, it was clearly possible to discern two groups in the results, one with a substantial increase in status, and one with a less dramatic increase. The group with the strong effects was characterised by sites with original eel densities at or below one individual • 100 m^{-2}, where eel was also the only tolerant species at the site (Fig. 2A; see Supplement 1: Fig. S2A-F and Fig. S3) for detailed visualization of these effects). Reducing eel catches by two individuals • 100 m^{-2} leads to more sites indicating higher ecological status and removing eels completely from the catch increased the status even further (Fig. 2B; also see Supplement 1: Fig. S3A-D). Modifying the VIX-index, so that eel is no longer classified as tolerant in the calculations, also lead to a substantial increase in number of sites classified in the 'Good' category (Fig. 2B). This increase was lower than when just removing eel from the catch, as a consequence of eel individuals still being included as neutral species (i.e., the proportion of intolerant species and proportion of lithophilic individuals will be lower than if eels are completely removed, reducing the index values slightly).

Modifying original data by increasing the estimated eel density generally decreased VIX values and consequently decreased the assessed ecological status derived from surveys in many cases (Fig. 3). Within the data subset consisting of only surveys with original presence of eel, the effect was rather small (especially when the density was only marginally increased by 0.1 eel per 100 m^2, which does not lead to any noticeable differences), since they were already negatively influenced by this prior presence of eel (Fig. 3A-B). With lower original eel densities, larger decreases in the VIX value were observed when adding eels to the catch (Fig. 3A). Adding more eels to the catch (0.1, 1, 2, 5, or 10 eels • 100 m^{-2}) progressively led to a higher proportion of surveys indicating less than 'Good' ecological status (Fig. 3B). Within the subset consisting of surveys without eel in the original catch, even a very marginal addition of eel (0.1 individual per m^2) could lead to substantial effects on status classification, and effects were more apparent when higher densities were added. Detailed examination of the decline in VIX due to one added eel per 100 m^2 showed that effects were relatively small when another tolerant species was present in the original data, but dramatic when no other tolerant species than eel were present (see the two distinct data clouds in Fig. 3C). Even with only 0.1 individual per 100 m^2 added, no surveys indicated 'High' ecological status anymore, and the majority of the surveys originally indicating 'Good' ecological status instead indicated less than 'Good' status (Fig. 3C-D). Further increases in eel density had substantially smaller additional effects (Fig. 3D), suggesting that presence in itself, rather than the relative density, of eel was driving much of the negative effect of eel on VIX values.

3.2. *Influence of eel on the status assessment for the second cycle of the water Framework Directive*

For rivers with eel presence at any given survey between 2016 and 2019, the mean effect of eels on the VIX value was −0.138 (median: −0.110; range: −0.528 – 0.00; interquartile range: −0.212 – −0.046; Fig. 4). The selected model for estimating effects of eels included log_{10}(eel density) and proportion of surveys with eel present ('eel presence'; parameter estimates in Table 1). Only the eel presence term was significant, but this is a consequence of strong collinearity between the factors, as running log_{10}(eel density) on its own results in significant effects (slope estimate: −0.08880, $p < 0.001$). Similarly, while not included among the candidate models with $\Delta AIC < 2$, a model based only on log_{10}(number of surveys) returned a significant relationship (slope estimate: 0.1042, $p < 0.001$). More surveys reduce the proportion of surveys with eels present, which drive the positive relationship. In addition to the analysed model, all three terms investigated as potentially influencing change in VIX ('number of surveys', 'eel presence', and 'eel density') are visualised in Fig. 4A-C, using non-linear regressions (generalised additive models within the *ggplot2* package for R). In brief, the non-linear regressions largely support the linear modelling results.

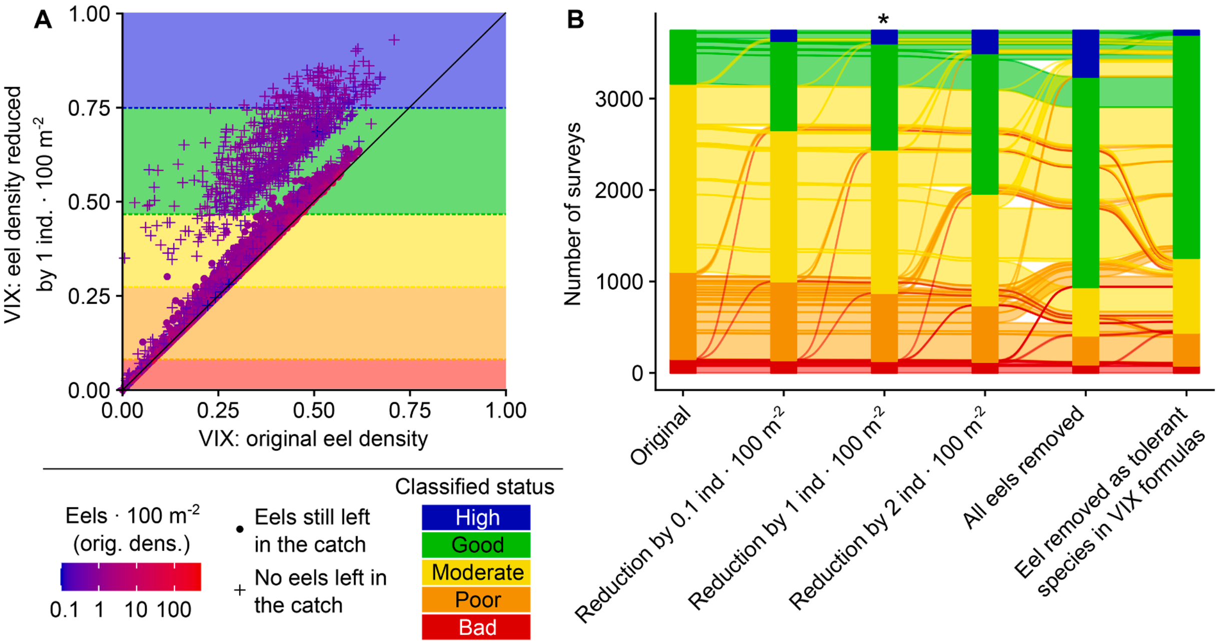

Fig. 2. Effects of manipulating original data by removing eel from the catch. A) Effects on VIX when removing 1 eel individual • 100 m^{-2} (if<1 eel • 100 m^{-2} were caught, the density was set to 0; indicated by '+' symbols). The diagonal black line shows the 1:1 relationship (no change). Points above the diagonal indicate an increase in the VIX ecological quality ratio. Coloured areas represent the status class boundaries along the y-axis. See Supplement 1: Fig. 2A-D for similar illustration of all manipulations. B) Alluvial plot showing the change in status classification when removing eel from the catches (only sites with eel presence included). The left-most bar shows the number of sites classified into each status class, based on original data. The following three bars show the change in status classification when reducing densities by 0.1, 1, 2 individuals • 100 m^{-2}. The two right-most bars illustrate the change in status classification if all eels are removed from the data and if eel is not considered a tolerant species in the VIX formulas (NB, the predicted reference values are still derived from data including eels). Asterisk (*) denote the data represented in panel A.

Increasing number of surveys in a stream decreases the negative effect of eels on VIX; with more surveys, the proportion of surveys with eels in the catch decreases as a consequence of eel being a relatively rare electro-fishing catch in most areas, and then the average negative effect on VIX also decreases (Fig. 4A). Increasing eel density at a given site increases the negative effect on VIX (Fig. 4B), as do increasing proportion of surveys with eel presence at a given site (Fig. 4C). These effects are expected, given how VIX is calculated (Supplement 1: Box S1, Table S3-S4). Plotting the results on a map over Sweden shows that the west coast of Sweden is the region which is most influenced by eel presence affecting assessed ecological status in recent years (2016–2019) (Supplement 1: Fig. S4-S5).

4. Discussion

In this paper, we demonstrate large negative impacts of eel presence and eel density on ecological status classification based on the Swedish fish-based index VIX. Given that VIX is commonly applied within the ecological status classification process for Swedish river water bodies this sensitivity to eel constitutes a potential problem for both water- and eel management. European eel is a native species which has been historically abundant, but now endangered. In fact, the presence of eel in itself may indicate a healthy ecosystem, especially with respect to longitudinal hydrological connectivity.

The classification of eel as a generally tolerant riverine species can be reasonably questioned, based on the existing literature. Assessments suggest that the eel's tolerance to anthropogenic impact is moderate to high, but also that this tolerance is context- and life-stage specific (Maceda-Veiga and De Sostoa, 2011; Segurado et al., 2011). Adult eels are indeed tolerant to many environmental impacts, in terms of survival, and a strong dominance of adult eels in a fish community could indeed be an indirect indicator for a disturbed system. However, human impact on freshwater habitats and connectivity among water bodies are candidate factors for the drastic decline in the European eel population (Bevacqua et al., 2015). From a perspective of classifying status of freshwater systems, the connectivity barriers' effects on the younger stages are of main importance. Adults too would be affected, but this effect would not be detected in river fish surveys since adults are affected when migrating out of the freshwater systems. Hence, absence of eels could be an indicator of negatively affected ecological integrity, in which case the eel should be assigned as intolerant – in stark contrast to its current classification in VIX and several other indices. However, to assess effects of disrupted connectivity one needs to know whether the survey site is located upstream of a migration barrier, a factor that is not included in the data used to calculate VIX. Furthermore, many Swedish inland eel stocks are enhanced or maintained through stocking by means of translocation (Dekker et al., 2018). Both presence *per se*, and high densities may therefore be associated with recent stocking events, although most stocking in freshwater is done in lakes and not in rivers (Dekker et al., 2018). Whether stocking affects Swedish river ecosystem communities has not been investigated. Studies in Portugal indicate that stocking of glass eel (ca. 0.9 individuals/m^2 available habitat) has no obvious negative impacts on biota in the stocked areas, so this action in itself may not warrant any major concerns about ecological status (Félix et al., 2020), unless the stocking densities are very high in relation to the available habitat. VIX does not consider whether individuals are stocked or naturally recruited, but this has obvious implications for evaluating the results of VIX-calculations. Stocked individuals, in particular recently stocked ones, are not reliable indicators of ecological status, which should be considered in future index-development. Overall,

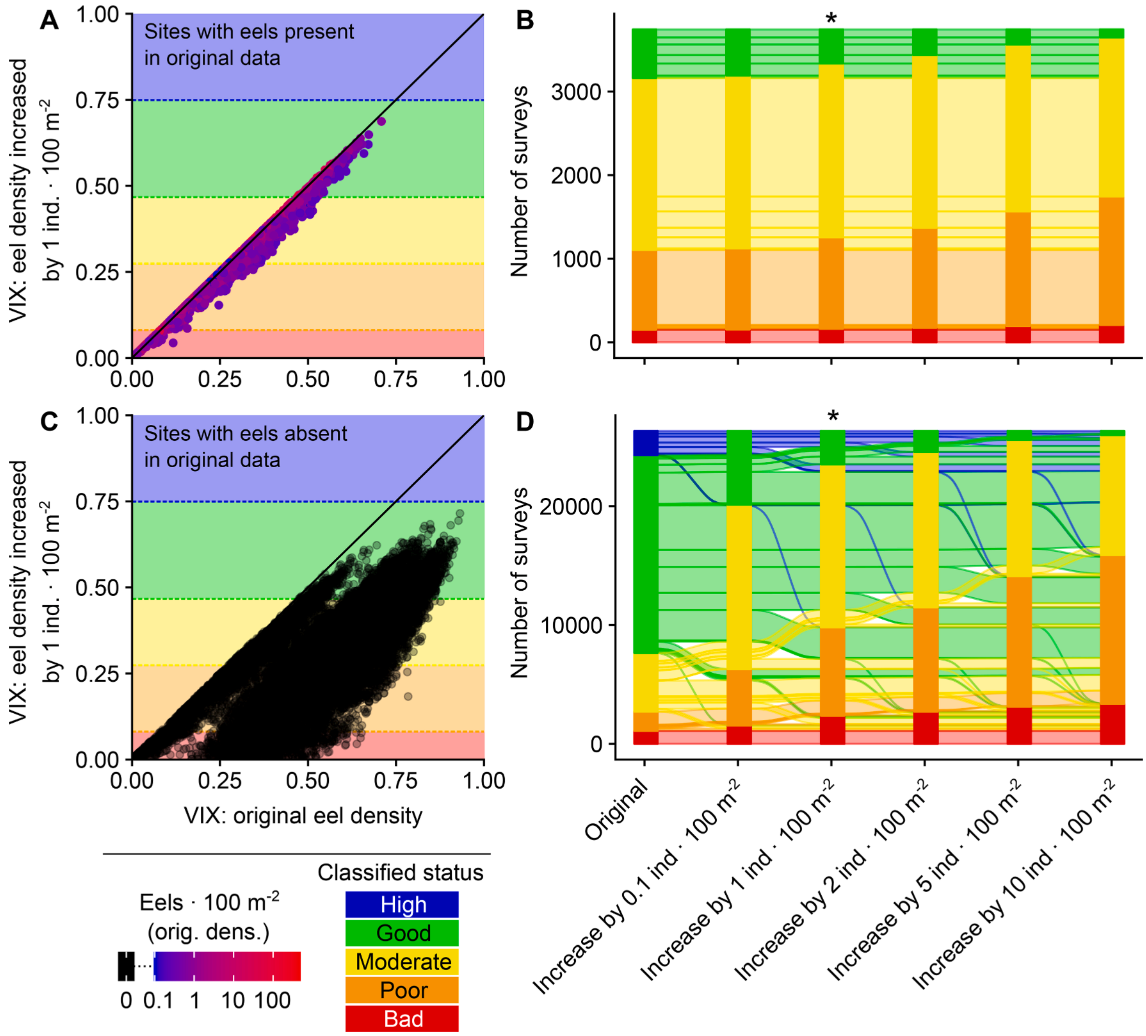

Fig. 3. Effects of manipulating original data by adding eel to the catch. A) Effects on VIX when adding 1 eel individual per 100 m^2, when eels were already present in the catch (x-axis title is the same as in C). The diagonal black line shows the 1:1 relationship (no change). Points below the diagonal indicate a decrease in VIX. Coloured areas represent the status class boundaries along the y-axis; see classes in D). B) Alluvial plot showing the change in status classification when adding eel to the catches from sites where eels were already present. The left-most bar shows the number of sites classified into each status class, based on original data. The following four bars show the change in status class when adding 0.1, 1, 2, 5, or 10 eels per 100 m^2 to the catch (x-axis labels are the same as in D). C) Effects on VIX when adding 1 eel individual per 100 m^2, when eels were not previously present in the catch. D) Alluvial plot showing the change in status classification when adding eel to the catches from sites where eels were not previously present. Bars represent the same modifications of catch data as in B). Asterisks (*) in panels B and D denote the data represented in panel A and C, respectively.

indices like VIX need information in addition to the data used for calculations to be properly evaluated. For the specific case relating to VIX, knowledge of local conditions or further investigations are needed to assess the ecological status when eel is present in the data used for status classification.

In a supplement to this study (Supplement 2) we show that there is no detectable negative relationship between eel presence and the presence of intolerant species and that, when coexisting, the abundance of intolerant species tends to increase when the abundance of eel increases. Hence, both eel and intolerant taxa appear to be favoured by the same environmental conditions. Of course, eel being favoured in good environmental conditions does not imply that they are not tolerant, since tolerance does not imply doing worse in good conditions. The analyses, however, suggest that improving conditions for intolerant species would likely also benefit eels, provided that they can migrate to the area in question. Given the negative effects that the mere presence of eel have on VIX, this means that environmental improvements may not lead to higher classifications of ecological status as long as VIX is used within the assessment. This is a likely outcome when river connectivity issues are addressed, but also when riverine habitats are restored. Both of these management actions constitute goals for Swedish and European water management (The Swedish Government, 2020; European Commission, 2022).

Based on *in silico* manipulation of empirical SERS data (i.e., reducing or increasing the eel density in the data, all else being equal) it is clear that increasing the eel abundance can reduce the assessed ecological status, as determined by VIX. Consequently, by removing eels one can also theoretically improve the reported ecological status (i.e., on paper, not in reality). The major issue is eel presence *per se*, although there are smaller-magnitude effects of increased density as well. The issue arises from the fact that the reference data used to construct VIX had low average abundance of tolerant species and individuals (Supplement 1: Table S2). This is a consequence of most electrofishing being conducted in river sections mainly suitable for juvenile salmonids (i.e., relatively shallow and with good flow) where most species classified as tolerant are naturally rare (Degerman and Sers, 1992). However, eel is one of the few “tolerant” species that regularly use such habitats (Degerman and Sers, 1992), and hence, this species is particularly problematic for the

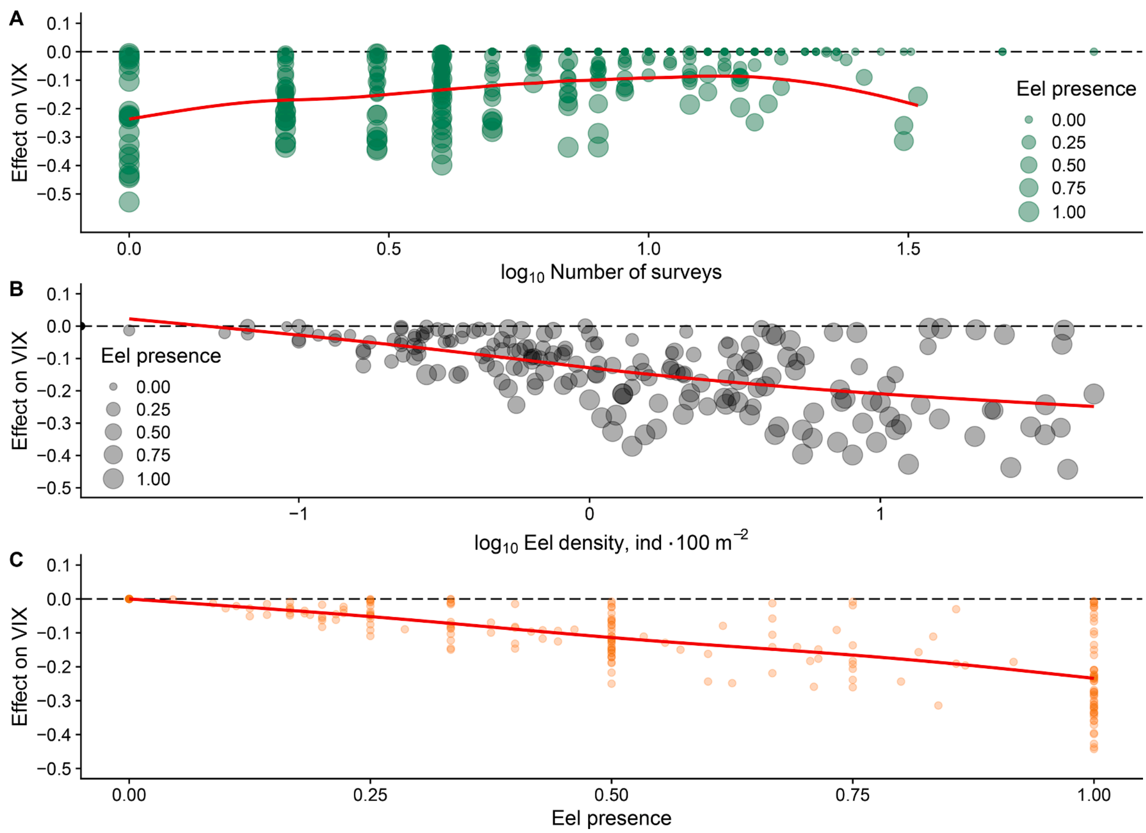

Fig. 4. Effects of eel in the catch on VIX values for the current (second) cycle of the EU Water Framework Directive (data from 2016 to 2019 included; the cycle ends in 2021). Effect is calculated as the difference between VIX as calculated based on catches with all eels removed and VIX as calculated based on original data. A) Effect on VIX as predicted by number of surveys from each classified river. All rivers within the "eel region" (see Materials and methods and Fig. 1A for definition) are included, but the non-linear local regression line (red) only depict the relationship for rivers with eels present in the catches (eel presence in terms of proportion of surveys including eel illustrated by point size). B) Effect on VIX as predicted by eel density. Only data from rivers where eels were present in the catch included. Non-linear local regression illustrated with red line. Eel presence in terms of proportion of surveys including eel illustrated by point size. C) Effect on VIX as predicted by proportion of surveys within a river with eel presence in the electrofishing catches. Non-linear local regression illustrated with red line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Parameter estimates from a linear model describing effects of catches of eel on VIX. Effect is calculated as the difference between VIX as calculated based on catches with all eels removed and VIX as calculated based on original data.

Parameter	Measurement	Estimate	SE	*t*	*p*
Intercept		0.00008	0.01728	0.005	0.996
$\log_{10}$(eel density)	Individuals • 100 m^{-2}	−0.01132	0.01316	−0.860	0.391
eel presence	Proportion of surveys	−0,22720	0.02950	−7.700	<0.001

index calculation. As a consequence of eels typically hiding during daytime (Kullander et al., 2012; López-Olmeda et al., 2012; Steendam et al., 2020), when electrofishing is conducted, their catchability can be relatively low and unpredictable (Lobon-Cervia et al., 1990; Benejam et al., 2012). Hence, when eels are present at a site being electrofished for status assessment, there will be a certain element of chance involved in the status classification, depending on whether eels were caught or not. As illustrated in Fig. 4A, the status for rivers with confirmed presence of eel increases with number of surveys conducted. This is likely an effect of an increased likelihood of including surveys without eel when the number of surveys increase, given that eels are relatively rare in the electrofishing catches in general (due to both behavioural characteristics and low abundance).

Based on the data available in SERS, it seems difficult to reach "High" ecological status in a river where eels are present, when using VIX as the status classification tool. One possible consequence of this could be that improvement of longitudinal connectivity for eel migration, e.g., by removing dams or installing eel passes or fauna passages next to migration barriers, could lead to a decreased assessed status in upstream areas of a river, even if the ecological functions and processes of the river actually comes closer to a natural reference condition. This indicates that the usage of VIX leads to a contradiction between the aims of the WFD target of achieving at least 'Good' status in all rivers, and the aims of increasing eel stocks according to the Eel Regulation. Increasing the eel stocks in Swedish rivers will likely cause a decline in their assessed ecological status in general.

The effects caused by the manipulation of eel densities in the original electrofishing data would be identical for any other species classified as 'tolerant', since the formulas are not species specific. For instance, adding one extra individual • m^{-2} of a 'tolerant' species not previously observed at the site has the same effect regardless of species. However, most of the other 'tolerant' species are thriving in lacustrine-like environments (Supplement 1: Table S1). Hence, these other species could be more relevant as tolerant indicator species in situations where anthropogenic impact modifies the river hydrogeomorphology to become deep and slow flowing. However, several of these other species also have riverine environments as natural habitats (e.g., sticklebacks *Gasterosteus aculeatus/Pungitius pungitius*, Eurasian perch *Perca fluviatilis*, common roach *Rutilus rutilus*, and common bream *Abramis brama*), in particular in lowland rivers, but often at sites not selected for electrofishing since the method focusses on salmonid habitats within the national monitoring programmes. The reference data used to develop VIX stems from catches made between 1955 and 2001, and is probably affected by the general reduction of eel in Europe, which has been ongoing for decades (Dekker et al., 2003, 2018). Hence, it is likely that eel presence and abundance under pre-industrial reference conditions would have been higher than what was observed in the VIX reference sites. However, the same may not be true for other tolerant species, given that VIX is specifically used to assess flowing salmonid habitats which typically lack the limnophilic species under reference conditions. Hence, it is not clear that the general predicted presence and abundance of tolerant species and individuals, excluding eels, are underestimated in VIX.

Given the sensitivity of the index to the presence of tolerant species, caution is warranted when determining ecological status of rivers in general, and in lowland rivers in south-western Sweden in particular (Supplement 1: Fig. S4-5). Guidance documents for using VIX (Swedish Agency for Marine and Water Management, 2018) specifically note that only rivers dominated by salmonid habitats can be classified with some confidence. For the specific application of VIX in Sweden, we hereby add the cautionary note that any presence of tolerant species may warrant closer examination of the data and the ecological condition of the stream, and that expert assessment may be required in many cases. Given the strong impact of tolerant species on VIX EQR-values, a simple automatic recommendation of "expert judgement is required" could be delivered from the data host whenever tolerant species are present in survey data.

From a wider international perspective, fish indices based on general classification of groups of species into guilds, e.g. species tolerant or intolerant to environmental perturbation, should be used with caution unless there is strong evidence for the groupings being relevant from an assessment perspective. Assigned tolerance classifications are likely only valid under certain conditions, which must be thoroughly defined in order to conduct a proper assessment of ecological status or integrity. Context and life-stage specificity of tolerance is likely a common characteristic of many species classified as "tolerant". Hence, defining a species' tolerance requires a thorough specification of the conditions and life-stages for which the tolerance applies to, and survey data need to be assessed in relation to survey site characteristics with this in mind.

The presented results point to the importance of having an adaptive strategy for status classification based on biotic indices. Indices may have to change over time when inadvertent effects are discovered, as part of an adaptive management process. Biotic indices generally represent simplifications of complex environments with intricate ecological interactions present. Thus, they should be regarded as one tool in a larger tool-box for determining the 'true' ecological status of a water body and not the ultimate answer in themselves. Indices can often be improved when knowledge about the ecosystems is improved, a cause of action which is suggested here. In the end, assessment must relate to the knowledge and application of the user. Since the European eel is used as a tolerant indicator species in several European fish indices (e.g., Belpaire et al., 2000; Pont et al., 2006; Beier et al., 2007; Vehanen et al., 2010), similar effects as demonstrated here may be present for other fish indices as well, albeit likely with different effect magnitudes.

5. Conclusions

This study identifies issues with assigning European eel as a tolerant species for the fish-based index VIX, with the main problem being that it generates contradictions between the aim to reach 'Good' ecological status and eel population recovery in freshwaters. Success in strengthening the eel population according to the Swedish Eel Management Plan will likely reduce the ecological status of Swedish rivers, as long as VIX is used in the status classification without further post-calculation evaluation or expert judgement. Until the identified issues are resolved, e.g., by implementing a new or updated fish-based index for Swedish conditions, ecological status classification using fish of Swedish rivers must rely partially on expert judgement based on knowledge about local ecological conditions, river community- and ecosystem ecology and the statistical properties of VIX. The presented results are not evidence for Swedish rivers being assessed as having unjustifiably low ecological status – it is indeed a possible situation, but it would have to be assessed on a case-by-case basis. Using complementary, more holistic, survey approaches such as eDNA metabarcoding (Blancher et al., 2022) could potentially improve the overall fish-based assessment, since larger parts of the river fish community in a river water body could be assessed in comparison to wading electrofishing (i.e. more types of habitats could be assessed). This could give a more balanced picture of the abundance of tolerant species not typically found in shallow wadable habitats.

CRediT authorship contribution statement

Joacim Näslund: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Håkan Wickström:** Investigation, Writing – review & editing. **Erik Degerman:** Conceptualization, Investigation, Writing – review & editing. **Josefin Sundin:** Investigation, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data and R code are available at the open figshare repository (https://doi.org/10.6084/m9.figshare.19434581) https://figshare.com/s/bbcf12c5cd6772703bff. All electrofishing data are also available through the SERS database: https://www.slu.se/elfiskeregistret.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109537.

References

Almer, B., Dickson, W., Ekström, C., Hörnström, E., Miller, U., 1974. Effects of acidification on Swedish lakes. Ambio 3, 30–36. https://www.jstor.org/stable/4312039.

Ask, L., Berntsson, K.-E., Holmberg, B., 1971. Olika vattens attraktivitet på ålyngel. Information från Sötvattenslaboratoriet, Drottningholm 1971-14, 1-11.

Bartoń, K., 2020. MuMIn: Multi-model inference. Version 1.43.17. CRAN. https://CRAN.R-project.org/package=MuMIn.

Beier, U., Degerman, E., Sers, B., Bergquist, B., Dahlberg, M., 2007. Bedömningsgrunder för fiskfaunans status i rinnande vatten – utveckling och tillämpning av VIX (Environmental quality criteria to determine the status of fish in running waters – development and application of VIX). Fiskeriverket informerar (Finfo) 2007:5. Gothenburg: Swedish Board of Fisheries. https://www.havochvatten.se/download/18.64f5b3211343cffddb2800018314/1348912834442/finfo2007_5.pdf.

Belpaire, C., Smolders, R., Vanden Auweele, I., Ercken, D., Breine, J., Van Thuyne, G., Ollevier, F., 2000. An Index of Biotic Integrity characterizing fish populations and the ecological quality of Flandrian water bodies. Hydrobiologia 434, 13–33. https://doi.org/10.1023/A:1004026121254.
Belpaire, C., Hodson, P., Pierron, F., Freese, M., 2019. Impact of chemical pollution on Atlantic eels: Facts, research needs, and implications for management. Curr. Opin. Environm. Sci. Health 11, 26–36. https://doi.org/10.1016/j.coesh.2019.06.008.
Benejam, L., Alcaraz, C., Benito, J., Caiola, N., Casals, F., Maceda-Veiga, A., de Sostoa, A., García-Berthou, E., 2012. Fish catchability and comparison of four electrofishing crews in Mediterranean streams. Fish. Res. 123–124, 9–15. https://doi.org/10.1016/j.fishres.2011.11.022.
Bergquist, B., Degerman, E., Petersson, E., Sers, B., Stridsman, S., Winberg, S., 2014. Standardiserat elfiske i vattendrag – en manual med praktiska råd. Aqua reports 2014:15. 165 pp. Drottningholm: Swedish University of Agricultural Sciences, Department of Aquatic Resources. https://pub.epsilon.slu.se/12124/.
Bevacqua, D., Meliá, P., Gatto, M., De Leo, G.A., 2015. A global viability assessment of the European eel. Global Change Biol. 21, 3323–3335. https://doi.org/10.1111/gcb.12972.
Birk, S., Bonne, W., Borja, A., Brucet, S., Courrat, A., Poikane, S., Solimini, A., van de Bund, W., Zampoukas, N., Hering, D., 2012. Three hundred ways to assess Europe's surface waters: an almost complete overview of biological methods to implement the Water Framework Directive. Ecol. Indic. 18, 31–41. https://doi.org/10.1016/j.ecolind.2011.10.009.
Blancher, P., Lefrançois, E., Rimet, F., Vasselon, V., Argillier, C., Arle, J., Beja, P., Boets, P., Boughaba, J., Chauvin, C., Deacon, M., Duncan, W., Ejdung, G., Erba, S., Ferrari, B., Fischer, H., Hänfling, B., Haldin, M., Hering, D., Hette-Tronquart, N., Hiley, A., Järvinen, M., Jeannot, B., Kahlert, M., Kelly, M., Kleinteich, J., Koyuncuoğlu, S., Krenek, S., Langhein-Winther, S., Leese, F., Mann, D., Marcel, R., Marcheggiani, S., Meissner, K., Mergen, P., Monnier, O., Narendja, F., Neu, D., Pinto, V.O., Pawlowska, A., Pawlowski, J., Petersen, M., Poikane, S., Pont, D., Renevier, M.-S., Sandoy, S., Svensson, J., Trobajo, R., Zagyva, A.T., Tziortzis, I., van der Hoorn, B., Vasquez, M.I., Walsh, K., Weigand, A., Bouchez, A., 2022. A strategy for successful integration of DNA-based methods in aquatic monitoring. Metabarcoding Metagenom. 6, 215–226. https://doi.org/10.3897/mbmg.6.85652.
Blomqvist, P., 2017. Biologisk undersökning av fiskfaunan inom Fylleåns kalkningsprojekt 2017: En undersökning av åtta elfiskelokaler. Länsstyrelsen i Hallands län Meddelande 2018:3. 37 pp. Halmstad: Länsstyrelsen i Hallands län, Enheten för naturvård & miljöövervakning. https://www.lansstyrelsen.se/halland/tjanster/publikationer/20183-biologisk-undersokning-av-fiskfaunan-inom-fylleans-kalkningsprojekt-2017.html.
Boëtius, I., Boëtius, J., 1985. Lipid and protein content in *Anguilla anguilla* during growth and starvation. Dana 4, 1–17. https://www.aqua.dtu.dk/-/media/institutter/aqua/publikationer/dana/dana_vol_4_pp_1_17.pdf.
Bohlin, T., Hamrin, S., Heggberget, T.G., Rasmussen, G., Saltveit, S.J., 1989. Electrofishing – theory and practice with special emphasis on salmonids. Hydrobiologia 173, 9–43. https://doi.org/10.1007/BF00008596.
Breine, J., Simoens, I., Goethals, P., Quataert, P., Ercken, D., Van Liefferinghe, C., Belpaire, C., 2004. A fish-based index of biotic integrity for upstream brooks in Flanders (Belgium). Hydrobiologia 522, 133–148. https://doi.org/10.1023/B:HYDR.0000029991.42922.a4.
Brundin, L., 1939. Resultaten av under perioden 1917–1935 gjorda fiskinplanteringar i svenska sjöar. Meddelanden från Statens undersöknings- och försöksanstalt för sötvattensfisket 16, 1–41.
CEN (European Committee for Standardization), 2003. Water Quality – Sampling of Fish with Electricity. European Standard. European Committee for Standardization, Ref. No. EN 14011:2003.
Council of the European Union, 2007. Council Regulation (EC) No 1100/2007 of 18 September 2007 establishing measures for the recovery of the stock of European eel. Official Journal of the European Union L 248, 22.9.2007, p. 17–23. http://data.europa.eu/eli/reg/2007/1100/oj.
County Board of Halland, 2019. Utvärdering av kalkningens effekter i vattendrag i Hallands län. Del 3 Målområden i länets norra del. Länsstyrelsen i Hallands län Meddelande 2019:06. 366 pp. Halmstad: Länsstyrelsen i Hallands län, Naturvårdsenheten. https://www.lansstyrelsen.se/halland/tjanster/publikationer/201906-utvardering-av-kalkningens-effekter-i-vattendrag-i-hallands-lan.html.
Degerman, E., Sers, B., 1992. Fish assemblages in Swedish streams. Nord. J. Freshw. Res. 67, 61–71.
Degerman, E., Fogelgren, J.-E., Tengelin, B., Thörnelöf, E., 1986. Occurrence of salmonid parr and eel in relation to water quality in small streams on the west coast of Sweden. Water Air Soil Pollut. 30, 665–671. https://doi.org/10.1007/BF00303330.
Degerman, E., Petersson, E., Sers, B., 2012. Analys av elfiskedata. Länsstyrelsen i Jönköpings län meddelande 2012:12. Jönköping: Länsstyrelsen i Jönköpings län. https://www.lansstyrelsen.se/jonkoping/tjanster/publikationer/2012/201212-analys-av-elfiskedata.html.
Degerman, E., Tamario, C., Watz, J., Nilsson, P.A., Calles, O., 2019. Occurrence and habitat use of European eel (*Anguilla anguilla*) in running waters: lessons for improved monitoring, habitat restoration and stocking. Aquat. Ecol. 53, 639–650. https://doi.org/10.1007/s10452-019-09714-3.
Dekker, W., 2016. Management of the eel is slipping through our hands! Distribute control and orchestrate national protection. ICES J. Mar. Sci. 73, 2442–2452. https://doi.org/10.1093/icesjms/fsw094.
Dekker, W., Casselman, J.M., Cairns, D.K., Tsukamoto, K., Jellyman, D., Lickers, H., 2003. Worldwide decline of eel resources necessitates immediate action: Québec Declaration of Concern. Fisheries 28, 28–30.
Dekker, W., van Gemert, R., Bryhn, A., Sjöberg, N., Wickström, H., 2021. Assessment of the eel stock in Sweden, spring 2021. Fourth post-evaluation of the Swedish eel management. Aqua reports 2021:12, 108 pp. Drottningholm: Swedish University of Agricultural Sciences, Department of Aquatic Resources. https://www.slu.se/globalassets/ew/org/inst/aqua/externwebb/sidan-publikationer/aqua-reports-2021-12.pdf.
Donadi, S., Sandin, L., Tamario, C., Degerman, E., 2019. Country-wide analysis of large wood as a driver of fish abundance in Swedish streams: which species benefit and where? Aquat. Conserv. Mar. Freshw. Ecosyst. 29, 706–716. https://doi.org/10.1002/aqc.3107.
European Commission, 2000. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for community action in the field of water policy. Official Journal of the European Communities 43:L 327/1, 22 December 2000. http://data.europa.eu/eli/dir/2000/60/oj.
European Commission, 2003. Common Implementation Strategy for the Water Framework Directive. Guidance document no. 7. Monitoring under the Water Framework Directive. Luxembourg: Office for Official Publications of the European Communities.
European Commission, 2018. Commission Decision (EU) 2018/229 of 12 February 2018 establishing, pursuant to Directive 2000/60/EC of the European Parliament and of the Council, the values of the Member State monitoring system classifications as a result of the intercalibration exercise and repealing Commission Decision 2013/480/EU. Official Journal of the European Union L 47, 20 February 2018. http://data.europa.eu/eli/dec/2018/229/oj.
European Commission, 2022. Proposal for a regulation of the European Parliament and of the Council on nature restoration. COM(2022) 304 final, 2022/0195 (COD). Brussels: European Commission. *https://environment.ec.europa.eu/publications/nature-restoration-law_en*.
Félix, P.M., Costa, J.L., Monteiro, R., Castro, N., Quintella, B.R., Almeida, P.R., Domingos, I., 2020. Can a restocking event with European (glass) eels cause early changes in local biological communities and its ecological status? Global Ecol. Conserv. 21, e00884.
Fjellheim, A., Raddum, G.G., Sagen, T., 1985. Effect of aluminium at low pH on the mortality of elvers (*Anguilla anguilla*), a laboratory experiment. Int. Verein. Theor. Angew. Limnol. Verhandl. 22, 2544–2547. https://doi.org/10.1080/03680770.1983.11897720.
Forsberg, G., 1986. Nypigmenterade ålyngels överlevnad och födoval i en försurad sjö. Information från Sötvattenslaboratoriet, Drottningholm 1986–8, 1–29.
GBIF, 2020. Global Biodiversity Information Facility. GBIF, Copenhagen. Available at: https://www.gbif.org/occurrence/map?q=Anguilla%20anguilla&country=SE.
Geeraerts, C., Belpaire, C., 2010. The effects of contaminants in European eel: a review. Ecotoxicology 19, 239–266. https://doi.org/10.1007/s10646-009-0424-0.
Halvorsen, S., Korslund, L., Gustavsen, P.Ø., Slettan, A., 2020. Environmental DNA analysis indicates that migration barriers are decreasing the occurrence of European eel (*Anguilla anguilla*) in distance from the sea. Global Ecol. Conserv. 24, e01245.
HELCOM, 2013. Species Information Sheet: Anguilla anguilla. HELCOM Red List Fish and Lamprey Species Expert Group, Helsinki https://helcom.fi/media/red-list-species-information-sheet/HELCOM-Red-List-Anguilla-anguilla.pdf.
ICES, 2021. European eel (*Anguilla anguilla*) throughout its natural range. In: Report of the ICES Advisory Committee, 2021. ICES Advice 2021, ele.2737.nea. 10.17895/ices.advice.7752.
Karr, J.R., 1981. Assessment of biotic integrity using fish communities. Fisheries 6, 21–27. https://doi.org/10.1577/1548-8446(1981)006<0021:AOBIUF>2.0.CO;2.
Kullander, S.O., Nyman, L., Jilg, K., Delling, B., 2012. Nationalnyckeln till Sveriges flora och fauna. Ryggsträngsdjur: Strålfeniga fiskar. Chordata: Actinopterygii. Uppsala: SLU Artdatabanken.
Larsen, B.M., Hesthagen, T., Thorstad, E.B., Diserud, O.H., 2015. Increased abundance of European eel (*Anguilla anguilla*) in acidified Norwegian rivers after liming. Ecol. Freshw. Fish 24, 575–583. https://doi.org/10.1111/eff.12170.
Lasne, E., Acou, A., Vila-Gispert, A., Laffaille, P., 2008. European eel distribution and body condition in a river floodplain: effect of longitudinal and lateral connectivity. Ecol. Freshw. Fish 17, 567–576. https://doi.org/10.1111/j.1600-0633.2008.00307.x.
Lilljeborg, W., 1891. Sveriges och Norges fiskar. Tredje delen (Vol. 3). Upsala: W. Schultz.
Lobon-Cervia, J., Bernat, Y., Rincon, P.A., 1990. Effects of eel (*Anguilla anguilla*) removals from selected sites of a stream on its subsequent densities. Hydrobiologia 206, 207–216. https://doi.org/10.1007/BF00014086.
López-Olmeda, J.F., López-García, I., Sánchez-Muros, M.J., Blanco-Vives, B., Aparicio, R., Sánchez-Vázquez, F.J., 2012. Daily rhythms of digestive physiology, metabolism and behaviour in the European eel (*Anguilla anguilla*). Aquacult. Int. 20, 1085–1096. https://doi.org/10.1007/s10499-012-9547-z.
Lundberg, R., 1899. Om svenska insjöfiskars utbredning (On the distribution of Swedish freshwaterfishes). Meddel. Kongl. Landtbruksstyrelsen 58, 1–87.
Maceda-Veiga, A., De Sostoa, A., 2011. Observational evidence of the sensitivity of some fish species to environmental stressors in Mediterranean rivers. Ecol. Indic. 11, 311–317. https://doi.org/10.1016/j.ecolind.2010.05.009.
Mihov, S., 2010. Development of fish based index for assessing ecological status of Bulgarian rivers (BRI). Biotechnol. Biotechnol. Equip. 24, 247–256. https://doi.org/10.1080/13102818.2010.10817844.
Noble, R.A.A., Cowx, I.G., Goffaux, D., Kestemont, P., 2007. Assessing the health of European rivers using functional ecological guilds of fish communities: standardizing species classification and approaches to metric selection. Fish. Managem. Ecol. 14, 381–392. https://doi.org/10.1111/j.1365-2400.2007.00575.x.
Oberdorff, T., Pont, D., Hugueny, B., Porchers, J.-P., 2002. Development and validation of a fish-based index for the assessment of 'river health' in France. Freshw. Biol. 47, 1720–1734. https://doi.org/10.1046/j.1365-2427.2002.00884.x.

Olivereau, M., Olivereau, J.M., 1997. Long-term starvation in the European eel: general effects and responses of pituitary growth hormone-(GH) and somalactin-(SL) secreting cells. Fish Physiol. Biochem. 17, 261–269. https://doi.org/10.1023/A:1007766426512.

Pike, C., Crook, V., Gollock, M., 2020. *Anguilla anguilla*. The IUCN Red List of Threatened Species 2020, e.T60344A152845178. https://doi.org/10.2305/IUCN.UK.2014-1.RLTS.T60344A45833138.en.

Podda, C., Palmas, F., Pusceddu, A., Sabatini, A., 2021. Hard times for catadromous fish: the case of the European eel *Anguilla anguilla* (L. 1758). Adv. Oceanogr. Limnol. 12, 9997. 10.4081/aiol.2021.9997.

Pont, D., Hugueny, B., Beier, U., Goffaux, D., Melcher, A., Noble, R., Rogers, C., Roset, N., Schmutz, S., 2006. Assessing river biotic condition at a continental scale: a European approach using functional metrics and fish assemblages. J. Appl. Ecol. 43, 70–80. https://doi.org/10.1111/j.1365-2664.2005.01126.x.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna https://www.R-project.org/.

Segurado, P., Santos, J.M., Pont, D., Melcher, A.H., Jalon, D.G., Hughes, R.M., Ferreira, M.T., 2011. Estimating species tolerance to human perturbation: Expert judgment versus empirical approaches. Ecol. Indic. 11, 1623–1635. https://doi.org/10.1016/j.ecolind.2011.04.006.

Sers, 2020. Swedish Electrofishing RegiSter – SERS. Swedish University of Agricultural Sciences, Department of Aquatic Resources https://www.slu.se/elfiskeregistret.

SLU Artdatabanken, 2020. Rödlistade arter i Sverige. Uppsala: Swedish University of Agricultural Sciences.

Soukup, P., Näslund, J., Höjesjö, J., Boukal, D.S., 2022. From individuals to communities: habitat complexity affects all levels of organization in aquatic environments. WIREs Water 9, e1575.

Steendam, C., Verhelst, P., Van Wassenbergh, S., De Meyer, J., 2020. Burrowing behaviour of the European eel (*Anguilla anguilla*): effects of life stage. J. Fish Biol. 97, 1332–1342. https://doi.org/10.1111/jfb.14481.

Swedish Agency for Marine and Water Management, 2018. Fisk i vattendrag – vägledning för statusklassificering. Havs- och vattenmyndighetens rapport 2018:37. 20 pp. Gothenburg: Swedish Agency for Marine and Water Management. https://www.havochvatten.se/data-kartor-och-rapporter/rapporter-och-andra-publikationer/publikationer/2018-12-10-fisk-i-vattendrag—vagledning-for-statusklassificering.html.

Swedish Agency for Marine and Water Management, 2019. Havs- och vattenmyndigetens föreskrifter om klassificering och miljökvalitetsnormer avseende ytvatten. Havs- och vattenmyndighetens författningssamling HVMFS 2019:25. Gothenburg: Swedish Agency for Marine and Water Management. https://www.havochvatten.se/vagledning-foreskrifter-och-lagar/foreskrifter/register-vattenforvaltning/klassificering-och-miljokvalitetsnormer-avseende-ytvatten-hvmfs-201925.html.

Tamario, C., Calles, O., Watz, J., Nilsson, P.A., Degerman, E., 2019. Coastal river connectivity and the distribution of ascending juvenile European eel (*Anguilla anguilla* L.): implications for conservation strategies regarding fish-passage solutions. Aquat. Conserv. Mar. Freshw. Ecosyst. 29, 612–622. https://doi.org/10.1002/aqc.3064.

The Swedish Government, 2020. Nationell plan för moderna miljövillkor. Regeringsbeslut 18, M2019/01768/nm. Stockholm: Swedish Ministry of the Environment. https://www.havochvatten.se/arbete-i-vatten-och-energiproduktion/vattenkraftverk-och-dammar/nationell-plan-for-omprovning-av-vattenkraft/nationell-plan-for-omprovning-av-vattenkraft.html.

The Swedish Parliament, 2004a. Miljöbalk (1998:808), 5 kap. Miljökvalitetsnormer och miljökvalitetsförvaltning. http://www.riksdagen.se/sv/Dokument-Lagar/Lagar/Svenskforfattningssamling/Miljobalk-1998808_sfs-1998-808/?bet=1998:808#K5.

The Swedish Parliament, 2004b. Vattenförvaltningsförordning (2004:660). https://rkrattsbaser.gov.se/sfst?bet=2004:660.

The Swedish Parliament, 2017. Förordning (2017:868) med länsstyrelseinstruktion. https://www.riksdagen.se/sv/dokument-lagar/dokument/svensk-forfattningssamling/forordning-2017868-med-lansstyrelseinstruktion_sfs-2017-868.

Trebitz, A.S., Hill, B.H., McCormick, F.H., 2003. Sensitivity of indices of biotic integrity to simulated fish assemblage changes. Environ. Manage. 32, 499–515. https://doi.org/10.1007/s00267-003-0061-y.

van Ginneken, V.J.T., Onderwater, M., Olivar, O.L., van den Thillart, G.E.E.J.M., 2001. Metabolic depression and investigation of glucose/ethanol conversion in the European eel (*Anguilla anguilla* Linnaeus 1758) during anaerobiosis. Thermochim. Acta 373, 23–30. https://doi.org/10.1016/S0040-6031(01)00463-4.

Vehanen, T., Sutela, T., Korhonen, H., 2010. Environmental assessment of boreal rivers using fish data – a contribution to the Water Framework Directive. Fish. Manage. Ecol. 17, 165–175. https://doi.org/10.1111/j.1365-2400.2009.00716.x.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. J. Open Source Software 4, 1686. 10.21105/joss.01686.