

Assessment of mortality during trap and transport in adult European eel

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ABSTRACT

Many fluvial water systems suffer from reduced or completely disrupted connectivity due to human activities, causing negative effects for species and ecosystems. Artificial transport past migration barriers, so called trap and transport, can be used as a management tool to mitigate fish population declines. The efficiency of trap and transport is, however, rarely evaluated, in particular for downstream transport of catadromous species such as the European eel. In this study we analysed seven years of trap and transport data (2016–2022), encompassing nearly 58,000 transported adult eels, to evaluate mortality during all steps of the trap and transport process (i.e., mortality in fishing gear, during holding, and during transport). We found that mortality rates were generally low for all steps, 0.2–1.4 % in the fishing gear, 0.6–2 % during holding, and 0.03–0.17 % during transport (percent per year on average), compared to expected mortality in turbines (estimated turbine mortality in the investigated area: 70% to >99 %). The factors affecting mortality differed across the trap and transport steps, with year, season (day of year), temperature, and mortality in the previous step (i.e., indicative of general stress in the previous step, and/or poor condition) being the factors having an effect. We conclude that trap and transport may cause relatively low mortality compared to turbines, but since it requires maintenance and human interference, restoration of connectivity should be the long-term goal.

1. Introduction

Water connectivity is currently and increasingly becoming disrupted due to human activities, and has been so for decades, which can lead to loss of biodiversity and disturbed ecosystems (Kindlmann and Burel, 2008; Grafton et al., 2013; Crook et al., 2015; Hidalgo et al., 2017). This is evident in rivers, where man-made migration barriers hamper the link between freshwater and marine environments (Crook et al., 2015). Rivers provide essential ecosystem services, such as a wide variety of habitats for numerous organisms, biogeochemical transformation of energy and matter, and physical transformation of the landscape (Limburg et al., 2001; Crook et al., 2015). Since organisms distribute non-randomly in the environment, dams and hydropower plants pose a severe threat through blocked migratory routes, fragmented habitats, and direct mortality (Jonsson et al., 1999). In addition, artificial waterbodies, such as reservoirs, often have limited or no flow connectivity with the surrounding catchment, thereby hindering migration to and from such habitats (Piper et al., 2020). Such issues can be mitigated by restoring connectivity through removal of migration obstacles or by constructing fish passage solutions. While awaiting such actions,

artificial transport (assisted migration) around migration barriers, so called trap and transport or trap and haul, can be used as a management tool to mitigate fish population declines (Ward et al., 1997). Trap and transport consist of active–manual (e.g., gill net, fyke net) or passive–automatic (e.g., elevator, trap) capture of fish above or below a barrier, followed by upstream or downstream relocation (Schmetterling, 2003; McDougall et al., 2013). It is for example used for upstream transport of adult salmonids (Nyqvist et al., 2019; Weigel et al., 2019), sturgeons (McDougall et al., 2013), and juvenile eel (Bogdan and Waluga, 1980; Boerrigter et al., 2015), and for downstream transport of adult eel (Piper et al., 2020), and juvenile salmonids (Ward et al., 1997; Evans et al., 2008). In general, trap and transport can be a good management measure if the alternative is to pass through one or several turbines where the accumulated fish passage success will be low, leading to a likely death (Algera et al., 2020). However, in order for this method to be beneficial at the population level, the transported fish need to continue their up- or downstream migration, eat and grow, then return the same path (in case of juvenile transport), reach a suitable spawning habitat, and succeed with spawning.

The European eel, *Anguilla anguilla*, is one species for which trap and

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transport is used as a management tool (Piper et al., 2020). The species is critically endangered (Pike et al., 2020) with a recruitment decrease of 92–99 % (ICES, 2024). It is hence essential to ensure that conservation efforts work as intended. The European eel is an obligate migratory species (Schmidt, 1922; Wright et al., 2022), and they are affected by migration barriers both during their upstream migration as recruiting juveniles, and during their downstream migration as adult silver eels (Tamarío et al., 2019; Algera et al., 2020; ICES, 2024). The European eel has a large distribution, covering all of Europe and northern Africa (Schmidt, 1912; Pike et al., 2020), with one panmictic stock across the entire distribution area (Enbody et al., 2021). A large proportion of the European eel's habitat is affected by migration barriers (Algera et al., 2020; Duarte et al., 2021), and barriers is listed as one of the causes for the population decline (ICES, 2024). Few migration barriers are equipped with any form of fish passage solution (Algera et al., 2020). Upstream migration can be aided by eel ladders, eel collector traps, or similar (Drouineau et al., 2015; Tamarío et al., 2019). Eels are also excellent climbers and can climb barriers or pass a barrier by migrating around it on land (Legault, 1988; Kerr et al., 2015). Hence, upstream migration is, in general, not the main issue with regards to barriers for the European eel, and they are present in many areas upstream of migration barriers (Tamarío et al., 2019; ICES, 2024). In addition, restocking, i.e., moving glass eels from areas with a supposed excess to areas with a deficit (ICES, 2016), is conducted also to areas upstream of migration barriers. To ensure that restocking functions as a successful management measure, it is important to ensure that the restocked eels can migrate downstream when they are adults. Similarly, naturally recruited eels present upstream of migration barriers must also be ensured a safe downstream migration route. Unfortunately, this is a much more difficult problem to solve, and the European eel suffer high levels of turbine mortality as silvering downstream migrants (cumulative mortalities with multiple dams: 70 % to >99 %, Calles and Christiansson, 2012; Leonardsson, 2012). Safe downstream passage can be achieved with the combination of angled bar racks and nature-like fishways (Calles et al., 2021). In many instances however, bar racks or other behavioural guidance past turbines is either extremely challenging, expensive, or impossible to install or operate, particularly in large systems (Algera et al., 2020). These are some of the main reasons why trap and transport is performed on the European eel.

Studies evaluating the efficiency of trap and transport have mainly focussed on upstream transport of anadromous species, finding that it can be a useful tool to aid spawning migration of salmonids (Nyqvist et al., 2019; Weigel et al., 2019) and sturgeon (Finney et al., 2006; McDougall et al., 2013). Fish may however move downstream after upstream transport (Swanberg, 1997), and such fallback behaviour could result in migratory delays, injury and mortality if the fish go back through the hydropower turbines (Boggs et al., 2004), or failed spawning/migration if there is no (or inefficient) alternative passage routes (Hagelin et al., 2016). Increased predation risk and physiological changes induced by stress have also been observed among transported individuals (Kemp, 2015). The efficiency of downstream transport has received far less attention (Lusardi and Moyle, 2017), in particular of catadromous species (Piper et al., 2020), with a few exceptions (Béguer-Pon et al., 2018). This follows a general pattern that salmonids are studied to a much greater extent than other diadromous species (Algera et al., 2020). It is important that evaluations include catadromous species since trap and transport programs can provide management benefits, but come with challenges given its artificial nature. There are some indications that the trap and transport process seem to fulfil the intention for eel, since trap and transported adult eels from reservoirs showed similar migration patterns as resident river eel during the first part of their migration (in a river towards the sea, Piper et al., 2020). Transport can however result in increased metabolism and cause mortality, as shown in juvenile eels, elvers, in the context of moving eels used for restocking (Bogdan and Waluga, 1980; Boerrigter et al., 2015). Whether the same is true for adult eels, i.e., whether downstream trap

and transport can result in alteration of physiological condition and/or mortality, seems to be largely missing in the scientific literature. Preliminary analyses of stress (deduced from heart rate) during trap and transport of eel in Sweden indicate that heart rate was elevated during the entire transport process, suggesting that the eels experienced stress from this handling (Sundin et al., 2023). Such stress could have negative implications, and any mortality that occurs during trap and transport must be considered for this management tool.

Here, we used existing data on mortality rates from trap and transport data sheets from 2016 to 2022 to evaluate mortality in adult European eel during all steps of the trap and transport process. We predicted that factors suspected to be stressful, such as high water temperature, extended holding periods prior to transport, and long transport time, would increase mortality rates.

2. Material and methods

2.1. Trap and transport procedure

The trap and transport procedure investigated here consisted of collecting adult eels by fishing with pound nets and then keeping them in submerged fish corves or tanks on land until transport (Fig. 1). The eels were then transported in water filled tanks and released downstream of the migration barriers. Transport was done individually from one fisher/collection site to the release site, or by making stops at several fishers/collection sites along the transport route and releasing all at one release site (Fig. 1).

2.2. Origin of the trap and transport data sheets

Data used in this study were extracted from existing data sheets from trap and transport events conducted in Sweden 2016–2022, obtained via the Swedish Inland Fishermen's Federation (Svenska Insjöfiskarens Centralförbund, SIC: <http://www.insjofiskare.se>). Most, but not all, data sheets were from trap and transport events performed within Energiforsk's program called "Krafttag ål" (<https://energiforsk.se/en/>, <https://energiforsk.se/program/krafttag-ål/>). The program Krafttag ål is a voluntary agreement between several hydropower companies, and, at the commencement of the project, the Swedish Board of Fisheries (the former agency responsible for fisheries related matters in Sweden), now the Swedish Agency for Marine and Water Management (Dekker and Wickström, 2015). At some trap and transport locations, data sheets detailing mortality and additional parameters (see data management section below) were filled out by the fisher and the transporter conducting each respective trap and transport event. The data sheet was designed by a researcher at the Department of Aquatic resources, Swedish University of Agricultural Sciences (hence, the project was partly initiated and executed by the hydropower industry, but the data sheet was designed by an independent researcher). Some trap and transport projects executed and funded outside of the Krafttag ål program also used these data sheets; those were also included in our analyses. Note that not all trap and transport projects executed in Sweden, funded by various actors, were included in our analyses. Only those that used the specific data sheet, and that had sent those data sheets to the Swedish Inland Fishermen's Federation, were included.

2.3. Data management

The existing data sheets analysed here were from trap and transport of adult eel from three catchment areas, each encompassing several locations and fishers, in south-western Sweden (Fig. 2). The data sheets contained data on name of fisher, fishing location, fishing gear, fishing/capture date (i.e., the date when the fishing gear was emptied), type of holding facility (submerged corf or flow through tank on land), transport date, transport time, name of transporter, size of transport tank(s), water temperature (in corf/tank at the time of fish pickup and in the transport



Fig. 1. Conceptual illustration of the trap and transport procedure (yellow dashed arrow along the vehicle transport route and yellow circles to the left and right in the illustration), in comparison to the alternative route through one or several hydropower plants and turbines (pink arrow along the route through the hydropower plant, circle to the left in the illustration, and cross in the turbine), and compared to the natural migration route in a system without migration barriers (blue arrow along the river route and circles to the left and right in the illustration). The trap and transport procedure for adult eel consists of collection from fishing gear or traps/fish collectors upstream of migration barriers, holding in submerged fish corves or tanks on land (to the left in the illustration), transport past the migration barriers, and release downstream of the migration barriers, towards the sea. ©Susanne Landis, SCIENSTRATION.

tank), and number of dead eels in the fishing gear, during holding, and after transport. The data sheets did not contain information about the size of the eels. Previous assessments of trap and transported eels within the project Krafttag ål however indicated that the majority of eels were classified as migrants according to Durif's silver index (stage FIV-FV, Durif et al., 2005; Durif et al., 2009), with an average weight of 1.3 kg and length of 850 mm (Dekker and Wickström, 2015; Wickström, 2015). Since the weight and length data from the previous assessments were from trap and transport events from the same project as the data analysed here (i.e., same eel collection methods and sites), we assume that the eels in the data analysed here would be approximately in the same size range, although this is not known for certain.

The eels had been caught with pound nets in freshwater lakes by commercial fishers and were then held near the site of capture until they were picked up for transport. The eels were either held in submerged corves, or on land in flow-through tanks. The submerged, perforated, corves ranged from 200 to 300 L, and the flow through tanks on land from 2000 to 3000 L. The fishers were fishing continuously until transport, adding more eels to the corves and tanks, and using more corves and tanks if the eel density per corve/tank became too high (i.e., avoiding risk to the welfare of the eels). Data on holding density could not be derived since information on the exact number of eels per corve/tank was not specifically asked for in the data sheet. The fishers relied on their experience to avoid overcrowding. Holding time (number of days kept in corve/tank) could not be derived from the data sheets since eels were added continuously to the corves/tanks. Instead, number of days between the earliest fishing/capture date and the transport date was used to calculate maximum holding time. Water temperature in corves and tanks were noted at the day of transport. The transporter collected eels from one up to six locations (from several fishers) per transport event, and each transport event was concluded within a day. The transporter noted the time of collection and the temperature of the tanks on the transport vehicle at each stop along the route. The eels were transported in tanks ranging from 400 to 1500 L (during instances when many eels were transported, a larger truck with several tanks was used). Eels from one or more locations and/or fishers were sometimes placed in the same transport tank, or distributed across two or more tanks, without noting the exact number of eels per tank. This means that the exact number of eels per tank (i.e., exact density) could not be derived, while number of eels per transport was known. In our analyses, all data relating to the transport, including temperature, were therefore averaged for each transport event. I.e., each transport is an effective observation that is an average based on data from up to six locations/fishers depending on the specific transport event. Once the release site had been

reached, transport time and number of eels that died during transport were noted when the eels were released.

The data from the data sheets ($N = 126$) were first entered into a spreadsheet and validated. Occurrences of zero values and missing data were checked with a contact person at SIC to confirm whether there were either a zero to report (a true zero value) or if data were missing (i.e., the zero corresponded to "no recording"). Due to mixed usage of zeros and empty cells, some data sheets could not be included in the analysis ($n = 25$), leaving 101 data sheets for the analyses, corresponding to 101 transport events encompassing 302 fishing/catch and holding events.

2.4. Statistical analyses

Data from the data sheets enabled us to evaluate mortality rates during the entire trap and transport process starting with mortality in the fishing gear, followed by mortality during holding, and finally the mortality rates after completed transport. The data were analysed as the proportion of dead eels during each phase in the trap and transport chain. Three logistic regression models were fitted with the proportion of dead eels reported in gear, during holding, and after transport, as the respective response variables. Each of these models had their own set of covariates based on the information available from the data sheets.

It was not possible to perform one single analysis across the trap and transport process since the level of data resolution differed between the three steps. Mortality in fishing gear and mortality during holding had the same number of observations (number of fishing/holding events, $n = 302$). For mortality during transport, on the other hand, data were analysed per transport event ($n = 101$), rather than per pick-up event per fisher, resulting in a lower number of observations compared to the other two analyses. This was done since the transport vehicle usually had more than one tank, and since eels from one or more locations and/or fishers were sometimes placed in the same transport tank, or distributed across two or more tanks, without noting the exact number of eels per tank, meaning that the exact number of eels per transport tank was unknown, while number of eels per transport event was known.

For the analysis of mortality in fishing gear we used a linear and quadratic effect of day of year, location, and year as explanatory variables. Day of year is a continuous variable (1–365) where the linear effect allows for an increasing effect for the first part of the year and the quadratic allows for a decreasing effect for the second part of the year (other patterns are also possible). Fishing location is a categorical variable encompassing where, how, and who was fishing. Year was also treated as a categorical variable that should capture potential variation

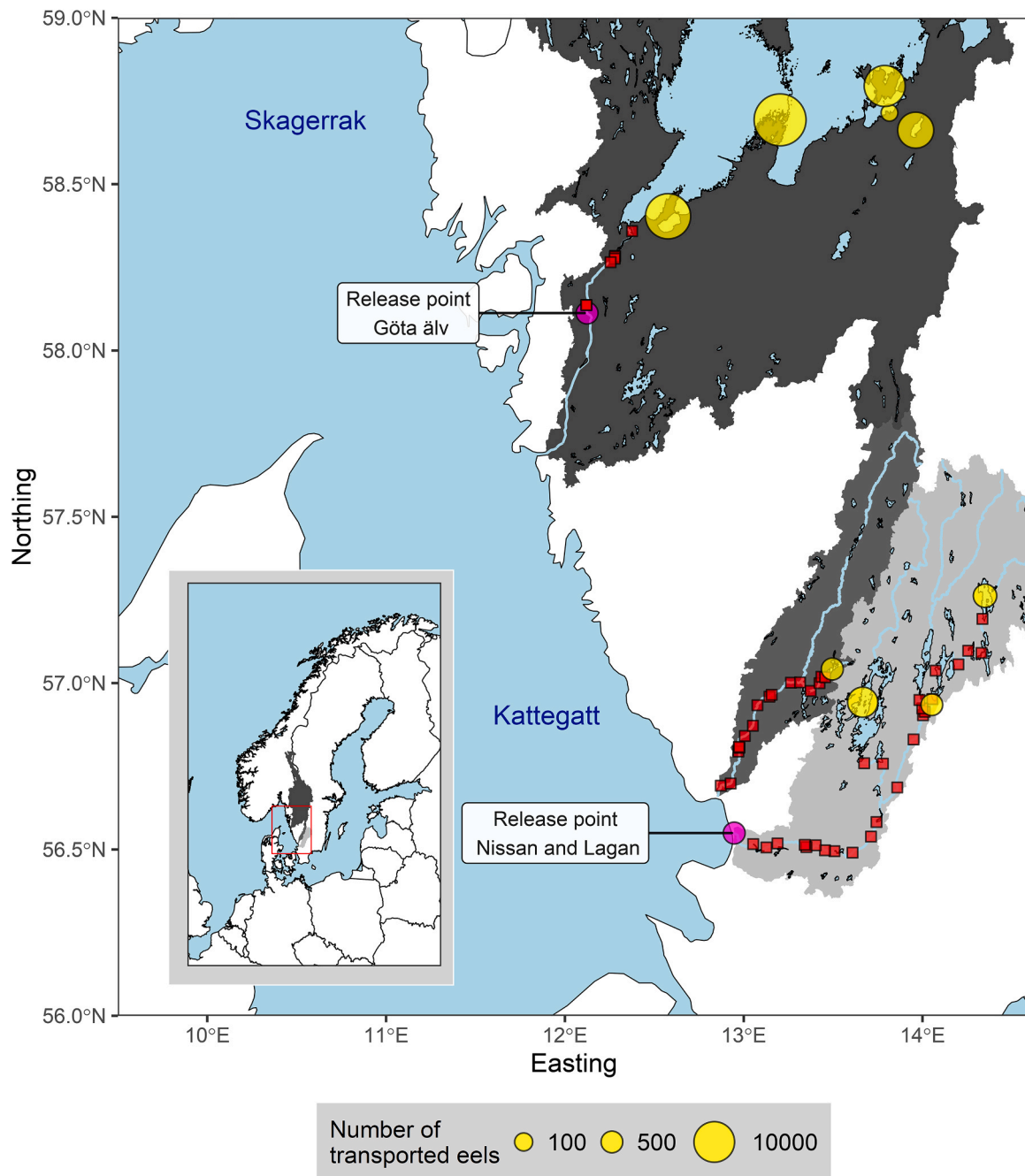


Fig. 2. Approximate collection sites (fishing sites, yellow circles) in south-western Sweden for trap and transport of adult European eel, and the respective approximate release sites (purple points) towards Kattegat and Skagerrak in the North Sea. The size of the yellow circles indicates the number of transported eels, shown as number of eels that survived the entire trap and transport process, from each location during 2016–2022 ($n = 101$ transport events, $n = 302$ fishing and holding events). Hydropower plants downstream of the collection site (i.e., that the eels were transported past) are shown in red squares; upstream plants and dams are not shown. The catchment areas are indicated in dark to light grey, from north to south: Göta älv, Nissan, and Lagan.

in mortality between years. These four variables were the only information available that could explain fishing gear mortality. In this model and the models below, the two day of year variables (linear and quadratic) were fitted jointly (Cade, 2015). This resulted in eight possible model combinations that were ranked by Akaike information criterion (AICc), with each explanatory variable included in four models. To estimate relative variable importance (RVI), in this model and the models below, we summed the AICc model weights for each model that included the explanatory variable. This step is described in detail below.

For the analysis of mortality during holding, eight explanatory

variables were available: a linear and quadratic effect of day of year, fishing location, year, proportion dead eels reported in the fishing gear (since mortality in the previous step can be indicative of general stress in the previous step, and/or poor condition of the eels in the fishing gear), corf/tank type (submerged corf or flow through tank on land), maximum number of days kept in corf/tank, and water temperature in corf/tank. The variable location was removed since the fishers at each location used either corves or tanks, and not a combination of the two, meaning that the effect of location and corf/tank was collinear. AICc showed that corf/tank had greater support than location, therefore location was removed from the analyses. Furthermore, the quadratic

effect of day of year were removed prior to model selection because it was not significant and the day of year effect was best explained by the linear term only. To investigate which variables had an effect on holding mortality, we performed model selection on a set of models that included all possible combinations of the six remaining explanatory variables. This resulted in 64 possible model combinations that were ranked by AICc, with each explanatory variable included in 32 models.

For the analysis of mortality during transport, variables were averaged for each transport event (as detailed above). Eleven explanatory variables were available: a linear and quadratic effect of day of year, proportion of dead eels reported in the fishing gear, maximum number of days kept in corf/tank, water temperature in corf/tank, the proportion of eels that were kept in a corf and that were kept in a tank before transport (0 for all in corf and 1 for all in tank), the proportion of dead eels reported in fish corf/tank, water temperature in the transport, difference in water temperature between corf/tank and transport tank, year, and transport time. The variable location was not included in any of the models since eels from several locations were transported together on the same day (as detailed above). Further, the variable water temperature in corf/tank was removed because it was correlated with water temperature in transport, and models with water temperature in transport had lower AICc than models with water temperature in corf/tank. Similar to the model on mortality in fishing gear, the linear and quadratic effect of day of year were fitted together. This resulted in ten explanatory variables and 512 models that were ranked by AICc, with each variable included in 256 models.

For the models described above, we calculated AICc weights (ω_i) and used these weights to rank the models. AICc weights are model probabilities that sum to 1 (Burnham et al., 2011). The closer the model weight is to 1, the more likely it is that the model is the best model given the data. The models' explanatory variables can also be ranked based on the model weights (Burnham and Anderson, 2004). The ranking of variables gives a relative variable importance (RVI) and is calculated by summing the AICc model weights (ω_+) for each model where the variable is present. RVI (ω_+) is presented on a scale from 0 to 1, where 1 is full support and 0 is no support for the variable having an effect on the response variable (Burnham and Anderson, 2004). RVI values for all parameters are presented in the results section below. A top ranking model does not imply that all variables included are significant at an $\alpha = 0.05$ (Sutherland et al., 2023), and hence, model summary statistics are included in the results section (Table 1). The AICc model rankings could not always determine one unequivocally best model, and because of this we used information from all models, and the variable parameters were averaged across models. Because our response variables were on the logit scale, model averaging should not be calculated on the untransformed parameters (Cade, 2015). Hence, model averages were calculated by making predictions for the fit and confidence intervals of each model and then transforming these to the original scale. Then weighted averages were calculated by using the model weights. The averages were calculated using shrinkage estimates, where parameters not included in the model takes the value zero (Bartón, 2022). This means that variables with low RVI will have model averaged estimates that approach zero. Model selection tables with the AICc ranking of all competing models are available as supplementary material (Tables S1–S3). The goodness-of-fit for each of the respective models was calculated using McFaddens' pseudo R^2 for logistic regression models (deviance of top model/deviance of null model, McFadden, 1974), with values between 0.2 and 0.4 representing excellent fits (McFadden, 1979). In addition, the goodness-of-fit for each respective model was also assessed using ROC-curves and area under the curve (AUC) values (Nam and D'Agostino, 2002; Carter et al., 2016).

To illustrate the potential effect of a specific predictor variable on mortality in fishing gear, during holding, and during transport, we plotted their model averaged partial regressions. This was done by allowing each focal predictor variable to vary across its range of values, and control for the remaining predictor variables in each model by fixing

Table 1

Parameter estimates and standard error (SE) from the best model for fishing gear mortality, mortality during holding, and mortality during transport, respectively, for adult European eel (*Anguilla anguilla*). The estimates and z-values indicate the strength and direction of the parameters on mortality, with associated p-values shown in the Pr(>|z|) column. Significance was determined at an alpha level of 0.05.

Response	Parameter	Estimate	SE	z-value	Pr(> z)	
Fishing gear	Intercept	-16.805	1.562	-10.76	< 0.001	
	Location B	-1.027	0.200	-5.12	< 0.001	
	Location C	-1.049	0.163	-6.45	< 0.001	
	Location D	-1.767	0.318	-5.56	< 0.001	
	Location E	-0.305	0.253	-1.21	0.227	
	Location F	-16.683	824.559	-0.02	0.984	
	Location G	-16.578	1147.357	-0.01	0.988	
	Location H	-16.414	1645.121	-0.01	0.992	
	Location I	-17.557	4253.396	0.00	0.997	
	Day of year linear	0.121	0.015	8.07	< 0.001	
	Day of year quadratic	-0.000	0.000	-8.11	< 0.001	
	Year 2017	-0.016	0.248	-0.06	0.949	
	Year 2018	0.452	0.224	2.02	0.043	
	Year 2019	-0.515	0.277	-1.86	0.063	
	Year 2020	-1.552	0.488	-3.18	0.001	
	Year 2021	0.269	0.255	1.05	0.292	
	Year 2022	0.571	0.225	2.54	0.011	
	Holding	Intercept	-5.637	0.221	-25.51	< 0.001
		Day of year linear	-5.285	1.009	-5.24	< 0.001
Mortality in fishing gear		18.885	3.312	5.70	< 0.001	
Corf or tank		0.528	0.116	4.55	< 0.001	
Temperature holding		0.044	0.013	3.25	0.001	
Maximum days in holding		0.013	0.008	1.57	0.116	
Year 2017		-0.200	0.175	-1.14	0.253	
Year 2018		-0.511	0.183	-2.80	0.005	
Year 2019		-0.582	0.183	-3.18	0.001	
Year 2020		-1.252	0.293	-4.28	< 0.001	
Year 2021		-0.672	0.223	-3.01	0.003	
Year 2022		-0.110	0.167	-0.66	0.510	
Transport		Intercept	-12.727	1.1842	-10.75	< 0.001
	Temperature transport	0.394	0.085	4.61	< 0.001	
	Day of year linear	-10.056	2.555	-3.94	< 0.001	
	Day of year quadratic	8.239	2.837	2.90	0.004	
	Mortality in fishing gear	38.343	14.796	2.59	0.010	
	Year 2017	0.791	0.632	1.25	0.210	
	Year 2018	-0.713	0.702	-1.02	0.310	
	Year 2019	-0.014	0.606	-0.02	0.981	
	Year 2020	-1.349	0.917	-1.47	0.141	
	Year 2021	-1.571	0.814	-1.93	0.054	
	Year 2022	-0.961	0.702	-1.37	0.171	

their parameter value at their respective average (Fox and Weisberg, 2018, 2019). In contrast to the partial regressions for each predictor variable, we estimated a mortality range based on our fitted values from each top ranked model and plotted these alongside the observed value of each predictor variable. These plots illustrate the minimum and maximum modelled mortality within the data range, and how the combined effect of predictors influences mortality.

All data handling and statistical analyses were done using R (version 4.2.2) (R Core Team, 2022). The packages included in "tidyverse" (Wickham et al., 2019), "sf", and "patchwork" packages (Pebesma, 2018; Pedersen, 2020) were used to manipulate data (mutate, select, filter, summarise, and arrange) and create figures and maps. Model effects were calculated using the "effects" package (Fox, 2003; Fox and Weisberg, 2019). The package "MuMIn" (Bartón, 2022) was used to calculate RVI and rank model combinations based on AICc. Roc-curves and AUC estimates were derived using the functions roc() and auc() in

the “pROC” package (Robin et al., 2011).

3. Results

3.1. Descriptive statistics

In total, number of transported individuals ranged between 4 491 and 10,764 eels per year (57,908 individual eels in total), and between 72 and 1 699 eels per transport event (Fig. 3a). The total mortality (i.e., mortality in gear, in holding, and during transport combined) ranged from 0.6% to 2 % per year on average (Fig. 3b). Average annual mortality rates in fishing gear ranged from 0.2% to 1.4 % (Fig. 3c), mortality during holding from 0.6% to 2 % (Fig. 3d), and mortality during transport from 0.03% to 0.17 %, per year on average (Fig. 3e). The average holding time that was 11.4 days, and the average transport time was 3.5 h.

3.2. Mortality rates

Mortality in fishing gear (pound nets) was affected by day of year (cumulative model weight DAY OF YEAR $\omega_+ = 1.00$), with the highest

mortality being reported during summer (peaking in mid-July, Fig. 4a). In late spring (April and May) and during fall (October and November), the mortality was lower (Fig. 4a). There were also differences in mortality across years (YEAR $\omega_+ = 1.00$), where mortality in the fishing gear was lower in 2020 compared to the other years (Fig. 4b). There were differences in mortality depending on location (LOCATION $\omega_+ = 1.00$), with some locations having lower fishing gear mortality than others (Fig. 4c). It should be noted that for four locations, the estimates could not be included in the figure since the estimates were very low and had high standard errors due to lack of data (Table 1). Hence, five (out of a total of nine locations) are included in Fig. 4c. All main effects in the model on fishing gear mortality were significant at an alpha level of 0.05 (Table 1). The McFaddens’ pseudo R^2 was 0.41, and the AUC-value was 0.81 (indicating good model fits). A model selection table with the AICc ranking of all competing models, and the ROC-curve, are available in the supplementary material (Tables S1, Figure S1).

Similar to mortality in fishing gear, mortality during holding was also affected by day of year (cumulative model weight DAY OF YEAR $\omega_+ = 1.00$), but this time the pattern was somewhat different, with greater mortality in late spring and summer (April-July), and lower in fall (October and November) (Fig. 5a). There was also an effect of year on

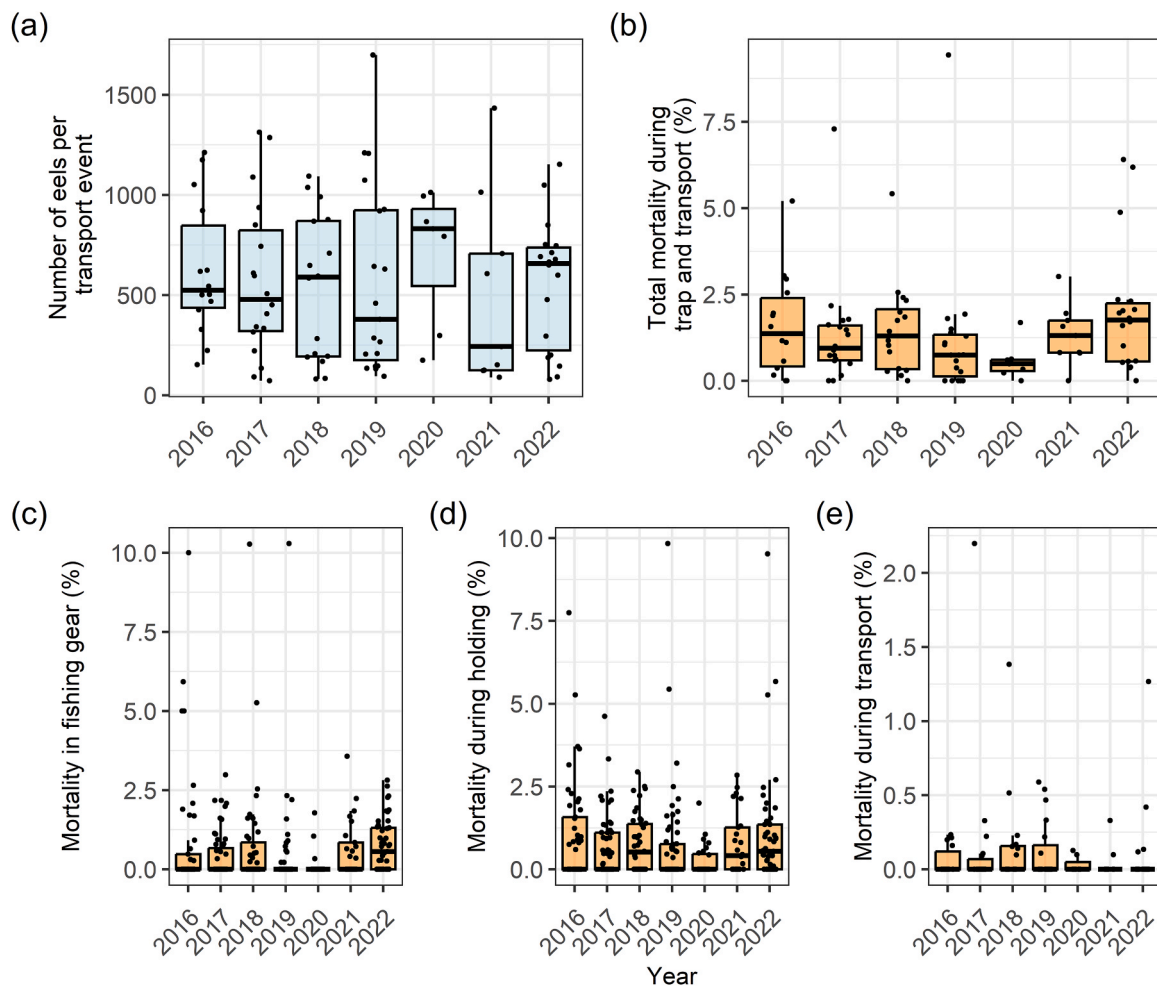


Fig. 3. Descriptive statistics and reported dead European eels (*Anguilla anguilla*) adults during trap and transport. Boxplots show: (a) total number of transported eels per trap and transport event per year, (b) total mortality during trap and transport per year, (c) mortality in gear per year, (d) mortality during holding per year, and (e) mortality during transport per year. The box represents the 25th and 75th percentile with the median value shown as a black line in the box, whiskers denote values lower than the 25th percentile and higher than the 75th percentile. Black points show raw data. Note the different y-axis scales between panels. Note that panel (b) and (e) on total and transport mortality include 101 observations, while panel (c) and (d) on fishing gear and holding mortality include 302 observations (since each transport event contained eel from several fishers/locations, which affected the resolution of observations). Note that the sum of mortality in the three steps (gear (c), holding (d), and transport (e)) is not equal to the total mortality in panel (b), since eels that died in a previous step of the trap and transport process are not included in the following step.

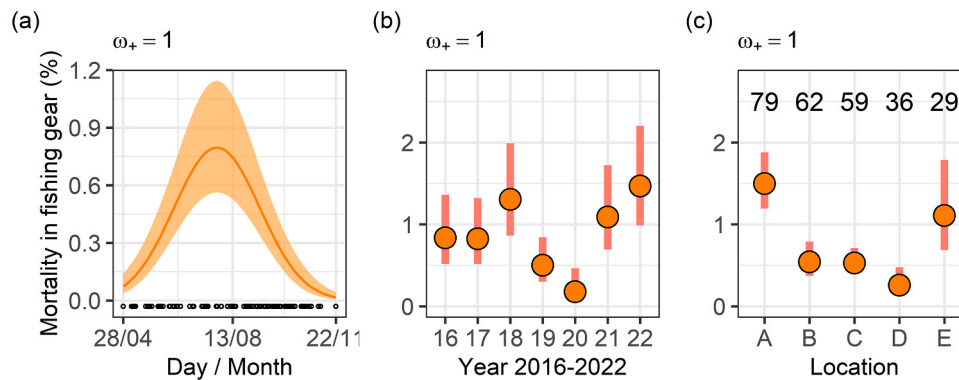


Fig. 4. Proportion of reported dead European eels (*Anguilla anguilla*) adults in fishing gear (pound net) (a) as a quadratic function of day of year (displayed as day/month), (b) as a function of year (2016–2022), and (c) as a function of fishing location. In panel (a) the average mortality for the five locations with the greatest number of observations is shown across day of year. Black circles show the observed x-values along the horizontal axis. In panel (c) the number of observations per location is shown, for the five locations where estimates could be included in the figure (estimates from all locations are presented in Table 1), the observations for location F–I were 20, 10, 6, and 1, respectively. Orange line and points show the models' partial regression estimates, shaded orange area show 95 % confidence interval. Relative variable importance values (ω_+) are included above each panel. Note the different y-axis scales between panels.

mortality during holding (YEAR $\omega_+ = 1.00$), with lower mortality in 2020 (Fig. 5b). In addition, mortality increased with increasing mortality in fishing gear (GEAR MORTALITY $\omega_+ = 1.00$), meaning that when mortality had been high in the fishing gear, it was also high during holding (Fig. 5c). Furthermore, mortality was greater in flow-through tanks on land than in submerged corves (CORF|TANK $\omega_+ = 1.00$, Fig. 5d) and higher temperatures within the range of 5–24 °C resulted in greater mortality (WATER TEMPERATURE $\omega_+ = 0.99$, Fig. 5e). The remaining variable maximum days in holding received weak support (MAX DAYS IN CORF|TANK $\omega_+ = 0.53$, Fig. 5f), but was however, based on AICc ranking of the 64 candidate models, still part of the top model. Not all main effects in the top model on holding mortality were significant at an alpha level of 0.05 (Table 1). The McFaddens' pseudo R^2 was 0.20, and the AUC-value was 0.65 (indicating good model fits). A model selection table with the AICc ranking of all competing models, and the ROC-curve, are available in the supplementary material (Tables S2, Figure S2).

Mortality during transport was also affected by day of year (cumulative model weight DAY OF YEAR $\omega_+ = 1.00$), again somewhat differently compared to fishing gear mortality and mortality during holding. Mortality was highest in early spring, then decreased abruptly from the end of April, reached near zero by June, and remained at low levels throughout the year (Fig. 6a). Furthermore, mortality increased with higher water temperatures during transport (TEMPERATURE $\omega_+ = 1.00$, Fig. 6b). The remaining variables received weak support according to the model weights, although mortality in fishing gear had a significant effect ($p < 0.01$, Table 1). Year had a weak effect on mortality during transport (YEAR $\omega_+ = 0.65$, Fig. 6c), with no distinguishable pattern in mortality across years. Mortality in the previous step (MORTALITY IN CORF|TANK $\omega_+ = 0.55$, Fig. 6d) and mortality in fishing gear (GEAR MORTALITY $\omega_+ = 0.53$, Fig. 6e) also received weak support, with a pattern indicating that when mortality had been high during holding and in the fishing gear, it was also high during transport (Fig. 6d, e). There was weak support for mortality to increase with longer transport time (TRANSPORT TIME $\omega_+ = 0.37$, Fig. 6f). The remaining three variables all had an effect approaching zero (CORF|TANK TYPE $\omega_+ = 0.26$, MAX DAYS IN CORF|TANK $\omega_+ = 0.26$, TEMPERATURE DIFF TRANSPORT VS CORF|TANK $\omega_+ = 0.30$). The McFaddens' pseudo R^2 was 0.52, and the AUC-value was 0.83 (indicating good model fits). A model selection table with the AICc ranking of all competing models, and the ROC-curve, are available in the supplementary material (Tables S3, Figure S3).

The predicted minimum, median, and maximum mortality in fishing gear were 0.015 (95 % CI: 0.006–0.036 %), 0.4 % (0.2–0.7 %), and 2.7 % (2.1–3.6 %), respectively (Fig. 7a). The same metrics during holding were 0.1 (0.1–0.2 %), 0.7 % (0.5–0.9 %), and 6.4 % (3.5–11.6 %), respectively (Fig. 7b). Finally, during transport the

predicted minimum, median, and maximum mortalities were 0.002 (0.0002–0.011 %), 0.04 % (0.01–0.11 %), and 1.07 % (0.28–4.04 %), respectively (Fig. 8).

4. Discussion

This study utilized existing data from trap and transport data sheets from 2016 to 2022, encompassing nearly 58,000 transported eels, to evaluate mortality during trap and transport in adult European eel. We found that the average mortality rate was generally low for all steps, 0.2–1.4 % in the fishing gear, 0.6–2.0 % during holding, and 0.03–0.17 % during transport (percent per year on average). Hence, most of the total mortality was related to fishing and holding, while mortality during transport itself was lower. The total mortality during all steps of the process (i.e., mortality in gear, during holding, and during transport) could however be up to 10 %. Combining the worst-case scenarios within the boundaries of the observed data showed that predicted mortality levels ranged (minimum and maximum) between 0.01 % and 2.7 % in the fishing gear, 0.1 % and 6.4 % during holding, and 0.002 % and 1.07 % during transport. Hence, both the observed and the predicted mortality during trap and transport was much lower compared to the expected mortality in turbines (Algera et al., 2020). The estimated total turbine mortality in the three river systems investigated here is 70 % to > 99 % (Göta älv: 70–90 %, Nissan: >99 %, Lagan: >99 %, Calles and Christiansson, 2012; Leonardsson, 2012).

Some of the investigated parameters affected mortality in fishing gear and during both holding and transport, while others only had an effect during parts of the process. Year had an effect on mortality in fishing gear and during holding, but not during transport. There were no clear consistent effects, but in year 2020 there was lower mortality in fishing gear and during holding, and in addition there was lower mortality in fishing gear in 2019. This is somewhat surprising, since the year 2020 was unusually warm in Sweden (www.smhi.se). While the data sheets do not contain any information that could potentially explain the lower mortality in 2020, seemingly random/inexplicable interannual variation in real-world datasets is not uncommon (Werner et al., 2020). Such results should however be interpreted with care given the difficulties associated with obtaining the needed statistical power to interpret interannual variation (Cauvy-Fraunié et al., 2020). Season, i.e., time of year, affected mortality during all steps of trap and transport, however not in the same way. For mortality in fishing gear, the highest mortality was noted during the summer, peaking in mid-July, and being lower in late spring (April and May) and during fall (October and November). This could be interpreted as a temperature effect, since this pattern follows how the water temperature is expected to look in Sweden.

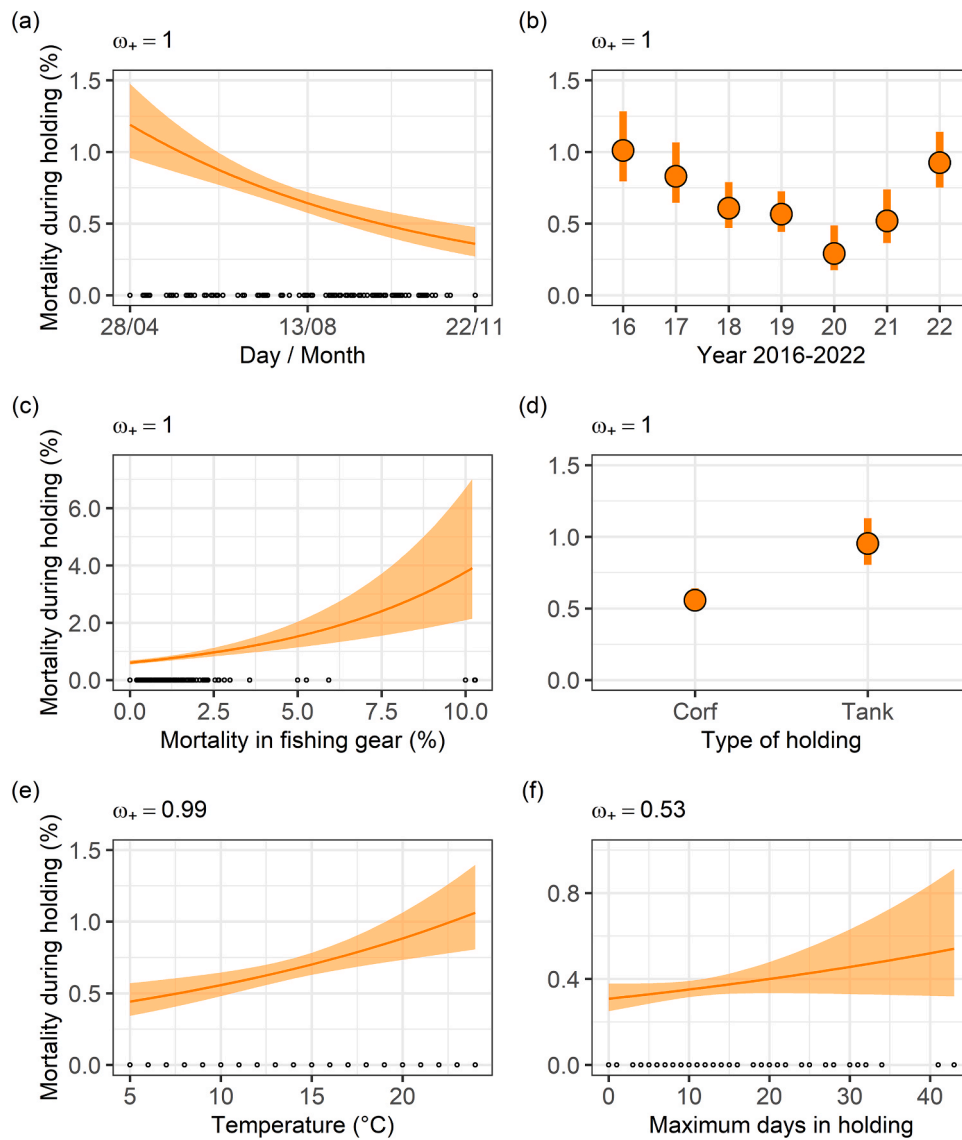


Fig. 5. Proportion of reported dead European eels (*Anguilla anguilla*) adults during holding (submerged corf or flow through tank on land) as a function of: (a) day of year (displayed as day/month), (b) year (2016–2022), (c) proportion of dead eels in the fishing gear, (d) corf/tank type, (e) water temperature in corf/tank, and (f) maximum days in holding. Orange lines and points show the models’ partial regression estimates, shaded orange areas show 95 % confidence interval. In (a), (c), (e) and (f), black circles show the observed x-values along the horizontal axis. Relative variable importance values (ω_+) are shown above each panel. Note the different y-axis scales between panels.

Temperature was however not part of the model since the data sheets did not contain data on water temperature at the site/time of fishing/emptying the gear. Mortality during holding followed a similar pattern regarding effect of season, with greater mortality during summer and lower in fall. For this step of the process, however, mortality was also high in spring (April, May), which cannot be explained by temperature. We do not know why mortality was high in spring (in addition to during summer), but the eels might be more sensitive to holding in spring after their winter dormancy. The European eel is not completely dormant during winter (Westerberg and Sjöberg, 2015; Rohtla et al., 2022). Being kept in a corf/tank may thus be particularly negative in spring when the eels have just started to be more active and started to forage (Methling et al., 2012; Reeve et al., 2022; Rohtla et al., 2022). For mortality during transport, the season effect again showed that mortality was greater during early spring, which could point to a similar sensitivity after dormancy as in mortality during holding. This could be related to exhaustion of stored energy, or potentially a suppressed immune system, after the dormancy period, which might influence stress

tolerance. After spring, mortality during transport decreased abruptly, reached near zero by early summer (June), and remained at low levels throughout the year. This pattern shows that there is an effect of season in the early spring on mortality during transport. This result should not be coupled with temperature effects, since those two variables were not collinear, and mortality did increase with increasing water temperature (which is well-supported in the literature, e.g., Sadler, 1979; Pauly, 1980). It should be noted that the transport time, on average 3.5 h, was much shorter than the holding time, on average 11.4 days, meaning that there is less time that can cause mortality. We do not know the soak time for the gear, but it was likely longer than the transport time. Mortality was also lower during transport compared to in fishing gear and during holding, and the effects should be interpreted taking this into account. There were also fewer datapoints, in general, for spring and autumn, meaning that the season effect should be interpreted with care. More studies would be needed to investigate if there are potential effects of winter dormancy that could be linked to greater sensitivity to handling.

Another of the analysed parameters that had an effect on mortality

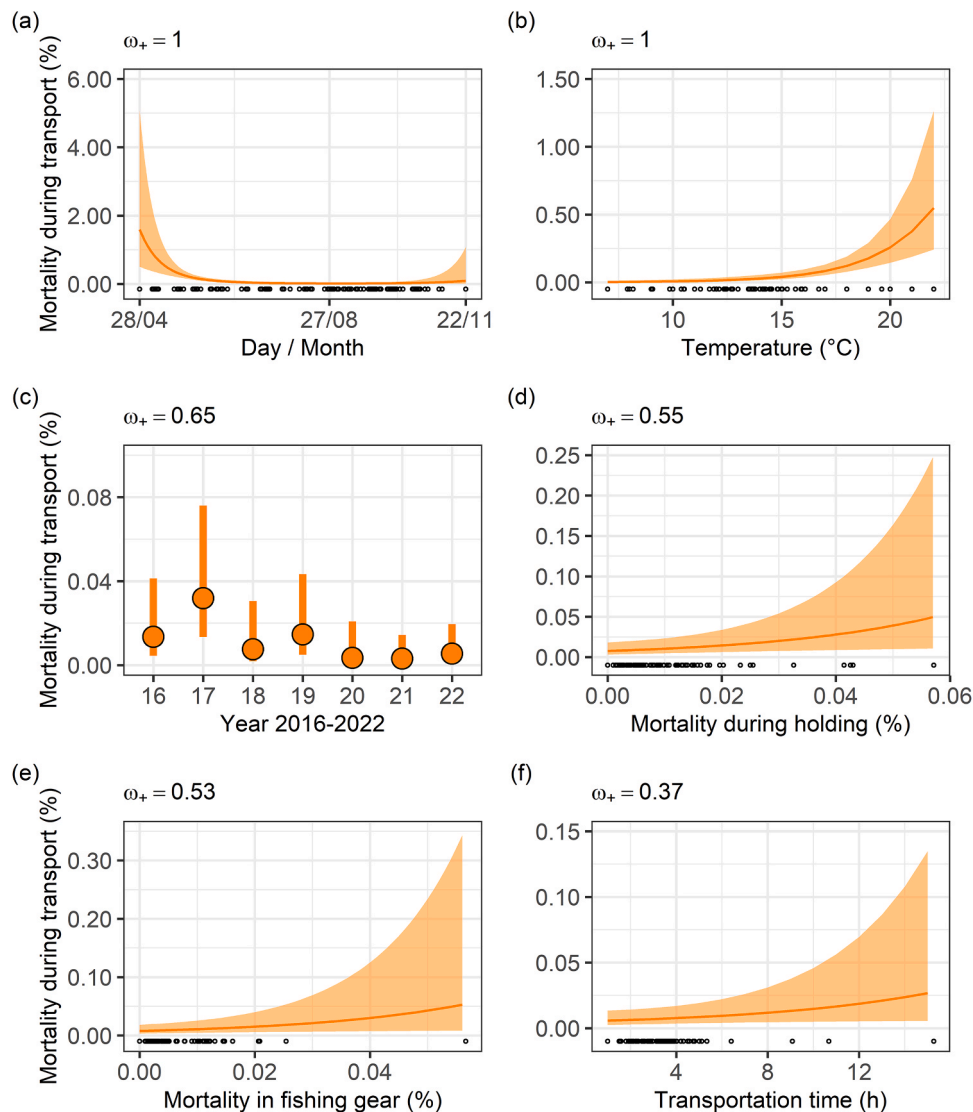


Fig. 6. Proportion of reported dead European eels (*Anguilla anguilla*) adults after transport as a function of: (a) day of year (displayed as day/month), (b) the average temperature in the transport tank, (c) year (2026–2022), (d) average mortality during holding, (e) average mortality in fishing gear, and (f) average transport time. Orange solid lines show the models’ partial regression estimates, shaded orange areas show 95 % confidence interval. Black circles in (a), (b), and (d) to (f) show the observed x-values along the horizontal axis. Relative variable importance values (ω_+) are shown above each panel. Note the different y-axis scales between panels.

during holding and transport was the variable “mortality in fishing gear”, which received strong support in the models for mortality during holding but weaker support in the models for mortality during transport, although significant in both top models. This result likely reflects that if mortality was high in the first step of the process, the eels were in poorer condition, and higher mortality is hence seen also in the next step. The reason why this parameter had limited effect during transport could be due to most injured and/or sick eels dying during the holding period, whereby a strong effect would not be present in the analysis of mortality during transport. Mortality in gear could be due to many factors, such as injuries caused by the fishing gear or potential injuries from predators, and might be difficult to avoid. Injuries and mortality can increase with longer fishing durations, i.e., longer set-times of the gear (reviewed in: Veldhuizen et al., 2018), and while soak time was unknown in this study, it could have had an effect. It might therefore be beneficial to empty the fishing gear as often as possible when the eels are fished for a trap and transport program. It could be better to collect eels for trap and transport programs using outlet traps, rather than fishing gear, since the risk of injuries is generally lower in traps compared to fishing gear (Uhlmann and Broadhurst, 2015). It has also been shown in glass eel that

push nets caused 42 % mortality (on average), while there was zero mortality for glass eel collected with hand nets or traps (Briand et al., 2012). Whether the same is true for adult fish has not been studied, to our knowledge. If using traps for adult eel collection, it is important that the trap is designed to minimize stress and injuries, and in addition offer protection from opportunistic predators.

Holding time and transport time did not have an effect on mortality, which may seem counterintuitive. It has, however, previously been reported that holding eels for a substantial amount of time may have little effect in general (Davidsen et al., 2011). For example, it has been reported that eels held as long as four months seemed largely unaffected and resumed normal migratory behaviour upon being released (Davidsen et al., 2011). It has also been shown that the handling associated with loading and unloading may be more stressful than the transport itself, for example in a study on commercial well boat transports of Atlantic salmon (*Salmo salar*) smolts (Iversen et al., 2005). Although an effect of holding and transport time was not observed here, it could be suggested to keep those at a minimum, as a precautionary approach. Holding and transport time may however be difficult to modify. Keeping the eels for some time before transport may be

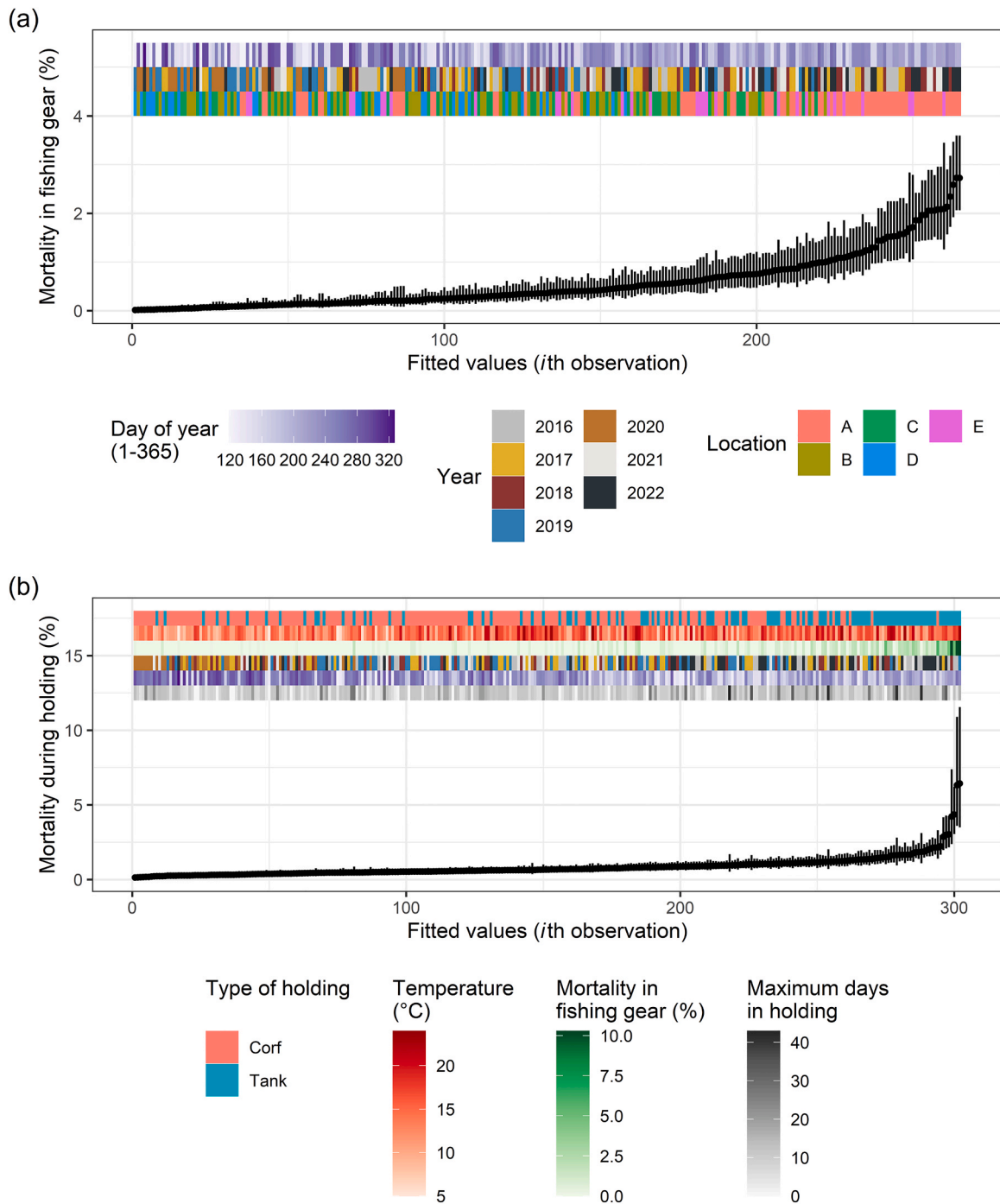


Fig. 7. Mortality range within the data boundaries (model predictions derived from the observed values in the data). Black data points represent the model fit, and point ranges denote the 95 % confidence intervals. In panel (a), alongside the fishing gear mortality, the predictor variables—day of year, year, and location—are color-coded for each observation. For example, tiles with an intermediate purple colour indicate summer and, together with locations A and E, have the highest mortality rates in fishing gear. Panel (b) shows the predictor variables: type of holding (submerged corf or tank on land), temperature during holding, mortality in fishing gear, maximum days in holding, day of year, and year, alongside the mortality during holding. Refer to the legend in panel (a) for day of year and year also in panel (b). In panel (a), the predictions from locations F to I have been removed as these locations could not be reliably estimated due to a low number of observations. Consequently, the number of observations differs between panel (a) and panel (b).

unavoidable; it may not be practically, or economically, feasible to transport and release the eels daily. Usually within trap and transport programs, eels are collected and accumulated over several days before transport and release. Similarly, transport time can be difficult to modify, but trap and transport from locations that are far away from a suitable release site could be avoided. Transport time may however be longer than given by the distance, due to the transporter fetching eels

from several locations, for financial reasons, thereby increasing transport time substantially. This could be avoided if economical constraints were not a concern.

An important aspect relevant for the analysis of mortality during transport is that mortality caused from gear and holding are relatively certain measures since this would be comparably easy to assess (any dead eel would be noted when the eels were moved from the gear to the

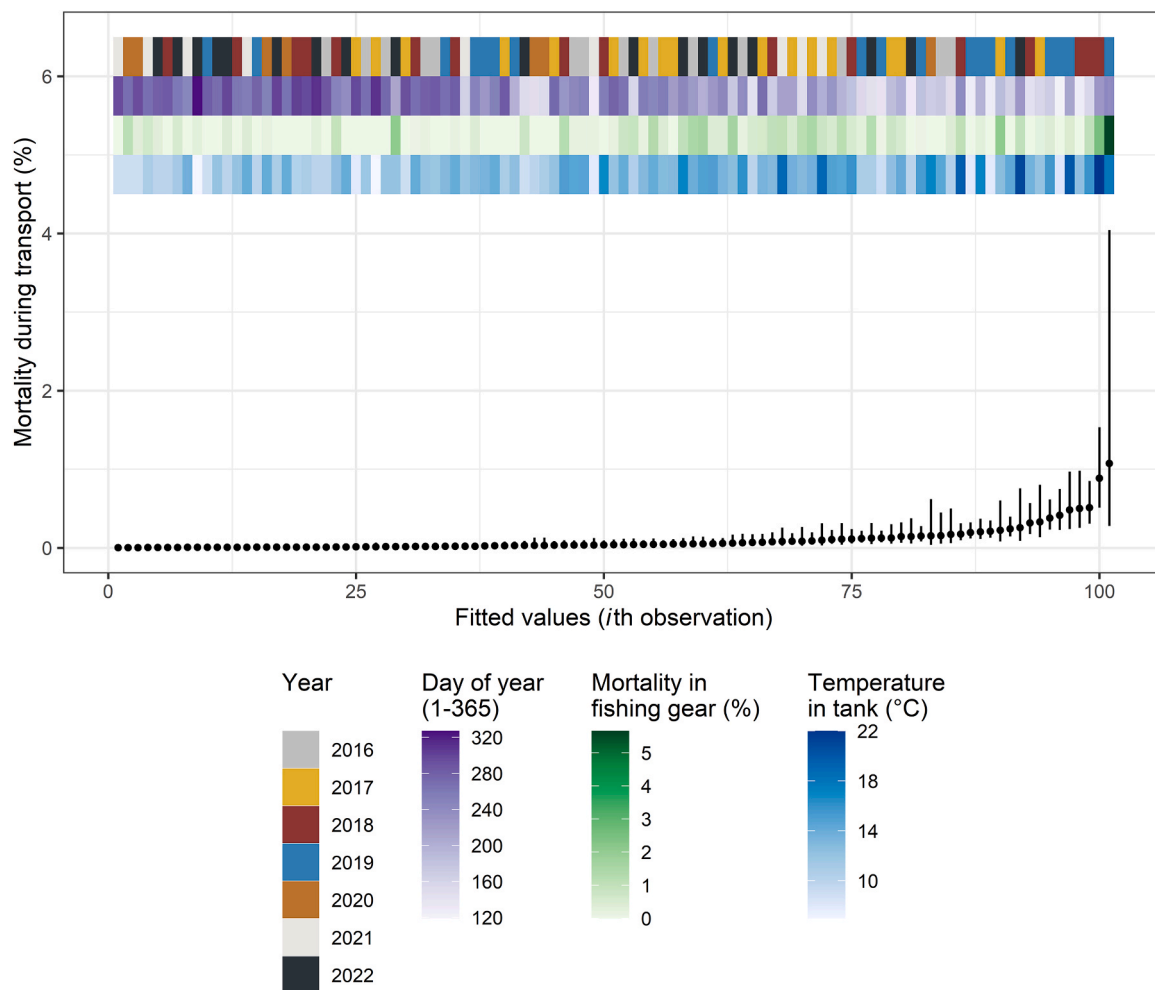


Fig. 8. Mortality range within the data boundaries (model predictions derived from the observed values in the data). Black data points represent the model fit, and point ranges denote the 95 % confidence intervals. Mortality during transport is plotted alongside the color-coded predictor variables: year, day of year, mortality in fishing gear, and temperature in transportation tank.

holding curves/tanks, and from holding to the transport tank). Mortality after transport might be more difficult to assess since the eels are released from the transport tanks into the water at the release site. Hence, there is less “hands on” handling of the eels during the release, and dead eels could therefore be overlooked. This means that the data on mortality during transport presented here is conservative, and that the actual mortality could be higher. This is particularly important to keep in mind given that most of the total mortality was related to fishing and holding, while mortality during transport was lower. In order to make sure that transport mortality is accurately assessed, the eels could for example be released from the transport vehicle into a keeping net and allowed to swim through an opening of the net. Any dead eel would then remain in the net and could be accurately counted. If using such a method, it would be important to ensure that this extra step would not cause any extra stress or risk of mortality during release.

While this study mainly has implications for the spawning migration of adult eel, it also has some relevance for the reallocation of juvenile eel from one area to another (i.e., restocking), since restocking is done also in areas upstream of migration barriers in watercourses lacking free migration pathways (Nordqvist, 1929; Nyström and Trybom, 1902; ICES, 2016). While awaiting actions to create open migration routes, such as dam removal or the construction of functional fish passage solutions, trap and transport is one of the few tools available to increase the survival of downstream-migrating eels which otherwise likely would die when passing through the hydropower turbines. Since many dams in

Europe and other countries were built during the first half of the 20th century, or even earlier, few or no eels have been able to migrate in a free-flowing river in these systems for several decades, and few have functioning fish passage solutions and/or so called fish friendly turbines, or other technical solutions aiming at reducing turbine mortality (Taft, 2000; Piper et al., 2018; Calles et al., 2021). Hence, in the absence of restocking, there would no longer be any adult eels in these systems and thereby no need for trap and transport. The eel’s role in the ecosystem would however have been lost, and biodiversity would have been reduced. Because the European eel has not yet been successfully reproduced artificially at a large scale, restocking relies exclusively on wild recruits, meaning that the net-benefit of restocking on the population level is unclear (ICES, 2016). Despite this, restocking has been one of the recommended management measures with the aim to aid the recovery of the eel stock since the implementation of the EU Eel Regulation in 2007 (Council Regulation No 1100/2007), and the subsequent establishment of national eel management plans. Fishing of glass eel for restocking purposes is however advised against in the latest ICES advice, as adopted by its Advisory Committee, ACOM, (ICES, 2023).

While safe downstream passage can be achieved with the combination of angled bar racks and nature-like fishways (Calles et al., 2021), such methods are in many instances either extremely challenging, expensive, or impossible to implement, particularly in large systems (Algera et al., 2020). Since trap and transport and other passage solutions require maintenance and human interference, are labour intensive,

and can cause stress and mortality in fish, these practises should only be considered as temporary or complementary measures (Verhelst et al., 2021). Restoration of connectivity should be the long-term management goal. This would also reduce or completely remove the need for restocking above migration barriers, and would follow the advice to avoid species-focused stocking, since this method can be outperformed by ecosystem-based management (Radinger et al., 2023). Barrier removal is sustainable for ecosystems and cost-efficient in the long term, and it is the only practice that can restore natural flow and connectivity (Bednarek, 2001).

5. Conclusion

We found that the average mortality rate of adult European eel was generally low for all steps of the trap and transport process, with most of the total mortality being related to fishing and holding, while mortality during transport was lower. The data on mortality during transport should however be viewed as conservative since the eels are released from the transport vehicle into the water at the release site and dead eels could hence be overlooked. On the contrary, any dead eel would be noted when moving eels from gear to holding, and from holding to transport. The observed mortality during trap and transport was much lower compared to the expected mortality in turbines, as the estimated total turbine mortality in the three river systems investigated was 70 % to > 99 % (Calles and Christiansson, 2012; Leonardsson, 2012). Turbine mortality is important not the least since most eels will not be caught and transported, but the majority of eels will still face turbine impingement and mortality even in locations where a trap and transport program is in place. In addition, this study only assessed one aspect of the potential effects of trap and transport on silver eels. In order for trap and transport to work as intended, the eels not only need to survive the process, but they need to continue their migration, reach a suitable spawning habitat, and succeed with spawning. Increased predation risk and physiological changes induced by stress have been observed among fish that have been transported (Kemp, 2015), and such effects could have negative implications for continued migration and spawning. Since the European eel is a panmictic species that undertakes a spawning migration that is thousands of kilometres long, and since the natural spawning behaviour to date has not been observed and the spawning location is not identified in detail (Schmidt, 1922; Enbody et al., 2021; Wright et al., 2022), studies investigating the long-term effects of trap and transport are virtually impossible to conduct. Eels could however be tracked with acoustic tags, across shorter distances and in areas where a receiver network can be setup, or with satellite tags that can provide long-distance migration data. Such studies would be needed to assess the complete effects of trap and transport.

Data and replication statement

A 7-year time series (2016–2022) of mortality during trap and transport in inland waters in western Sweden, with release sites towards Skagerrak and Kattegat, the North Sea. Trap and transport data sheets contained data on number of eels found dead in the fishing gear, mortality during holding in corves and tanks, and number of eels found dead after transport (Table 2). Data on mortality in gear and during holding were analysed per fishing/holding event. Data on mortality during transport were analysed per transport event (Table 2).

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Table 2
Data and replication parameters.

Scale of inference	Observational unit	Number of observations at this scale	Response variables and units
Temporal: multi-annual (7 years). Spatial: Inland waters in western Sweden with release sites towards Skagerrak and Kattegat, the North Sea.	Fishing/catch and holding events per fisher and time, transport events with eel from several fishers grouped per transport.	302 fishing/catch and holding events, 101 transport events.	Proportion of adult dead eels reported in gear, corf/tank, and after transport.

CRediT authorship contribution statement

Philip Jacobson: Writing – review & editing, Conceptualization. **Birgitta Jacobson:** Writing – review & editing, Validation, Data curation. **Konrad Karlsson:** Writing – review & editing, Visualization, Formal analysis. **Josefin Sundin:** Writing – review & editing, Writing – original draft, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare no competing interest. Note that while the data sheets were designed by a researcher, they were filled out by fishers and transporters, and no part of the trap and transport process was executed by researchers. Most of the data included in this paper originates from trap and transport events funded by the hydropower industry.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2025.107264](https://doi.org/10.1016/j.fishres.2025.107264).

Data availability

The data and script used for statistical analyses are archived in the figshare repository, together with the complete model selection tables with the AICc ranking of all competing models (figshare.com/s/eef9a40f5b34751bc3a6, DOI: [10.6084/m9.figshare.28123547](https://doi.org/10.6084/m9.figshare.28123547)), following best practices guidelines for public data archiving (Roche et al. 2015). Due to international General Data Protection Regulation (GDPR) law, names of fishers or transporters are not included in any publicly archived data files. Since fishers could be identified by location, the publicly archived files also do not contain the actual name of location or the coordinates, instead a generic code is provided for each location.

References

- Algera, D.A., Rytwinski, T., Taylor, J.J., Bennett, J.R., Smokorowski, K.E., Harrison, P. M., Clarke, K.D., Enders, E.C., Power, M., Bevelhimer, M.S., 2020. What are the relative risks of mortality and injury for fish during downstream passage at hydroelectric dams in temperate regions? A systematic review. *Environ. Evid.* 9, 3.
- Bartón, K. 2022. **MuMin: Multi-Model Inference; R Package Version 1.47.1.** (<https://CRAN.R-project.org/package=MuMin>).
- Bednarek, A.T., 2001. Undamming rivers: a review of the ecological impacts of dam removal. *Environ. Manag.* 27, 803–814.
- Béguet-Pon, M., Verreault, G., Stanley, D., Castonguay, M., Dodson, J.J., 2018. The migration of stocked, trapped and transported, and wild female American silver eels through the Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* 75, 2024–2037.
- Boerrigter, J.G., Manuel, R., van den Bos, R., Roques, J.A., Spanings, T., Flik, G., van de Vis, H.W., 2015. Recovery from transportation by road of farmed European eel (*Anguilla anguilla*). *Aquac. Res.* 46, 1248–1260.
- Bogdan, E., Waluga, D., 1980. The effect of transport on the quality of eel stocking material. *Aquaculture* 20, 139–146.
- Boggs, C., Keefer, M.L., Peery, C., Bjornn, T.C., Stuehrenberg, L.C., 2004. Fallback, reascension, and adjusted fishway escapement estimates for adult Chinook salmon and steelhead at Columbia and Snake River dams. *Trans. Am. Fish. Soc.* 133, 932–949.
- Briand, C., Sauvaget, B., Girard, P., Fatin, D., Beaulaton, L., 2012. Push net fishing seems to be responsible for injuries and post fishing mortality in glass eel in the Vilaine estuary (France) in 2007. *Knowl. Manag. Aquat. Ecosyst.* 02.
- Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behav. Ecol. Sociobiol.* 65, 23–35.
- Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociol. Methods Res.* 33, 261–304.
- Cade, B.S., 2015. Model averaging and muddled multimodel inferences. *Ecology* 96, 2370–2382.
- Calles, O., and J. Christiansson. 2012. **Ålens möjlighet till passage av kraftverk: En kunskapsammanställning för vattendrag prioriterade i den svenska ålförvaltningsplanen samt exempel från litteraturen.**
- Calles, O., Elghagen, J., Nyqvist, D., Harbicht, A., Nilsson, P.A., 2021. Efficient and timely downstream passage solutions for European silver eels at hydropower dams. *Ecol. Eng.* 170, 106350.
- Carter, J.V., Pan, J., Rai, S.N., Galandiuk, S., 2016. ROC-ing along: evaluation and interpretation of receiver operating characteristic curves. *Surgery* 159, 1638–1645.
- Cauvy-Fraunié, S., Trenkel, V.M., Daufresne, M., Maire, A., Capra, H., Olivier, J.-M., Lobry, J., Cazelles, B., Lamouroux, N., 2020. Interpretation of interannual variability in long-term aquatic ecological surveys. *Can. J. Fish. Aquat. Sci.* 77, 894–903.
- Crook, D.A., Lowe, W.H., Allendorf, F.W., Erős, T., Finn, D.S., Gillanders, B.M., Hadwen, W.L., Harrod, C., Hermoso, V., Jennings, S., 2015. Human effects on ecological connectivity in aquatic ecosystems: integrating scientific approaches to support management and mitigation. *Sci. Total Environ.* 534, 52–64.
- Davidson, J.G., Finstad, B., Økland, F., Thorstad, E.B., Mo, T.A., Rikardsen, A.H., 2011. Early marine migration of European silver eel *Anguilla anguilla* in northern Norway. *J. Fish. Biol.* 78, 1390–1404.
- Dekker, W., Wickström, H., 2015. **Utvärdering av målen för programmet Krafttag ål. Energiforsk 103.** ISBN: 978-91-7673-103-1.
- Drouineau, H., Rigaud, C., Laharanne, A., Fabre, R., Alric, A., Baran, P., 2015. Assessing the efficiency of an elver ladder using a multi-state mark–recapture model. *River Res. Appl.* 31, 291–300.
- Duarte, G., Segurado, P., Haidvogel, G., Pont, D., Ferreira, M.T., Branco, P., 2021. Damn those damn dams: fluvial longitudinal connectivity impairment for European diadromous fish throughout the 20th century. *Sci. Total Environ.* 761, 143293.
- Durif, C., Dufour, S., Elie, P., 2005. The silvering process of *Anguilla anguilla*: a new classification from the yellow resident to the silver migrating stage. *J. Fish. Biol.* 66, 1025–1043.
- Durif, C., Guibert, A., Elie, P., 2009. Morphological discrimination of the silvering stages of the European eel. In: Casselman, J.M., Cairns, D.K. (Eds.), *Eels at the edge. Science, status, and conservation concerns.* American Fisheries Society Symposium, pp. 103–111.
- Enbody, E.D., Petterson, M.E., Sprehn, C.G., Palm, S., Wickström, H., Andersson, L., 2021. Ecological adaptation in European eels is based on phenotypic plasticity. *Proc. Natl. Acad. Sci.* 118.
- Evans, A.F., Wertheimer, R.H., Keefer, M.L., Boggs, C.T., Peery, C.A., Collis, K., 2008. Transportation of steelhead kelts to increase iteroparity in the Columbia and Snake rivers. *North Am. J. Fish. Manag.* 28, 1818–1827.
- Finney, S.T., Isely, J.J., Cooke, D.W., 2006. Upstream migration of two pre-spawning shortnose sturgeon passed upstream of Pinopolis Dam, Cooper River, South Carolina. *Southeast. Nat.* 5, 369–375.
- Fox, J., 2003. Effect displays in R for generalised linear models. *J. Stat. Softw.* 8, 1–27.
- Fox, J., Weisberg, S., 2018. Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. *J. Stat. Softw.* 87, 1–27.
- Fox, J., Weisberg, S., 2019. *An R companion to applied regression, third edition.* Third edition. Sage publications.
- Grafton, R.Q., Pittock, J., Davis, R., Williams, J., Fu, G., Warburton, M., Udall, B., McKenzie, R., Yu, X., Che, N., 2013. Global insights into water resources, climate change and governance. *Nat. Clim. Change* 3, 315–321.
- Hagelin, A., Calles, O., Greenberg, L., Nyqvist, D., Bergman, E., 2016. The migratory behaviour and fallback rate of landlocked Atlantic salmon (*Salmo salar*) in a regulated river: does timing matter? *River Res. Appl.* 32, 1402–1409.
- Hidalgo, M., Kaplan, D.M., Kerr, L.A., Watson, J.R., Paris, C.B., Browman, H.I., 2017. Advancing the link between ocean connectivity, ecological function and management challenges. *ICES J. Mar. Sci.* 74, 1702–1707.
- 2016 ICES. 2016. **Report of the Workshop on Eel Stocking (WKSTOCKEEL), 20–24 June 2016, Toombbridge, Northern Ireland, UK.** ICES CM 2016/SSGEPD:21.
- ICES. 2023. **ICES Advice on fishing opportunities and conservation for the European eel (*Anguilla anguilla*) throughout its natural range.** Report of the ICES Advisory Committee ele.2737.nea.
- ICES, 2024. **Joint EIFAAC/GFCM/ ICES Working Group on Eels (WGEEL).** ICES Sci. Rep. 6, 90.
- Iverson, M., Finstad, B., McKinley, R.S., Eliassen, R.A., Carlsen, K.T., Evjen, T., 2005. Stress responses in Atlantic salmon (*Salmo salar* L.) smolts during commercial wild boat transports, and effects on survival after transfer to sea. *Aquaculture* 243, 373–382.
- Jonsson, B., Waples, R.S., Friedland, K., 1999. Extinction considerations for diadromous fishes. *ICES J. Mar. Sci.* 56, 405–409.
- Kemp, P.S., 2015. Impoundments, barriers and abstractions: impact on fishes and fisheries, mitigation and future directions. *Freshw. Fish. Ecol.* 717–769.
- Kerr, J.R., Karageorgopoulos, P., Kemp, P.S., 2015. Efficacy of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel (*Anguilla anguilla*) and river lamprey (*Lampetra fluviatilis*) at an experimental Crump weir. *Ecol. Eng.* 85, 121–131.
- Kindlmann, P., Burel, F., 2008. Connectivity measures: a review. *Landscape Ecol.* 23, 879–890.
- Legault, A., 1988. Le franchissement des barrages par l'escalade de l'anguille. Etude en Sèvre Niortaise. *Bull. Fr. De la Peche Et. De la Piscic.* 1–10.
- Leonardsson, K., 2012. **Modellverktyg för beräkning av ålförluster vid vattenkraftverk.** Elforsk rapport 12, 36.
- Limburg, K.E., Swaney, D.P., Strayer, D.L., 2001. River Ecosystems. In: Asher Levin, S. (Ed.), *Encyclopedia of Biodiversity.* Elsevier, pp. 213–231.
- Lusardi, R.A., Moyle, P.B., 2017. Two-way trap and haul as a conservation strategy for anadromous salmonids. *Fisheries* 42, 478–487.
- McDougall, C., Hrenchuk, C., Anderson, W., Peake, S., 2013. The rapid upstream migration of pre-spawn Lake Sturgeon following trap-and-transport over a hydroelectric generating station. *North Am. J. Fish. Manag.* 33, 1236–1242.
- McFadden, D., 1974. Conditional logit analysis of qualitative choice behavior. In: Zarembka, P. (Ed.), *Frontiers in Econometrics.* Academic Press, New York, pp. 105–142.
- McFadden, D., 1979. Quantitative methods for analyzing travel behaviour of individuals: Some recent developments. In: Stopher, D.H.P. (Ed.), *Behavioural travel modelling.* Cambridge University Press, Cambridge, pp. 279–318.
- Methling, C., Steffensen, J., Skov, P.V., 2012. The temperature challenges on cardiac performance in winter-quietest and migration-stage eels *Anguilla anguilla*. *Comp. Biochem. Physiol. Part A: Mol. Integr. Physiol.* 163, 66–73.
- Nam, B.-H., D'Agostino, R.B., 2002. Discrimination index, the area under the ROC curve. In: Huber-Carol, C., Balakrishnan, N., Nikulin, M.S., Mesbah, M. (Eds.), *Goodness-of-fit tests and model validity.* Springer Science, New York, pp. 267–279.
- Nordqvist, H., 1929. **Försök rörande import och inplantering i svenska sjöar av engelsk glasål.** Skrifter utgivna av Södra Sveriges Fiskeriförening. 60–86.
- Nyqvist, D., Zagars, M., Calles, O., Comoglio, C., 2019. Behavior of trap-and-transported Atlantic salmon spawners of hatchery origin in the Daugava River system (Latvia). *J. Limnol.* 78.
- Nyström, A., Trybom, F., 1902. **Uppgångsrännor för ålyngel vid Trollhättan.** Svensk Fiskeritidskrift, 11.
- Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES J. Mar. Sci.* 39, 175–192.
- Pebesma, E., 2018. Simple features for R: standardized support for spatial vector data. *R. J.* 10, 439–446.
- Pedersen, T.L. 2020. **Patchwork: The composer of plots, R package version 1.1.1.** (<http://CRAN.R-project.org/package=patchwork>).
- Pike, C., C. V. and M. Gollock. 2020. **Anguilla anguilla.** The IUCN Red List of Threatened Species e.T60344A152845178.
- Piper, A.T., Rosewarne, P.J., Wright, R.M., Kemp, P.S., 2018. The impact of an Archimedes screw hydropower turbine on fish migration in a lowland river. *Ecol. Eng.* 118, 31–42.
- Piper, A.T., Rosewarne, P.J., Wright, R.M., Kemp, P.S., 2020. Using 'trap and transport' to facilitate seaward migration of landlocked European eel (*Anguilla anguilla*) from lakes and reservoirs. *Fish. Res.* 228, 105567.
- Radinger, J., Matern, S., Klefoth, T., Wolter, C., Feldhege, F., Monk, C.T., Arlinghaus, R., 2023. Ecosystem-based management outperforms species-focused stocking for enhancing fish populations. *Science* 379, 946–951.
- Reeve, C., Rowsey, L.E., Speers-Roesch, B., 2022. Inactivity and the passive slowing effect of cold on resting metabolism as the primary drivers of energy savings in overwintering fishes. *J. Exp. Biol.* 225, jeb243407.
- Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., Müller, M., 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinform.* 12, 1–8.
- Roche, D.G., Kruuk, L.E., Lanfear, R., Binning, S.A., 2015. Public data archiving in ecology and evolution: how well are we doing? *PLoS Biol.* 13, e1002295.
- Rohtla, M., Moland, E., Skiftesvik, A.B., Thorstad, E.B., Bosgraaf, S., Olsen, E.M., Browman, H.I., Durif, C.M., 2022. Overwintering behaviour of yellow-stage European eel (*Anguilla anguilla*) in a natural marine fjord system. *Estuar., Coast. Shelf Sci.* 276, 108016.
- Sadler, K., 1979. Effects of temperature on the growth and survival of the European eel, *Anguilla anguilla* L. *J. Fish. Biol.* 15, 499–507.

- Schmetterling, D.A., 2003. Reconnecting a fragmented river: movements of westslope cutthroat trout and bull trout after transport upstream of Milltown Dam, Montana. *North Am. J. Fish. Manag.* 23, 721–731.
- Schmidt, J., 1912. The reproduction and spawning-places of the fresh-water eel (*Anguilla vulgaris*). *Nature* 89, 633–636.
- Schmidt, J., 1922. The breeding places of the eel. *Philos. Trans. R. Soc. Lond. Ser. B* 211, 179–208.
- Sundin, J., Jacobson, B., van Gemert, R., Persson, J., Myrenås, E., Jacobson, P., 2023. Stress hos europeisk ål under sumpning och transport – effekter av fångst och transport. *Aqua notes Uppsala: Institutionen för akvatiska resurser* 25. <https://doi.org/10.54612/a.4r2gje6cg>.
- Sutherland, C., Hare, D., Johnson, P.J., Linden, D.W., Montgomery, R.A., Droge, E., 2023. Practical advice on variable selection and reporting using Akaike information criterion. *Proc. R. Soc. B* 290, 20231261.
- Swanberg, T.R., 1997. Movements of bull trout (*Salvelinus confluentus*) in the Clark Fork River system after transport upstream of Milltown Dam. *Northwest Sci.* 71, 313–317.
- Taft, E., 2000. Fish protection technologies: a status report. *Environ. Sci. Policy* 3, 349–359.
- 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.
- Team, R.C., 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Uhlmann, S.S., Broadhurst, M.K., 2015. Mitigating unaccounted fishing mortality from gillnets and traps. *Fish Fish* 16, 183–229.
- Veldhuizen, L., Berentsen, P., De Boer, I., Van De Vis, J., Bokkers, E., 2018. Fish welfare in capture fisheries: a review of injuries and mortality. *Fish. Res.* 204, 41–48.
- Verhelst, P., Reubens, J., Buysse, D., Goethals, P., Van Wichelen, J., Moens, T., 2021. Toward a roadmap for diadromous fish conservation: the Big Five considerations. *Front. Ecol. Environ.* 19, 396–403.
- Ward, D.L., Boyce, R.R., Young, F.R., Olney, F.E., 1997. A review and assessment of transportation studies for juvenile Chinook salmon in the Snake River. *North Am. J. Fish. Manag.* 17, 652–662.
- Weigel, D., Koch, I., Monzyk, F., Sharpe, C., Narum, S., Caudill, C.C., 2019. Evaluation of a trap-and-transport program for a threatened population of steelhead (*Oncorhynchus mykiss*). *Conserv. Genet.* 20, 1195–1199.
- Werner, C.M., Stuble, K.L., Groves, A.M., Young, T.P., 2020. Year effects: interannual variation as a driver of community assembly dynamics. *Ecology* 101, e03104.
- Westerberg, H., Sjöberg, N., 2015. Overwintering dormancy behaviour of the European eel (*Anguilla anguilla* L.) in a large lake. *Ecol. Freshw. Fish.* 24, 532–543.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. *J. Open Source Softw.* 4, 1686.
- Wickström, H., 2015. Trap and transport av ål från Lagan 2014 - Fördjupad kvalitetskontroll. Swedish University of Agricultural Sciences. Dnr: SLU. aqua.2015.5.5-5.
- Wright, R.M., Piper, A.T., Aarestrup, K., Azevedo, J.M.N., Cowan, G., Don, A., Gollock, M., Rodriguez Ramallo, S., Velterop, R., Walker, A., Westerberg, H., Righton, D., 2022. First direct evidence of adult European eels migrating to their breeding place in the Sargasso Sea. *Sci. Rep.* 12, 15362.