

When the Eel Meets Dams: Larger Dams' Long-Term Impacts on *Anguilla anguilla* (L., 1758)

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Diadromous fish, like the European eel Anguilla anguilla (L., 1758), are highly threatened by dams that disrupt river connectivity, consequently impeding fish movements to reach feeding and spawning habitats. In this study, variation in eel occurrence between a historical period (1940-1970) and recent data (2016-2020) was assessed throughout the Sardinian rivers' network (more than 450 sites). Using Boosted Regression Trees (BRT) we investigated relationships between eel's occurrence and a set of spatial and temporal environmental variables including a set of dams' construction features for each period. An overall decrease by 65% of eel's occurrence was noticed during the ca. 80-years period under scrutiny. Considering a subset (105 and 88 sites for the historical and the recent period, respectively) characterized by the presence of larger dams (height >15 m), eel's occurrence dropped by 85%. Conversely, eel's occurrence dropped only by ca. 44% in dam-free sites. During the historical period, eel's occurrence was mostly affected by time since the initial habitat fragmentation, flow, distance to dams, connectivity, and dams' height. In the most recent period, eel's occurrence is mostly affected by dams' building year, dam-to-sea distance, and, again, dams' height. Results pinpoint that dams' construction features and the time from their construction have significant negative effects on eel's occurrence. Addition of future effective eel restoration practices, apart any other adverse environmental stressor, must consider dams' removal, wherever socially sustainable or alternatively, the modification of construction features of dams (like excessive height) and the addition of fish ladders.

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INTRODUCTION

Freshwaters are biodiversity hotspots with 13,000 fish species inhabiting rivers and lakes (Lévêque et al., 2008). Free-flowing rivers provide migration routes for aquatic and riparian species, allow the transportation of sediments and nutrients, enable groundwater recharge, and mitigate flooding (Poff et al., 1997; Tickner et al., 2020). At the same time, rivers are essential elements for biodiversity and humans' wellbeing (Addams et al., 2009; Russi et al., 2013). Rivers are among the most threatened ecosystems by anthropogenic disturbances (Vörösmarty et al., 2010) including a large variety of obstacles (e.g., dams and weirs, road crossings, hydroelectric power plants, water abstraction for irrigation, flood control systems for municipal water security) (Welcomme, 1995; Jungwirth et al., 2000; Nilsson et al., 2005). Dams' construction has seen an acceleration worldwide during 1950/ 1960s (Dynesius and Nilsson, 1994; Postel and Richter, 2003; MacGregor et al., 2009), and more than two thirds of larger rivers have been fragmented (Grill et al., 2015). At present, ca. 2.8 million dams

are operating and roughly 3,700 major dams are being constructed or planned (Zarfl et al., 2015; Grill et al., 2019).

Environmental alterations caused by anthropogenic obstacles affect the natural hydrology and connectivity of stream networks, and their ability to transport sediments (Bednarek 2001; Fullerton et al., 2010; Grill et al., 2015; Rincón et al., 2017). Modifying the river flow (Grill et al., 2015), dams pose increasing threats to freshwater ecosystems and mobile biota, particularly fish (Arthington et al., 2016). These barriers play a role in the degradation of water quality (Chowdhury and Kipgen, 2013; Galipeau et al., 2013; Opperman et al., 2019; Barbarossa et al., 2020), cause variations in temperature and water flows (Poff et al., 1997; Richter et al., 2010; Opperman et al., 2017), impair biodiversity, and in particular impede migration, threat the spawning habitats and alter the natural gene flows (Silva et al., 2018; Wilkes et al., 2018; Birnie-Gauvin and Aarestrup, 2019), ultimately increasing the risk of extinction of fish (Lucas and Baras, 2001; Ding et al., 2018). In addition, to adequate habitat for spawning and development, fish require connectivity to migrate freely between different areas of the river and to lakes and to the sea. High connectivity between freshwater and marine habitats facilitates the exchange of matter, energy, and nutrients, with species contributing to the longitudinal transfer and supporting important ecosystem services (Holmlund and Hammer, 1999). For instance, anthropogenic intervention in river discharge result in reduced flushing up to unnaturally extended periods of estuary mouth closure and reduce the connectivity between freshwater habitats and the sea (Potter et al., 2010; Lloyd et al., 2012; Podda et al., 2020). In many estuarine systems, especially those with Mediterranean climate, sand bars are deposited during low flow periods at the river mouth, resulting in truncation of the connection between freshwater and marine habitats (Potter et al., 2010; Suari et al., 2019; Podda et al., 2020). These interruptions and the river flow alteration can have severe implications especially for diadromous species (Gillanders et al., 2003), like the European eel Anguilla anguilla (L., 1758). This diadromous species demonstrates high plasticity in habitat use (Daverat et al., 2006), and is currently exposed to numerous threats along the migratory routes in both marine and freshwater realms (Culurgioni et al., 2014, 2015; Bevacqua et al., 2015; Aalto et al., 2016; Baltazar-Soares et al., 2014; Dekker and Beaulaton, 2016; Drouineau et al., 2018; Podda et al., 2021). Because of these hazards, A. anguilla is progressively declining since the 1970s (ICES, 2021), and is currently classified as Critically Endangered (CR) (IUCN, 2014; Pike et al., 2020) and protected according to the European Council regulation 1100/2007 (EC, 2007).

One of the major threats to the European eel is the presence of large instream barriers restricting access to juveniles leaving the sea after recruitment (Dekker, 2003; Piper et al., 2013; Tamario et al., 2019). The more so as the natural recruitment is the only source of supply of the species (Pedersen and Rasmussen, 2016). Despite their extraordinary climb ability, only a minor proportion of eels can successfully overcome large dams (White and Knights, 1997). Furthermore, direct mortality and sublethal injuries can occur during obstacle passages because of impingements on hard structures, even in the absence of turbines (Bruijs and Durif, 2009). Moreover, increased costs of metabolic energy caused by obstacle passage may have a delayed impact on eel's migration success and fecundity (Van Ginneken and van den Thillart, 2000). Delays induced by dams can impair escapement, especially when the migration suitability window is limited (Verbiest et al., 2012; Drouineau et al., 2017).

In this study, the impacts of large dams on the occurrence of the European eel *A. anguilla* in the Sardinian hydrographic district (Central-Western Mediterranean) have been investigated considering how the pre and post dams' building can affect the long-term presence of eels. We studied relationships among current and historical occurrence of the European eel hypothesizing potential negative effects of a set of temporal, spatial, and dams' related descriptors using a multivariate approach.

MATERIALS AND METHODS

Study Area

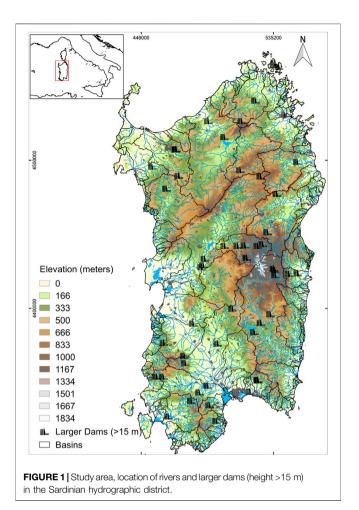
Sardinia (Italy) is the second largest island in the Mediterranean $(area = 24,106 \text{ km}^2)$. Its hydrographic district coincides with the entire regional territory (Figure 1). The Sardinian hydrographic network is characterized by a reduced number of perennial rivers and the prevalence of intermittent streams (Palmas et al., 2022). Mediterranean climate is typically bi-seasonal with severe drought summer and rainy autumn/winter that determine irregular flow and strong seasonal hydrological fluctuations (Sabatini et al., 2011, 2018; Palmas et al., 2020; Podda et al., 2020). Average annual precipitations range from 500 to 900 mm (De Waele et al., 2010; Moccia et al., 2020). Artificial interruptions of longitudinal river continuity, like dams, strongly influence the annual hydrological cycle of these streams (Naselli-Flores and Lugliè, 2014). An increasing construction of artificial barriers has been observed since the end of the 19th century to provide water for human use (Marchetto et al., 2009; Montaldo and Sarigu, 2017).

Eels' Data

Two datasets were collected in the frame of the monitoring program for the official Fish Inventory of the Sardinian region (VV.AA., 2022).

The point-to-point historical occurrence data available from 1940 (1940–1970, hereafter historical period), derive from scientific and informative publications of regional origin for a total of 238 sites (**Supplementary Table S1**), and were georeferenced in a Geographical Information System (GIS) through the Open-Source Software Quantum Gis 2.18.3 (QGIS) (http://www.qgis.org/).

Recent occurrence data (2016–2020; hereafter current period) were collected for 214 sites. Surveys were conducted mainly during the dry season using electrofishing (0-4 Ampere, 0-600 Volt) in habitats ranging from sea level to 1,262 m a.s.l. For comparisons, current data were then integrated into the GIS layer including historical data. Sites have been selected in proportion to the amplitude of the hydrographic basin and in order to have a historical continuity with the data deriving from the previous historical period allowing an appropriate spatial



coverage in relation to the extension of the whole hydrographic network of Sardinia (VV.AA., 2022).

Datasets were analyzed separately, and sites influenced by at least one downstream dam were identified. In each dataset, sites located on free-flow rivers or under dams have been analyzed separately from those located above dams.

Data Analysis

Twelve variables, ten continuous and two dummies, have been investigated as potential factors explaining the eel's occurrence related to dams' effects. The variables were subdivided into four categories: temporal, spatial, dams' features, and site-specific, respectively (**Table 1**). Geospatial information on dams were acquired from the Regional Land Information System of Sardinia (RAS, 2021).

Differences between the percentage of eel's occurrence during the historical and recent period were evaluated using the X² test (*p*-value < 0.05). Pairwise collinearity in explanatory variables was examined by scatter plots to exclude redundancy between paired variables disregarding combinations with Spearman's rho >0.7. Variables were discarded from the pairwise combination based on the Variance Inflation Factor (VIF) discarding observation with VIF > 3 (Zuur et al., 2010).

The set of dams' descriptors for the two datasets was fitted using Boosted Regression Tree models (BRT) (Friedman 2001; Elith et al., 2008). BRT is a machine-learning method for data exploration and analysis recently introduced into the fields of ecology and conservation biology (Déath, 2007; Elith et al., 2008). BRTs are suited to select the most relevant predictors from a large set of candidate variables, do not depend on the normality and homoscedasticity of the data, integrate nonlinear responses, and reduce the problem of 'overfitting' (Elith et al., 2008). BRTs allow to calculate multiple regression models (regression trees) and include an adaptive method to combine many simple models to give improbe predictive performance (boosting). Within the BRT model, terms that are used to optimize predictive performance are represented by the learning rate, tree complexity, and bagging factor (Friedman, 2001; Elith et al., 2008). BRTs were adjusted with a learning rate to return an optimal number of regression trees (1,000-1,500), which has been associated with data overfitting. Trees' complexity of two refers to the number of nodes in a tree that has been selected (Elith et al., 2008). We use tree complexity to control the number of nodes, to set the maximum number of interactions between predictor variables that are possible, and we used a bagging factor of 0.5 (Friedman, 2001). Variable selection is not necessary for constructing BRTs because they generally ignore non-informative predictors (Elith et al., 2008). The BRT analysis was conducted using the Bernoulli family of occurrence. For visualizing the results, we calculated the partial dependencies that depict the relationships between the response and each predictor variable while controlling for the average effects of the remaining predictors (Friedman, 2001; Friedman and Meulman, 2003).

Our approach did not allow to assess confidence intervals for BRTs, used when a large number of BRT sub-models are fitted. The partial dependence plots for parameters with a contribution >10% were used to visualize the effect of each variable on eel's occurrence. As this method does not deliver *p*-values, but uses internal validation processes, BTRs performance were evaluated using the amount of total deviance explained (%) and cross-validated correlation between model prediction and observed data (CV correlation) (Derville et al., 2016; Nieto and Mélin, 2017; Ju et al., 2021; Saha et al., 2021). Statistical analyses were conducted using the opensource R software (R Core Team, 2021). Specifically, *gbm* (Greenwell et al., 2020), and *dismo* (Hijmans et al., 2011) packages for BRT analyses, and partial dependence plots with smoothing for each variable.

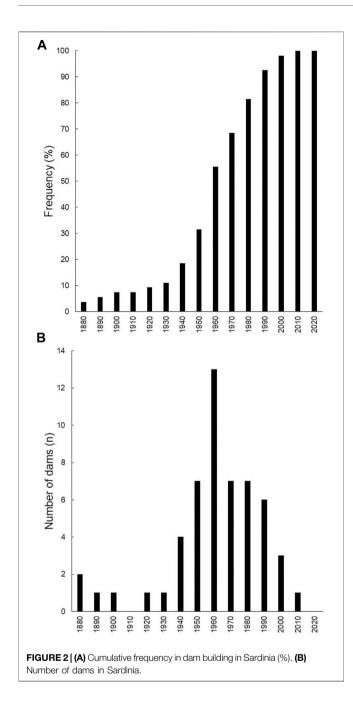
RESULTS

Dams in the Sardinian Hydrographic District

Although the first dam in Sardinia date back to the end of the 19th century, a rapid increase in dams' construction has been observed from the late 1960s to the late 1990s (**Figure 2A**). More than 50% of the 54 larger dams (>15 m height, mean height \pm Standard Deviation—SD, 42.5 \pm 22.3 m) were built between 1940 and 1960 (**Figure 2B**), with two of the most recent dams not completely built yet. Furthermore, Sardinia is currently

TABLE 1 | Description of the investigated variables.

Variable Name (ABBREVIATION)	Description	Туре	Unit
Year of fragmentation (FRAGMENTATION)	Number of years since dam construction compared to sampling year or the year of construction of the oldest dam in cases with multiple dams	Temporal	
Year of dam building (YEAR)	Year of construction of the nearest dam downstream the site	Temporal	
Height (HEIGHT)	Dam height	Dam	m
		feature	
Volume (VOL)	Dam volume	Dam	m ³
		feature	
Flow (FLOW)	Dam flow	Dam	m ^{3s-1}
		feature	
Elevation (ELEV)	Elevation above sea level	Dam	m
		feature	
Distance of the dam from the site (D_STA)	The distance of the dam from the site	Spatial	km
Distance of the dam from the sea (D_SEA)	The distance of the dam from the sea	Spatial	km
Dendritic Connectivity Index (DCI)	Proxy of the fragmentation of the longitudinal river connectivity caused by dams in relation to the presence of eels.	Spatial	%
(Cote et al., 2009)	DCI = 100 I L ⁻¹ where I is the current length of the river from the sea to the first barrier without fish passage, and L is		
	the maximum historical eel migration distance for each site		
Number of dams (DAM)	Number of downstream dams in each site	Site-	1 or 2 in the historical dataset
		specific	From 1 to 6 in the current dataset
River mouth condition (MOUTH)		Site-	0 = closed, for rivers which don't flow into a
		specific	lagoon
			1 = open, rivers which flow into a lagoon
Fishing pressure (FISH)	Presence of fishing pressure along the river to its river mouth, (http://www.sardegnaagricoltura.it)	Site-	0 = absence of fishing activities
		specific	1 = presence of fishing activities



lacking river flow regulations, and fishways or fish ladders are mainly absent or not working with one single exception (i.e., Casteldoria dam, height = 26.6 m, $40^{\circ}53.3843 \text{ N}-08^{\circ}53.7534 \text{ E}$, recently built, 2015).

Eel's Occurrence in Sardinian Rivers

Comparing sites correspondence (one observation per site for each dataset) between the historical and the current datasets, a total of 54 sites matched (23% and 25% of number of sites, respectively). The analysis of the historical period (1940–1970) revealed that eel's occurrence amounted of ca. 95% (**Figure 3A**). In the current period (2016–2020) we observed a strong

contraction (ca. 65%, X^2 , p < 0.001) of eel's occurrence, which decreased to only 30% (**Figure 3B**).

Considering only sites with downstream dams (88 and 105 sites for the historical and current period, respectively), eel's occurrence dropped from 92% to 7% respectively, with a total (statistically significant) decrease of ca. 85% (X^2 , p < 0.001). In this subset, the proportion of sites influenced by downstream dams was ca. 37% and 49% for the two periods, respectively.

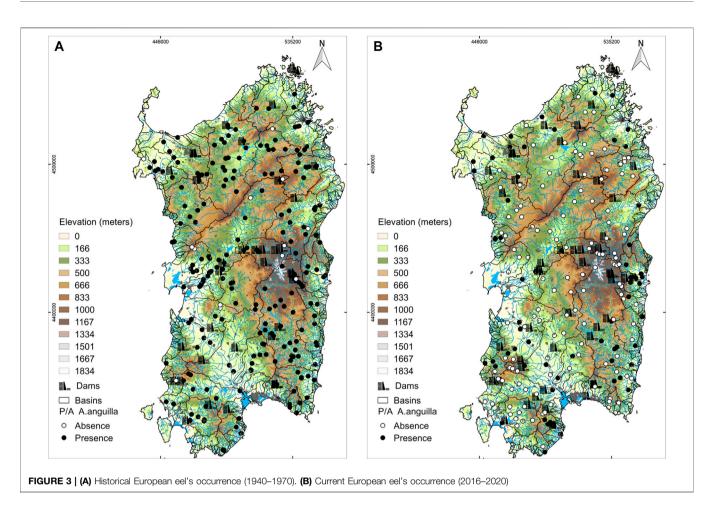
During the historical period, 96% of free flow sites (i.e., sites without dams or sites without downstream dams) had eels, whereas in the current period this value dropped to 52%, with a decreasing rate between the two periods of ca. 44% (X^2 , p < 0.001).

Effect of Larger Dams on Eel's Occurrence

After analyzing dams' descriptors through Spearman correlation (**Supplementary Figures S1, S2**) and using VIF score >3 as a threshold (**Supplementary Tables S2, S3**), only eight descriptors were included for the modeling of the data from the historical period, and seven for the current one. Five descriptors were common between the datasets: dendritic connectivity index (DCI), height (HEIGHT) and flow (FLOW) of dams, river mouth condition (MOUTH), and fishing pressure (FISH). The predictors in the modeling of the historical period also included the temporal fragmentation (FRAGMENTATION), the distance of dams from each site (D_STA) and the dams' elevation (ELEV), while the year of dams' building (YEAR) and the distance of dams from the sea (D_SEA) were included in the modeling of the current period.

The historical BRT model shows that five descriptors cumulatively explain 88.4% of the model: FRAGMENTATION (relative contribution = 22.3%), FLOW (22.2%), D_STA (14.7%), DCI (14.6%), HEIGHT (14.6%). Explained deviance (51%) and CV correlation (0.40) suggest that the relationships between dams' characteristics and the eel's occurrence are quite robust. The partial dependence plots obtained after BRT models (Figure 4) show that the contribution of FRAGMENTATION to eel's occurrence is greatest 20 years after dams' building. The difference across that threshold is very narrow, with a value of 91% and 94% occurrence, below and above downstream dams, respectively. The contribution of FLOW to eel's occurrence is maximum over a threshold of ca. 1,300 m^3s^{-1} , with a value of 87% below and 100% above the threshold. The highest effect of D STA is observed more than 5 km far from dams, where mean eel's occurrence is 75%, whereas at closer sites this value is 96%. The HEIGHT effect was highest above ca. 60 m, where eel's occurrence (100%) was higher than that (90%) in sites with downstream dams <60 m height. The index of river connectivity (DCI) has the highest effect on eel's occurrence within the interval of 60%-80% DCI with mean eel's occurrence of 86% below 60% of DCI, and 100% above this threshold.

The BRT model for the most recent period reveals that three descriptors, YEAR (54.6% of relative contribution), D_SEA (21.3%), and HEIGHT (13.4%), explain cumulatively 91% of the model. There is well goodness of fit of the BRT with an explained deviance of 62% and a CV correlation of 0.67. The partial dependence plots obtained after BRT models (**Figure 5**) show that the effect of dams' age is highest (25%) after 1980 (i.e., dams with less than ca. 40 years) and drops to 2% in more



recent years. The contribution of D_SEA to eel's occurrence is highest below 20 km, with the highest mean occurrence (13%) in sites close to the sea and the lowest (2%) in the farthest ones. The highest contribution of HEIGHT is observed for dams between 30 and 80 m, which have a mean eel's occurrence of 5%. In sites with dams <30 m occurrence is 10%, whereas in sites with dams >80 m (some of which are still not completed) the mean eel's occurrence is 7%.

DISCUSSION

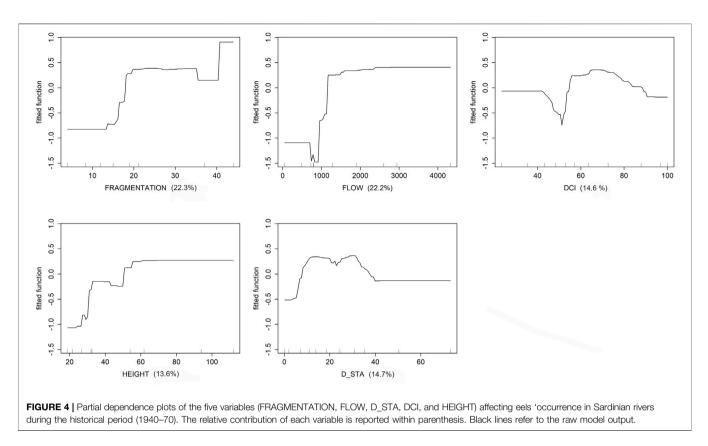
Impacts of Large Dams on Eel's Occurrence

A. anguilla is worldwide ranked as critically endangered species due to an ample array of often synergistic, anthropogenic threats (Jacoby et al., 2015; Miller et al., 2016; Drouineau et al., 2018). Moreover, the presence of dams, causing a physical interruption of river connectivity, river flow reduction or modification, and loss and deterioration of habitats, may also critically affect eel's survival during their freshwater life stage (Feunteun, 2002; Tamario et al., 2019; Watz et al., 2019).

The dramatic decline of the European eel's recruitment reported worldwide (Dekker, 2003, 2004; ICES, 2021) also affects the Sardinian rivers' network, where we observed a huge decrease in eel's occurrence. Indeed, considering only free-flow sites (i.e., sites in dam-free rivers or sites without downstream dams), the European eel occupied most of the main Sardinian rivers until the 1970s (ca. 95%). The overall 44% reduction in species' occurrence between the two periods in these sites suggests that a relevant proportion of such a decline is independent by dams. Nevertheless, the decline of eel's occurrence in Sardinian rivers is also severely affected by damming with eel's occurrence in sites above dams dropping by 85% between the two periods. Our results, ultimately, confirm that dams have a severe impact on eels due to the fragmentation of migration habitats and the alteration of river flow (Poff and Schmidt, 2016; Dias et al., 2017).

We hypothesized that dams' height (Larinier, 2001; Merg et al., 2020), dams' age (Atkinson et al., 2020) and the decreased river flow due to the oldest dams (Legault et al., 2003) could negatively affect eel's migration.

In both periods under scrutiny, as expected, the height of dams could have had a negative effect on eel's occurrence and such an impact was lower during the old period but severely exacerbated in recent years. In the most recent period, the eel's occurrence above dams >80 m high is, counterintuitively, higher than that in lower dams. This apparent discrepancy can be ascribed to the fact that especially some of the very tall dams (>80 m) were built only very recently, thus the presence of eels above the dam stems from times before the dam was finalized or filled. For catadromous fish,



including eels, climbing out of the water to surpass a barrier is challenging and linked to high metabolic costs (Edeline et al., 2004; Briand et al., 2005; Bult and Dekker 2007).

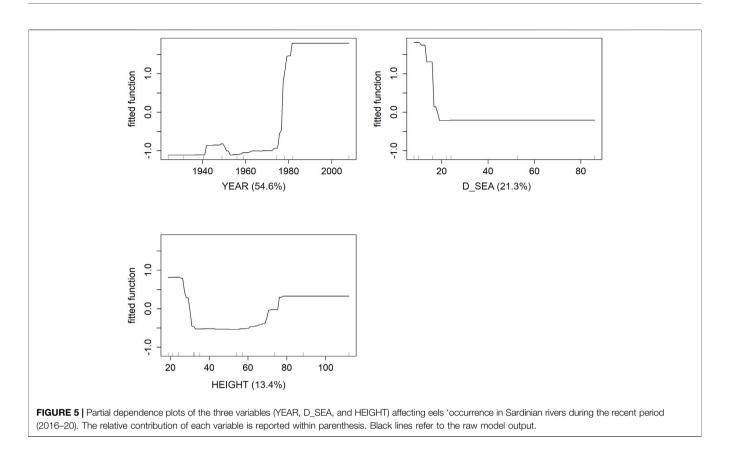
The age of the dams (estimated using either year of construction-in the most recent period-or temporal fragmentation-in the old one) negatively influence eel's occurrence. We contend that the oldest dams installed in Sardinia, possibly due to technical and financial limitations, have been built in rivers of lower order or in the upper part of the rivers, thus having a minor negative effect on the overall river connectivity (Segurado et al., 2013). In the most recent period, the strongest impact of fragmentation by dams could be attributable to the technological progress and modernization that allowed building dams with more effective water retention and, thus, the stronger capacity of interrupting the river flow in more downstream river sections (Haidvogl, 2018; Merg et al., 2020). Nevertheless, the effect of river flow is a major factor influencing eel's occurrence only in the old period. The minimum or nihil effect of river flow and the DCI index on eel's occurrence in the most recent period could be attributable to the very low river flow in the last 30 years, caused by prolonged drought, which, most probably impaired eels' ability to migrate upstream. The negative effect of dams appears more evident during the old period, when either river flow or the DCI index explains significant proportions of eel's occurrence variations. The major role of river flow and the DCI index, in the old period only, and their ininfluence in the most recent one, is corroborated by the intensity of water flow involved in the route choice (Legault et al., 2003), causing the silencing of environmental stimuli when it is too low (Trancart

et al., 2018, 2020) and, in the most extreme cases, interrupting downstream (Durif, 2003) and upstream migration (Podda et al., 2020).

In both periods, the distance from the sea explains significant proportions of eel's occurrence. The more distant from the sea the more probable is the presence of natural (and artificial) obstacles to be crossed by fish (Merg et al., 2020), which, indeed, becomes a severe impediment to migration, especially when river connectivity is limited due to low river flow.

Giving Future to the European Eel

Our study reveals that different dams' attributes can explain the current decline of A. anguilla. Along with damming, other factors, associated with excessive human pressure but also with climate change, are severely impairing eel's occurrence. To foster the conservation of the European eel, many authors have pushed to mitigate its commercial exploitation (Nielsen and Prouzet, 2008; Henderson et al., 2011; Aalto et al., 2016; ICES, 2021). In addition, we contend that a strong effort should be paid to eliminate highly impacting artificial barriers or, at least, to mitigate their impacts with more sustainable actions, tools, and devices. While creating unobstructed migration routes between the spawning area in the sea and freshwater growth habitats could be preferable (Feunteun, 2002; Drouineau et al., 2018; Rodeles et al., 2021), the removal of artificial barriers could be, locally, socially, and economically impracticable. Some attempts have been made and succeeded with other catadromous endangered species (Graf, 2003; Stanley and Doyle, 2003; Harris et al., 2016), including the American eel



Anguilla rostrata (Lesueur, 1817) (Hitt et al., 2012; Turner et al., 2018). The removal of artificial barriers could be not exempt from collateral negative effects, including, for instance, the facilitation of biological invasions (Rahel, 2013; Milt et al., 2018), the spill of toxic sediments, and sudden changes in hydromorphology (Stanley and Doyle, 2003; Gangloff, 2013).

Except these general suggestions, in our context it could be crucial to control and reducing the uptake of water for human use above dams and, at the same time, ensuring a Minimum Vital Flow (MVF; Moccia et al., 2020) that guarantees the morphological, hydrological, physical-chemical, and biological integrity downstream will enable the protection of eel's habitats in the short and long term (Dudgeon et al., 2006). A potentially compensative solution for partial restoration of dammed river connectivity, without eliminating dams, could also profit of the construction of artificial fishways to allow eels' passage beyond dams (Seliger and Zeiringer, 2018), management measures both still lacking in Sardinia. Moreover, it would be advisable that any management, operation, and maintenance of large dams in Sardinia would be implemented within a regional control system aimed at harmonizing and standardizing information to support a correct use and management of these structures. Although this study was conducted on a purely regional scale, our results highlighted the major impact of dams on the European eel's occurrence in Sardinian rivers and its apparent worsening in the last 10 years. We conclude that, based on the general current crisis of this species, urgent actions are needed worldwide to restore their habitats by

reducing humans' pressure, ensuring a minimum vital flow, abating, wherever possible, artificial barriers to river connectivity, or, at least, implementing natural migration routes with artificial fishways.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

CP led conceptualization, field sampling, data curation, software realization, statistical analysis, formal writing, and original draft. FP conducted field sampling, software realization, writing, review, and editing. AP contributed for the supervision, writing, review, and editing. AS led the project administration, supervision, writing, review, and editing.

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SUPPLEMENTARY MATERIAL

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