



Review Paper

The decline of the ecosystem services generated by anadromous fish in the Iberian Peninsula

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Abstract This work aims to present an historical review of the ecosystem services provided by anadromous fish (i.e., species that migrate from the sea to the river to spawn) throughout Human time, as well as of the main related threats, focusing on the Iberian Peninsula region. Anadromous fish provide important provision, cultural, regulatory and supporting ecosystem services across their distribution range and have been extensively exploited by humans since prehistoric times. In the Iberian Peninsula, sea lamprey, allis and twaite shads, sea trout, Atlantic salmon and European sturgeon were once abundantly present in

several river basins covering what is now Portuguese and Spanish territory. These species have suffered a severe decline across their distribution range, mainly due to habitat loss and overexploitation. Considered regal delicacies, these fishes were once a statement on the tables of the highest social classes, a much appreciated bounty for the poorer population and are still an important part of the local gastronomy and economy. Such high economic and cultural interest encouraged intensive fishing. Currently, management efforts are being implemented, pairing habitat rehabilitation (e.g., construction of fish passes in obstacles to migration such as weirs and dams) with sustainable fisheries. Considering the present climate change scenario, these species are bound to endure increased pressures, demanding novel management approaches to ensure population numbers that are able to secure their sustainable exploitation.

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Introduction

Freshwater ecosystems are known to comprise the highest relative fish species richness on the globe, with 58% of species inhabiting inland waters (over 18,000, according to Nelson et al., 2016), and to support a variety of aquatic communities that provide a

wide range of ecosystem services (ES). The provision of food and cultural services that generate a direct source of income, the regulatory services such as nutrient transportation, or the supporting services such as nutrient cycling, are some examples of ES (see Sect. 2 for details) that can be supported by fish inhabiting freshwater (MA, 2005). However, the degradation of these ecosystems has been occurring at a fast pace and the status of the species, and consequently the services they provide, are becoming considerably deteriorated (Su et al., 2021).

According to the European Red List of Threatened Species, 37% of European freshwater fish species are considered threatened (Freyhof & Brooks, 2011). On what concerns specifically migratory fish, major impacts have been reported during the last five decades, causing an estimated global decline of 76%, and an even more pronounced decline of 93% for the European region (WWF, 2020). Throughout human history, freshwater fish have become an important resource for the establishment of populations worldwide, including the Iberian Peninsula (hereinafter Iberia). Evidence dates back to prehistoric times, with increasing importance until nowadays, accompanying the growing demand for protein associated with human population expansion (see Sect. 3). Among the fish found in rivers, the anadromous species, those that migrate from the feeding areas at sea to the spawning grounds in freshwater, have been particularly important for human provision, possibly due to the large aggregations formed and temporal predictability of the spawning runs. Presently, anadromous species are considered particularly threatened due to a multitude of anthropogenic pressures, which in turn has consequences in the ES they generate (see Sect. 4). In Iberian rivers these pressures are amplified by climate change, leading to a sharp decline in the availability of freshwater and consequently reducing the quality and quantity of habitat accessible to these species (Almeida et al., 2018).

This work aims to present a historical overview of the ES generated by anadromous fish in Iberia. It begins with a brief description (Sect. 2) of the key aspects of anadromous species and a comprehensive identification of the ES they generate, according to the Millennium Ecosystem Assessment classification (MA, 2005). This is followed by a historical analysis of the evolution of ES provided by anadromous species and their importance to human populations in

Iberia from prehistoric to modern ages (Sect. 3). The main threats and pressures to anadromous species and to the sustainable and rational exploitation of associated ES are detailed in Sect. 4. Current management efforts and measures that may be further developed towards the sustainability of the ES are outlined in Sect. 5. This review ends (Sect. 6) by addressing future perspectives for the ES provided by anadromous species and the measures considered necessary to sustainably enhance, or at least maintain, the services provided.

Anadromous fish: who are they and what ecosystem services they provide

Diadromous fish use both marine and freshwater environments to complete their life cycle, migrating between them to feed and reproduce. In the case of anadromous fish, spawning occurs in freshwater, and therefore several species have been commercially targeted in Iberian rivers for centuries by riverine communities (e.g., Stratoudakis et al., 2016; Almeida et al., 2021).

Anadromous species occurring in Iberia include the sea lamprey, *Petromyzon marinus* L. (Fig. 1a, b), the European river lamprey, *Lampetra fluviatilis* L., the allis shad, *Alosa alosa* L. (Fig. 1c), the twaite shad, *Alosa fallax* (Lacépède 1803), the sea trout, *Salmo trutta* L. (Fig. 1d), the Atlantic salmon *Salmo salar* L. and the European sturgeon (*Acipenser sturio* L.) (Collares-Pereira et al., 2021). All occur in both Portugal and Spain, with the exception of the European river lamprey and the European sturgeon. The first is Regionally Extinct in Spain since the construction of the Cedillo dam in river Tagus, which, at the time, blocked its migration to Spanish waters (Doadrio, 2001). In Portugal it is also considered rare and classified as Critically Endangered (Cabral et al., 2005). The European sturgeon is Regionally Extinct in Portugal, where its presence was historically detected in Douro, Tagus and Guadiana. In Spain it is classified as Endangered (EN) even though its presence has not been detected since 1992 in Guadalquivir (Doadrio et al., 2011). Globally it is classified as Critically Endangered.

The Atlantic salmon has always been found in small numbers in Portuguese waters, where it is classified as Critically Endangered (Cabral et al., 2005).

Fig. 1 Examples of anadromous fish targeted by freshwater commercial and recreational fisheries in the Iberian Peninsula: **a** and **b** sea lampreys *Petromyzon marinus* L. captured by a large fyke net, locally named “botirão”, used by professional fishermen in river Mondego (*Image*: Esmeralda Pereira); **c** allis shad *Alosa alosa* L. captured downstream the Coimbra dam during the spawning migration to the upstream stretches of river Mondego (*Image*: Ana Filipa Belo); **d** trout *Salmo trutta* L. captured by a fly fishing catch-and-release angler in river Mondego (*Image*: Manuel Pedroso)



Currently, the species is only regularly found in river Minho and, less frequently, in the rivers Lima, Cávado and Douro. It is more widespread in Spain, where it is classified as Endangered (Doadrio, 2001; Collares-Pereira et al., 2021). The sea trout, even though also classified as Critically Endangered in Portugal, has a wider distribution, occurring in the North of Spain (i.e., Galicia, Asturias, Cantabria, Biscay, Gipuzkoa and Navarre basins (Álvarez et al., 2010)) and in the North and Centre of Portugal (i.e., Minho, Lima, Cávado, Douro, Vouga and Mondego basins), which is currently the southern limit of its distribution (Collares-Pereira et al., 2021).

All these species provide important ES, as presented in Fig. 2 and Table 1. Their conservation status and population trends, however, emphasise that species-specific management and conservation actions should be applied, to maintain the associated ES or enhance them in the medium-long term.

In the present work, the ES delivered by anadromous fish in Iberia are identified considering the Millennium Ecosystem Assessment classification (MA), which was the first comprehensive global assessment of the consequences of ecosystem change for human well-being (MA, 2005). It states that approximately 60 percent of the ES evaluated during the Millennium Ecosystem Assessment—MA (2001–2005) are being

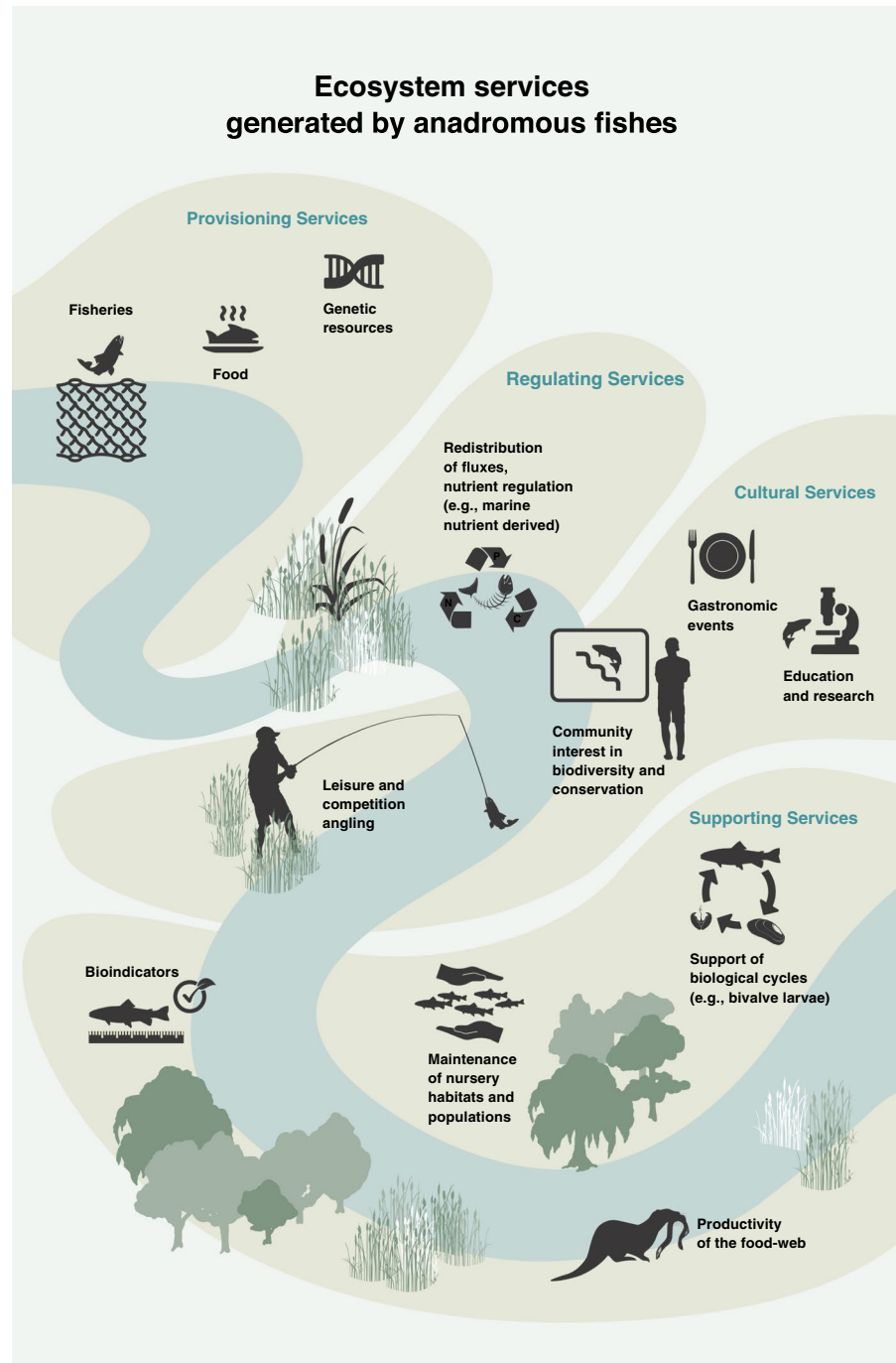
degraded or used unsustainably, with major implications for development, poverty alleviation and the strategies needed by societies to cope with and adapt to long-term environmental change. In this assessment, the ES are divided into four categories, including provisional, cultural, regulatory, and supporting services. Provisioning ES are products that can be traded, consumed or used directly, thus they are the desired ‘end-products’ of nature, providing visible benefits to society (e.g., food, materials, and energy). Cultural ES are intangible benefits derived by spiritual, emotional, recreational or educational activities (MA, 2005; Haines-Young & Potschin, 2010). The regulatory ES (e.g., nutrient transportation) and the supporting ES (e.g., nutrient cycling) are relevant ES provided by anadromous fish as their life cycle involves migration between freshwater and marine environments.

The importance of anadromous fish throughout human time

Prehistoric times

Evidence for the importance of freshwater fisheries to human populations dates back to prehistoric

Fig. 2 Examples of ecosystem services generated by anadromous fishes in the Iberian Peninsula



times. According to zooarchaeological records, the exploitation of freshwater fish started to be identified most commonly after the Last Glacial Maximum that occurred approximately 20,000 years ago (Richards et al., 2001). The quantity and predictability of anadromous fish spawning runs is considered to have

played an important role in the subsistence and settlement strategies of prehistoric humans (Banks, 2000). Stable isotope analysis of human and animal specimens from mid-Holocene in north-eastern North America confirmed that anadromous fish were an important seasonal component of human diet

Table 1 Ecosystem Services (ES) generated by the anadromous species occurring in Iberia, from the literature, following MA classification (MA, 2005)

Species	ES identification	Description	Examples	References
Allis shad (<i>Alosa alosa</i> L.)	Provisioning	Food (i.e., nutritional source)	Iberian gastronomy (e.g., fried shad with bread and roe mix)	Lillebø et al. (2020) (Vouga basin), O'Higgins et al. (2019) and Gastronomias (1997a, b)
		Fisheries (i.e., socio-economic value)	High commercial value (e.g., 10 €/kg to 16 €/kg, depending on the year)	Azeiteiro et al. (2021), Baglinière et al. (2003), Bao et al. (2015), Braga et al. (2022) (Minho basin); Lillebø et al. (2020) (Vouga basin); Mota et al. (2016) and Stratoudakis et al. (2016, 2020) (Mondego basin)
		Genetic resources (i.e., gene pool or genetic material available for human exploitation)	Stocks identification and respective management	Baglinière et al. (2003)
	Cultural	Gastronomic events (i.e., gastronomic festivals; gastronomic brotherhoods)	Gastronomic festivals in several basins (Minho, Douro, Vouga, Mondego, Tagus) Gastronomic Brotherhoods (e.g., Confraria do Debulho de Sável; Confraria Gastronómica "O Moli-ceiro"; Confraria Gastronómica do Sável e da Lampreia)	Lillebø et al. (2020) and O'Higgins et al. (2019) (Vouga) Gastronomias (1997a, b) Archeevo (2022)
		Art, folklore and traditional know-how	Open-air Palaeolithic parietal art site in the Côa Valley (Portugal)	Mercier et al. (2006)
		Community interest in biodiversity and conservation	Cultural/heritage value in the river Minho Conservation efforts/legacy/conservation value	Braga et al. (2022), Azeiteiro et al. (2021) and Mota et al. (2016)
			Appendix III of the Bern Convention and Appendix II of the European Union's Habitats Directive of 1992	Mota et al. (2015)
		Conservation interest in the OSPAR (The Convention for the Protection of the Marine Environment of the North-East Atlantic)		Mateus et al. (2015) and OSPAR (2021)
	Education and Research	Research model (e.g., biology, migration biochemistry and physiology, ecology, hybridization studies)		Alexandrino (1996), Belo (ongoing), Eiras (1981) and Mota (2014)

Table 1 (continued)

Species	ES identification	Description	Examples	References
Sea lamprey (<i>Petromyzon marinus</i> L.)	Regulating	Redistribution of fluxes and nutrient regulation (e.g., marine nutrient derived)	Nutrients flux from sea and estuary to river with mortality of spawners Provide nitrogen and phosphorous subsidies throughout western Europe	Baglinière et al. (2003) and Mota and Antunes (2012) Poulet et al. (2021)
	Supporting	Productivity of the food-web Support of biological cycles (e.g., host species) Maintenance of nursery habitats and populations	Sea lamprey diet Sea lamprey host Freshwater environment during the embryo–larval stage play an important role in development	Braga et al. (2020) Silva et al. (2014) Baglinière et al. (2003)
	Provisional	Bioindicators Food (i.e., nutritional source) Fisheries (i.e., socio-economic value)	Excellent indicator of connectivity and biological quality Iberian gastronomy (e.g., Lamprey rice) High market value (e.g., Average range of Lamprey Unit Price to the intermediate buyer: 10,00 € to 40,00 €)	Baglinière et al. (2003) Mateus et al. (2012) and reviewed in Braga et al. (2020) Andrade et al. (2007), Mateus et al. (2012), Almeida et al. (2018), reviewed in Braga et al. (2020) and Almeida et al. (2021)
Cultural	Genetic resources (i.e., gene pool or genetic material available for human exploitation)	Genetic compatibility between sea lamprey male and female plays an important role in hatching success	Rodríguez-Muñoz and Tregenza (2009)	
	Gastronomic events (i.e., gastronomic festivals; gastronomic brotherhoods)	Dozens of gastronomic festivals take place every year in Portugal Gastronomic Brotherhoods (e.g., “Confraria da Lampreia de Pena-cova”) Roman-age stone foundations of lamprey traps constructed in riverbeds (“Pesqueiras”)	Reviewed in Almeida et al. (2021) Gastronomias (1997a, b) (http://www.gastronomias.com/confrarias/) Leite (1999), Fernandes (2017), Reviewed in Araújo et al. (2016) and Almeida et al. (2021)	
	Art, folklore and traditional know-how Community interest in biodiversity and conservation	Community interest (Council of the European Communities, 1992) Conservation interest in the OSPAR (The Convention for the Protection of the Marine Environment of the North-East Atlantic)	Andrade et al. (2007), Almeida et al. (2008), Maitland et al. (2015) and reviewed in Braga et al. (2020)	

Table 1 (continued)

Species	ES identification	Description	Examples	References
River lamprey (<i>Lampetra fluviatilis</i> L.)		Education and Research	“Living fossil” Research model (e.g., ecological, human diseases)	Smith et al. (2013) and reviewed in Braga et al. (2020)
	Regulating	Redistribution of fluxes and nutrient regulation (e.g., marine nutrient derived)	Life-history contributions (e.g., adult spawners mortality)	Nislow and Kynard (2009), Araujo et al. (2013a) reviewed in Braga et al. (2020)
	Supporting	Productivity of the food-web	European otter (<i>Lutra lutra</i> L.) and Great Cormorant (<i>Phalacrocorax carbo</i> L.) diet	Magurran et al. (2010) and reviewed in Braga et al. (2020)
			Algae and macroinvertebrates nutrients assimilation from sea lamprey carcass subsidies	Weaver et al. (2016)
		Maintenance of nursery habitats and populations	Strong connectivity between the protection of riparian vegetation and the fluxes of organic matter responsible for sea lamprey ammocoete development	Dias et al. (2019)
		Bioindicators	Bioindicator of ecosystem state (e.g., studies with larvae)	Araujo et al. (2013b)
	Cultural	Community interest in biodiversity and conservation	Conservation interest (e.g., listed in Annex No. II to the EC Habitats Directive (92/43/EEC) of 21 May 1992 on the protection of natural habitats and wild fauna and flora)	Renaud (2011), Mateus et al. (2012), Ferreira et al. (2013), Maitland et al. (2015) and Mateus et al. (2016)
		Education and Research	“Living fossil” Research model (e.g., species ecology and evolution)	Mateus et al. (2012), Ferreira et al. (2013), Maitland et al. (2015) Mateus et al. (2016)
	Regulating	Redistribution of fluxes and nutrient regulation (e.g., marine nutrient derived)	Similar to sea lamprey	No studies
	Supporting	Productivity of the food-web	Food for consumers in the food web (predators similar to sea lamprey)	No studies
	Maintenance of nursery populations and habitats	Similar to sea lamprey	No studies	
	Bioindicators	Similar to sea lamprey	No studies	

Table 1 (continued)

Species	ES identification	Description	Examples	References
Sea trout (<i>Salmo trutta</i> L.)	Provisioning	Food (i.e., nutritional source)	Iberian gastronomy (e.g., diverse iberian dishes)	Roden (2016)
		Fisheries (i.e., socio-economic value)	Commercial fishing is prohibited in Portuguese rivers, except in river Minho (International Section), with restricted measures. In Spain, in addition to the fishing licence, it is required the payment of an additional surcharge and the report of all catches (e.g., Average range of trout price per kilo to the intermediate buyer: 5,00 € to 20,00 €)	Antunes et al. (2015) and Almeida et al. (2018)
		Genetic resources (i.e., gene pool or genetic material available for human exploitation)	Population differentiation	Vera et al. (2019)
	Cultural	Leisure and competition angling	Popular target species on recreational fisheries activities, providing the development of the local economy and the transfer of local ecological knowledge	ICES (2013) and Almeida et al. (2018)
		Gastronomic events (i.e., gastronomic festivals; gastronomic Brotherhoods)	Gastronomic value in Iberian Peninsula	ICES (2013) and Almeida et al. (2018)
		Art, folklore and traditional know-how	Fly Fishing competitions (e.g., World Fly Fishing Championship, in Asturias 2022)	No studies
		Community interest in biodiversity and conservation	Conservation interest	ICES (2013) and Almeida et al. (2018)
		Education and Research	Research model (e.g., fisheries studies)	Mota et al. (2016)
	Regulating	Redistribution of fluxes and nutrient regulation (e.g., marine nutrient derived)	Life-history contributions (e.g., adult spawners mortality)	Näslund et al. (2015)

Table 1 (continued)

Species	ES identification	Description	Examples	References
	Supporting	Productivity of the food-web	European otter (<i>Lutra lutra</i>) and sea lamprey diet	Novais et al. (2010) and Braga et al. (2020)
		Support of biological cycles (e.g., host species)	Sea lamprey and bivalve larvae host	Taeubert and Geist (2017) and Braga et al. (2020)
		Maintenance of nursery populations and habitats	Important target species in restocking programs Maintaining nursery populations and habitats (including gene pool protection)	Campos et al. (2007), Caballero et al. (2007) and Marco-Rius et al. (2013)
		Bioindicators	Indicator of high environmental quality, promoting sustainable tourism	Álvarez et al. (2010) and Almeida et al. (2018)
Atlantic salmon (<i>Salmo salar</i> L.)	Provisioning	Food (i.e., nutritional source)	Iberian gastronomy (e.g., Gratinado de Salmão or Salmón del Bidasoa en Parrilla)	Roden (2016) and IPMA (2022a, b)
		Fisheries (i.e., socio-economic value)	Commercial fishing is prohibited in Portuguese rivers, except in river Minho (International Section), with restricted measures. In Spain, in addition to the fishing licence, it is required the payment of an additional surcharge and the report of all catches High market value (e.g., Average range of Atlantic salmon price per kilo to the intermediate buyer: 30,00 € to 70,00 €)	NASCO (2005), Caballero (2013), Antunes et al. (2015) and Almeida et al. (2018)
		Genetic resources (i.e., gene pool or genetic material available for human exploitation)	Population fitness	Gabián et al. (2022)
	Cultural	Leisure and competition angling	Recreational fisheries	OSPAR (2010), Almeida et al. (2018) and Arca (2020)
		Gastronomic events (i.e., gastronomic festivals; gastronomic brotherhoods)	Gastronomy festival and events in Galicia (Spain)	OSPAR (2010), Almeida et al. (2018) and Arca (2020)
		Art, folklore and traditional know-how	Salmon Sculpture in river Pas and Asón (Cantabria, Spain)	No studies

Table 1 (continued)

Species	ES identification	Description	Examples	References
		Community interest in biodiversity and conservation	Conservation interest in the OSPAR (The Convention for the Protection of the Marine Environment of the North-East Atlantic) and NASCO (North Atlantic Salmon Conservation)	OSPAR (2010), Almeida et al. (2018) and Arca (2020)
		Education and Research	Research model (e.g., fisheries studies)	Mota et al. (2016)
Regulating		Redistribution of fluxes and nutrient regulation (e.g., marine nutrient derived)	Life-history contributions (e.g., adult spawners mortality)	Näslund et al. (2015)
Supporting		Productivity of the food-web	Sea lamprey diet	Braga et al. (2020)
		Support of biological cycles (e.g., host species)	Sea lamprey and bivalve larvae host	Taubert and Geist (2017) and Braga et al. (2020)
		Maintenance of nursery habitats and populations	Maintaining nursery populations and habitats (including gene pool protection)	Saura et al. (2006)
			Target species of restocking programs for the conservation of their populations	Caballero and García (2004) and Saavedra-Nieves et al. (2021)
	Bioindicators		Indicator of a healthy environment, promoting sustainable tourism	Álvarez et al. (2010)



Fig. 3 Open-air Palaeolithic parietal art site in the Côa Valley (Portugal). Representation of a fish dating between 23,000 and 17,000 years, here identified to be an allis shad *Alosa alosa* L. (Image: Luis Belo)

(Ledogar et al., 2018). Zooarchaeological evidence collected in different northern Spain Palaeolithic sites seems to point to a constant pattern of exploitation of freshwater fish with high incidence in the human diet (Adán et al., 2009). In most sites, salmonids represented the main fish resource (Adán et al., 2009), as recorded in other European regions, like France, where it was considered crucial in the human diet during the Upper Palaeolithic (Hayden et al., 1987).

An indicator of the importance of salmon, and other anadromous species, for our ancestors is the parietal art (Adán et al., 2009). Palaeolithic art representations of fish are rare (Zotkina & Cleyet-Merle, 2017), when compared with other animal groups such as mammals. However, such representations can be found in Iberia in Palaeolithic sites such as the Tito Bustillo and El Pindal caves in Asturias, Spain (Adán et al., 2009) and in the Fariseu site in river Côa (Fig. 3), a tributary of the river Douro in Portugal (Mercier et al., 2006). This parietal art symbolises the fusion of human and animal worlds, and the animals represented are considered to be the ones more central to their survival whether because of food provision (e.g., bison, horse), or because of the danger that they pose (e.g., predators such as big cats).

One of the animals represented on the Fariseu site is a fish. The species represented on this open-air parietal art site is still to be identified but taking in consideration the ichthyofauna that might have occurred on the river Côa, the external morphology

of the carved fish, and the fact that shad vertebrae were identified at the site (Gabriel & Béarez, 2009), it is reasonable to assume that it is a representation of a shad. Taking in consideration the relative height of the fish body, most probably an allis shad.

Archaeological excavations at the Lapa do Picaireiro cave in central Portugal have revealed faunal remains confirming the consumption by Palaeolithic humans of fish species belonging to the Cyprinidae and Clupeidae taxonomic families (Bicho et al., 2003). Although they could not identify the genus/species, it is possible the fish may have been *Alosa* sp.

Roman and Muslim occupation

During the Roman Empire, fish resources and derivative products were considerably exploited, having an important role in the economy (e.g., Botte, 2009; Marzano, 2013, 2018; Garnier et al., 2018; Trentacoste et al., 2018). Across the empire, fish factories dedicated to the production of salted fish (*salsamenta*) and other fish-products (*garum*, *liquamen* and *allec*) were established, some of the most important located in Iberia (Garnier et al., 2018). However, no evidence of anadromous species was recorded in these fish factories, located along the coast, where essentially sardines (*Sardina pilchardus* (Walbaum, 1792)) appear in large percent in vast excavations (Garnier et al., 2018).

Anadromous species were probably more exploited in the freshwater reaches of rivers where they would be easier to catch (Aarts et al., 2004) and not on coastal areas, including estuaries, where marine species would have greater importance due to their abundance (e.g., sardines; Marzano, 2013; Garnier et al., 2018). The fact that the main route of migration for anadromous species are normally the deeper channels with stronger water currents also makes them easier to catch in the upper and narrower river stretches (Aarts et al., 2004). In Europe it is possible to find more archaeological remains of these species associated with this period. According to Neer et al. (2005), bones of small clupeids (e.g., caudal vertebrae and operculum) dating from around the middle of the second century AD were found in a Roman street located in Belgium. These bones were identified as belonging to the species allis shad (*A. alosa*) or twaite shad (*A. fallax*). Modern data on species abundance, distribution, and respective fish size indicate that these

species would be captured further upstream from the estuaries, during spring or early summer and used later in the production of fish sauces. Remaining traces of twaite shad associated with fish sauce were also found in the excavation of a shipwreck in the Rhône at Arles (France), which served as food for ship crews (Marzano et al., 2018).

During the Arab occupation of Iberia, freshwater fisheries provided important resources as well. In Moorish Spain (Al-Andalus society, 711–1492), fish, although not valued as a delicacy or having any religious connotation, was a frequent item in the diet, especially for poorer people living near rivers and coastal areas. Amid the species eaten, allis shad, sturgeon and trout were amongst the most consumed (Salas-Sálvado et al., 2006). Findings such as shad remains found in Saltés, from the Almohad period of Muslim Spain, support this theory (Lentacker & Eryvynck 1999). In Portugal, evidence of sturgeon consumption dating from the thirteenth century was detected for the first time in excavations conducted in the Archaeological field of Mértola (“casa II”) (Antunes et al., 1996).

Socioeconomic information for this period appears to be sparse and scattered. Although some geographical treatises and cookbooks provide some information about fishing activities in Al-Andalus, they often only confirm information from the Roman period. Furthermore, Islamic documents remain untranslated into European languages, as is the case with documents from the Almohad period (reviewed in Muniz et al., 2020), making access to bibliographic information related to this period of history difficult.

Ancient fish traps

Ancient fishing weirs, called *pesqueiras*, have been used in NW Iberia to target anadromous fish during their spawning migrations. The oldest known *pesqueiras* date back to 700 AD and were built in river Minho. This timing coincides with the transition towards a more intensively used agricultural landscape (Viveen et al., 2014). The *pesqueiras* are fixed stone constructions, the result of the transformation by man of riverbank bedrocks at certain fishing sites (Leite, 1999). They are often located in stretches where the river narrows due to bedrock channels that extend from the bank towards the river bed (Araújo

et al., 2016; Fig. 4). The *pesqueiras* have been built throughout time by master masons who had a deep knowledge of river flows and currents (Leite, 1999). The huge amount of work involved in the construction of these infrastructures can only be justified by the value attributed to the fishery product they target.

To build the *pesqueiras*, skilled workers carved the rock along the bank to obtain steps at different heights to set the nets (Leite, 1999). The *pesqueiras-caneiros* are the most elaborate in terms of construction because at certain locations a vertical slot on the fishing weir wall allows to place a hoop-net targeting mainly the sea lamprey (Fig. 4). At the *pesqueira* end, a specific kind of net—*cabaceira*—with a small trap is also used to take advantage of the counter-flow effect created by the fishing weir.

The *pesqueiras* are commonly referred to in monastic documentation from the ninth century onwards. Since then, the construction and ownership of *pesqueiras* has moved progressively from monastic origins into private hands (Araújo et al., 2016). Currently, professional fishing still occurs in *pesqueiras* from rivers in Galiza (Spain), and Minho and Lima rivers in Portugal. In Portugal, the owners of the *pesqueiras* have to pay annually a property tax to the municipality.

Middle ages—first evidences of overexploitation

Between the 5th and the fifteenth centuries, several fishing methods were available and their employment was dependent on ingenuity and financial means of the fisherman. Capture methods included simple fishing lines, manual capture, the use of several types of traps like the *pesqueiras*, which were very common and widespread in Iberia (e.g., Leite, 1999; Almeida, 1978 in Machado et al., 2014; Matos Filipe et al., 2020). During this period in history, the first evidence of concerns related with the overexploitation of these resources emerged.

Fishing was intensive to supply an avid and growing population and promoted by cultural and religious motives (Santos et al., 2012). Fish consumption was allowed by the Catholic Church as a replacement of meat since the seventh century, which was forbidden for a full third of the year, increasing the efforts of fishermen to secure these prized goods (Hoffman, 2001). In the fourteenth century, fish consumption,



Fig. 4 Fishing weir (*pesqueira*) at river Minho used to target anadromous species in Northwestern Iberian Peninsula rivers (**a** Image: Bernardo Quintella). Some weirs have vertical slots

where a specific kind of hoop net (*botirão* in Portuguese) is placed to trap fish (**b** Image: Gabriela Cardoso)

especially fresh, was in fact a symbol of status (Aparisi, 2021). Elite groups preferred fresh fish, but a considerable number of preserved fish was traded to supply regions far from the sea, especially the poorer communities which depended on brined, salted or dried fish (Hoffman, 2001).

Anadromous species such as sturgeon, salmon, lamprey and trout were among the preferred and were present at refined tables, allis shad and twaite shad however seemed to be consumed by all social classes (Oliveira Marques, 1971; Cabau, 2021). For instance, among Princess Mata d’Armanyac (fourteenth century) gastronomic preferences we can find trout, sturgeon, salmon and lamprey, among others (Cabau et al., 2021). Among all the anadromous species, the Atlantic sturgeon was the rarest and represented a clear sign of wealth. Its exploitation was closely controlled by the monarchs in Iberia in order to ensure the supply of this delicacy (Viterbo, 1799 in Santos et al., 2012; Cateura, 2021). However, the Atlantic sturgeon seems to have been less abundant in Iberia than in other parts of Europe (Ludwig et al., 2011). Either due to its rareness or to the large sizes it could attain, sturgeons captured the interest of the highest social classes. In 1321 a specimen caught in river Tagus (Portugal, Montalvo), was so large (total length=3.4 m; weight=192.5 kg) that King Dinis

made sure the occurrence went on record (Coelho, 1992).

Contrary to sturgeon rareness, shads’ value seemed to rely on high abundances. In the river Tagus, shad fisheries were so profitable that entire communities seasonally abandoned their usual trade and moved from coastal to riverine areas to profit from this activity (Pedrosa et al., 2018). Anadromous species represented an important contribution to the economy of the region where they occurred since they were consumed locally but were also traded to supply other areas of the country and even exported. In Portugal, in the fifteenth century, an important amount of gold and silver was traded for allis shad with merchants from Castile and other countries (Coelho, 1992; Pedrosa et al., 2018). For example, shads caught in the river Tagus in fishing concessions property of Prince Henrique’s were salted and sold in Ceuta (Coelho, 1992).

Signs of over exploitation become obvious early on. Fishermen were apprehensive of the impacts of large fishing traps, the *caneiros*, which blocked the river preventing migratory fish from spawning. For the *Caneiro de Abrantes*, in 1455, fishermen requested the King that the barrier should be open at least from April to June to ensure fish spawning. Also in river Tagus, in June 1462 a Royal Charter

mentioned shad shortage and the problems it caused. Restrictions regarding the fishing gear were applied, since barrier nets, using a very small mesh size, and the use of poison such as the *trovisco*, were considered to be killing the juvenile fish migrating downstream and thus reducing the bounty provided by the adults (Baldaque da Silva, 1892; Coelho, 1992). Evidence of fishing regulations implemented to secure fishing stocks is abundant, however it seems that it was not always respected or it did not apply to everyone (Lobo, 1812 in Batista et al., 2012).

Modern times—the beginning of the decline

During the eighteenth century rulers of both Portugal and Spain took advantage of the technological advances and promoted the fisheries sector development to feed the growing population, decrease the dependence on imported goods and/or boost the economy (Santos et al., 2012; Corrales, 2014). An economic and sustenance mind set was at play, promoting gear efficiency and capture rate, while completely disregarding ecological concerns (Santos et al., 2012).

Pressure was increasing and new techniques were adopted in response to the growing demand for fishery goods. In Catalonia for instance, trawling nets pulled by oxen were employed to meet the needs by improving fishing efficiency (Shaw & Díaz, 1988). Furthermore, besides the popular *pesqueiras*, several types of fyke nets (*botirão* and *camboas*) and other trapping nets, trammel and gill nets, beach seine nets (*xávega*), harpoons type gear (*galheiro* and *bicheiro*) and rakes (*fisga*) with adaptations according with the target species and mesh size allowed, were used to secure these prized goods (Baldaque da Silva, 1892; Almeida et al., 2021).

During this period, anadromous fish were still the most valuable inland river fisheries across the Peninsula, throughout the eighteenth century until the late nineteenth–early twentieth centuries (Baldaque da Silva, 1892; Hurtado et al., 2009). Fishing communities were known to migrate along the Portuguese territory in order to better profit from the fishing resources available, as previously observed in the Middle Ages (Souto, 2003; Pedrosa et al., 2018; Aparisi, 2021). In Ria de Aveiro (central Portugal), for instance, changes in the sedimentary regime along the coast caused periodic fluctuations in fisheries

production, which made the region either very profitable or not at all. When yields were low, local communities were incited to travel along the coast searching for better fishing locations, usually by the sea. Temporary settlements (*Palheiros*) gave way to permanent and important riverine communities. Some of the known fishing expeditions were to the rivers Tagus and Sado to profit from the shad seasonal spawning migration. The fish caught was then sold across the trading routes established by these communities (Baldaque da Silva, 1892; Souto, 2003).

In the river Minho, reports for the customs posts of Lanhelas, Seixas and Caminha during the fishing seasons show that salmon was the most expensive species when compared to shad and lampreys, with a price ranging from 4 to up to ten times the price of lamprey (Baldaque da Silva, 1892). Lamprey was still more expensive than shads, but the amount of allis shad captured in the river Minho made up for the slightly lower price and gathered the most revenue. In river Lima, shads appear to have been less abundant or desired than sea lamprey, and salmon were rare. Either due to record quality or a natural occurrence, the number of fish reported for the river Minho was far superior to the amounts registered in the neighbouring Lima (Baldaque da Silva, 1892).

By the twentieth century stocks suffered further decline and some of the Iberian rivers produced little to none of the anadromous species mentioned before (Andrade, 1995; Costa et al., 2001; Lopez et al., 2007; Antunes et al., 2015; Almeida et al., 2021). The most affected was the sturgeon. According to Nobre (1931), sturgeons occurred in Portugal in the beginning of the twentieth century in the basins of rivers Douro, Tagus and Guadiana and were still common in the Douro. The Guadalquivir and the Ebro might have been the most important rivers for sturgeons in Iberia (Ludwig et al., 2011; Cateura, 2021). In 1931, a factory dedicated to processing sturgeon for caviar and smoked flesh was set up in the Guadalquivir, an indicator of sturgeon abundance in the system. This factory, together with the construction of the Alcala del Rio dam, is thought to have been the demise of the species in this river basin (Férrandez-Pasquier, 1999; Ludwig et al., 2011). Moreover, an abrupt decline in shad captures was observed around the 1950s in several Iberian basins (e.g., Minho, Tagus, Guadalete, Ebro) rendering the once most



Fig. 5 Shad landings in River Douro (Porto, Portugal), an extraordinary bountiful day, April 1st 1965 (*image*: Henrique Moreira / Arquivo JN)

abundant anadromous fisheries much less profitable (Andrade, 1995; Costa et al., 2001; Lopez et al., 2007; Antunes et al., 2015) (Fig. 5). Salmon fisheries were also not impervious to the diminishing tendency of the anadromous fishes that the twentieth century brought. According to Baldaque da Silva (1892), by the late nineteenth century this species was already very rare in Portuguese rivers, with the exception of the Minho, where it was legally captured and sold at a very high price. Salmon was more abundant in the Spanish Atlantic rivers. However, decline was still observed in the region by the late nineteenth, early twentieth centuries, with salmon disappearing from some rivers by the 1980s (Moreno, 2003). Finally, while sea lamprey in the nineteenth century was commercially captured in 22 Spanish rivers, currently it is restricted to three rivers in Northwestern Spain (Araújo et al., 2016; Almeida et al., 2021). Nevertheless, lamprey seems to have acquired a new importance economically and culturally, especially in Portugal, as the other anadromous species became less abundant and consequently less profitable (Teixeira & Ribeiro, 2013; Almeida et al., 2021).

As described in this section, humans have taken advantage of anadromous resources since

prehistoric times in Iberia. Exploitation of these resources escalated with population growth and technology evolution, contributing to intense fishing efforts, which together with other anthropogenic pressures (see next section) dictated the species decline.

Factors affecting the sustainability of anadromous fish ES

Considering their highly complex life-cycles, which include long migrations between different habitat types (i.e., river and sea), with specific requirements (e.g., longitudinal connectivity, good water quality, hydromorphological integrity) (Lucas & Baras, 2001; see Sect. 2 for more detail), and adding their significant socioeconomic interest, anadromous fish have always been subjected to several pressures and threats. These contributed greatly to the poor conservation status that some of these species face nowadays throughout their global distribution, but particularly in Iberia, the southern limit of distribution for several of them, ultimately impacting the exploitation of related ES. Threats such as aquatic pollution, which in some cases can result in bioaccumulation problems (Wilhelm, 2009; Shesterin, 2010) as these species are highly consumed by humans in regions like Iberia (e.g., sea lamprey and shads; Lochet et al., 2008; Pedro et al., 2013; Madenjian et al., 2021), or the introduction of non-indigenous species, particularly of large predatory fish (e.g., pikeperch, *Sander lucioperca* L., and the European catfish, *Silurus glanis* L. (Boulêtreau et al., 2018, 2020, 2021)), can lead to negative ecological and economic consequences (Pimentel et al., 2005; Simberloff, 2011; Landos et al., 2021). Detailed information about these specific threats on anadromous fish species and related ES is still scarce, especially for the Iberian region. On the other hand, main threats contributing to the decline of anadromous stocks in Iberia, such as dam construction and operation, overfishing and poaching, and climate change, are addressed in more detail in this section.

Dams and other obstacles

The construction of dams and other obstacles is, arguably, the most well-known, and perhaps

currently the most pressing threat to anadromous fish species and, consequently, to the sustainability of related ES (Larinier, 2001; Lucas & Baras, 2001; Poff & Zimmerman, 2010; van Puijenbroek et al., 2019). In a recent study by Belletti et al. (2020), a total of 629,955 barriers of multiple types and purposes were identified in Europe. Just in Iberia, 31,079 structures were counted, and this number is probably an underestimation, considering the number of new barriers that are constantly being identified in ongoing studies. By the time of the Water Framework Directive (WFD) implementation, Portugal was already impacted by almost 200 large dams (over 15 m high, or between 10 and 15 m and a volume over 1 hm³) and in the last 20 years another 65 were built and more than 8,000 small obstacles were identified (PGRH 2016–2021). This has contributed to an estimated 80% loss of accessible habitat for anadromous species such as the sea lamprey in all major rivers of Iberia (Mateus et al., 2012).

The construction of barriers across rivers, sometimes multiple and large obstacles in cascade, usually leads to the inevitable loss of longitudinal connectivity of impounded watercourses (Bunn & Arthington, 2002), significantly affecting fish migrations between different habitats, which are a mandatory component of these species' life-history (Lucas & Baras, 2001). The presence of an impassable barrier, as most large dams are, can lead to isolation of populations, failed recruitment, reduced gene flow and local extinction of populations in a more drastic scenario (Dudgeon et al., 2006; Hughes et al., 2009). Daming impacts are more detrimental to anadromous fish when impassable barriers are built in tidal areas, completely preventing the access of anadromous fish to riverine habitat and compromising the success of their migration and reproduction, with obvious negative results in the future viability of local populations (Wright et al., 2016; McCartin et al., 2019; Alcott et al., 2021).

For anadromous fish, not only adult upstream migration is impaired by these obstacles, as juveniles at some point of their life-cycle need to return to the sea and are often faced with problems such as increased mortality by passing through turbines (Pracheil et al., 2016; Thorstad et al., 2017), migratory delay due to reduced flow velocity in dam reservoir (Marschall et al., 2011; Huusko et al., 2018), or

high exposure to predation by large piscivorous fish that inhabit the upstream lentic habitats (Gauld et al., 2013; Schwinn et al., 2017).

Besides the more obvious barrier effect, dams are also the most significant modifier of downstream riverine habitat, as they can artificially regulate the entire flow regime in many ways, from the sediment dynamics and channel morphology, through thermal regime and other chemical conditions, to the habitat structure, which in turn influence composition, structure and life-histories of riverine fish assemblages (Naiman et al., 2008; Poff & Zimmerman, 2010; Olden & Naiman, 2010; Toffolon et al., 2010; Bruno et al., 2013). For migratory species, such as anadromous fish, who are strongly dependent on environmental cues during their different life-stages, especially from temperature and flow patterns (Lucas & Baras, 2001), these artificial and sometimes unpredictable environmental changes can completely disrupt their natural migratory behaviour.

Dam construction and operation also contribute to a decline of fisheries production in impounded rivers (e.g., Richter et al., 2010), affecting the sustainable exploitation and valorisation of ES in these regulated aquatic ecosystems and leading to major social and economic impacts (Poff & Schmidt, 2016). Socio-economically, changes in fish fauna downstream of hydropower dams are known to affect commercial fisheries, respective yields and market values, as well as decrease the potential for sustainable exploitation of socioeconomic and cultural aspects linked to angling and recreational fishing activities (Hughes, 2015; Arantes et al., 2019).

Perhaps the most well-known anadromous species in Europe is the Atlantic salmon, which, together with its congener, the trout (both the anadromous and resident ecotypes), are among the most iconic and valuable species for recreational fisheries. Unfortunately, the species has undergone a general decline. Recruitment of Atlantic salmon's European stock has diminished almost threefold, from 8 to 3 million, since the early 1970s (Friedland et al., 2009). Among other threats, river fragmentation by dams and other obstacles is frequently reported as the main cause of this decline (Lucas & Baras, 2001; Thorstad et al., 2008; Limburg & Waldman, 2009). In Iberia, for example, which represents the southern limit for the global distribution of this species, salmon populations have suffered a considerable loss in the past 30–40 years

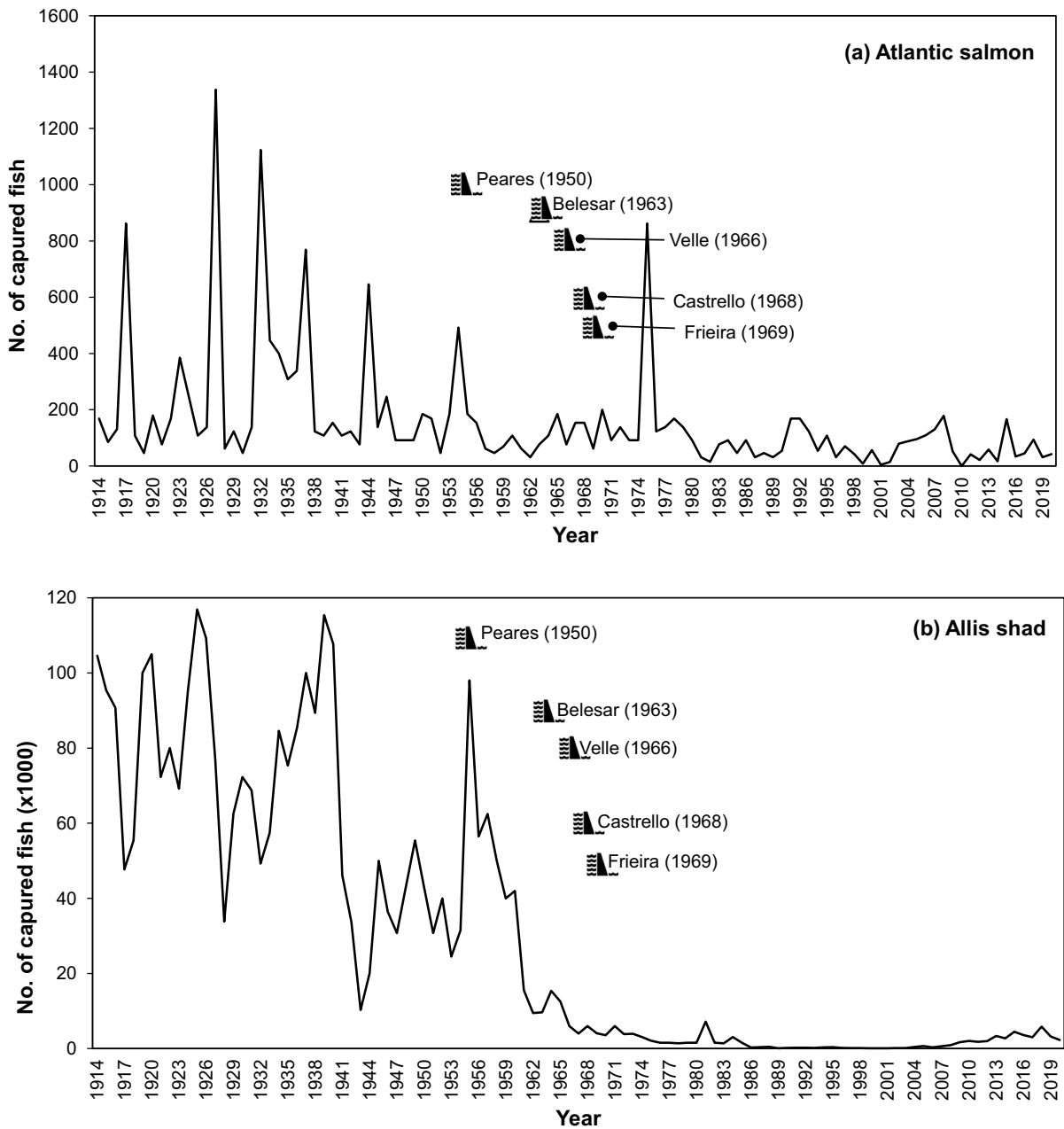


Fig. 6 Time series (1914–2020; black line) of **a** Atlantic salmon *Salmo salar* L. and **b** Allis shad *Alosa alosa* L. landing reports in the river Minho, together with the date of construc-

tion of main dams (black symbols) on this river. Landing data for both species were provided by the local authorities (*data source*: provided in 2021 by Capitania do Porto de Caminha)

(with reductions of an estimated 90% in Portugal and 60–70% in Spain; Nicola et al., 2018; Lennox et al., 2021) (Fig. 6a).

Allis shad and sea lamprey are other emblematic anadromous species that have suffered severe habitat

and population losses in Europe. Allis shad abundance has been decreasing across its natural distribution area, raising concerns among academic and governmental agencies responsible for the management of related fisheries (Rougier et al., 2012; Stratoudakis

et al., 2016). The collapse of this species' stocks has been attributed to several stressors, but habitat reduction due to river impoundment seems to be more significant (Rougier et al., 2012; Alcott et al., 2021). In Iberia, allis shad is still present in most northern and central river basins (Mota et al., 2016; Nachón et al., 2019), but, for example, in the Minho river, the species reported catches decreased from over 100,000 fish in 1914 to less than 5,000 in 2020 (Mota et al., 2016), a declining trend that seems to be related to the considerable reduction of available habitat on Minho's main stretch (Fig. 6b). For sea lamprey, both disruption of migratory movements and habitat degradation caused by dams or other obstacles are well-recognized threats to the persistence of populations of this species throughout its natural distribution range (Clemens et al., 2021; Moser et al., 2021). In Iberia, Mateus et al. (2012) estimated that 80% of sea lamprey habitat has been lost due to this stressor.

Overall, dams generally result in negative impacts on riverine and anadromous fish, and related fisheries. In this case, the loss in fish yield can sometimes be partially compensated by new fisheries in some large reservoirs, however this does not generally maintain biodiversity value and may only represent a temporary benefit (Brink et al., 2018). In many cases, dams have been constructed in series on the same river or watershed and the combined effects are particularly deleterious to anadromous fish stocks. Even if each dam is equipped with functional fish pass devices, there are still incremental, and sometimes substantial, losses of fish at each obstacle.

Overfishing and poaching

Overfishing and poaching represent different threats to anadromous fish species and to the related ES. Overfishing occurs when the fishing is held in an unsustainable way, and not enough mature adults survive to breed and guarantee a healthy population, often caused by inadequate management and fisheries regulations (Möllmann & Diekmann, 2012). Poaching, or illegal fishing, is usually carried out by those without suitable licence, with illegal gear, who fish over a defined quota or target prohibited species or sites (Ma, 2020).

Commercial fishing is an important activity due to its high socioeconomic value, especially the fisheries related with anadromous fish (e.g., sea lamprey,

shad) which are of particular interest and value in the southern regions of Europe, such as Iberia (Almeida et al., 2018). When anadromous fish return to the rivers, adults are particularly susceptible to commercial fishing, which consequently prevents the ones that are caught from spawning and completing their life cycles (ICES, 2015; Dadswell et al., 2021). Some anadromous fish, especially sea lamprey and shad, due to their high economic value (Pereira et al., 2013; Valadares & Ribeiro, 2013) and still relative abundance guaranteeing some level of profitability of the fishing effort, are a preferred target of both professional fishermen and poachers (ICES, 2015).

In Portugal, commercial fishermen legally target sea lamprey and shad in eight main river basins (Minho, Lima, Cávado, Douro, Vouga, Mondego, Tejo, Guadiana), while salmon is caught only in the river Minho. In Spain, lamprey fisheries occur only in the rivers Ulla, Tea and Minho and for allis and twaite shad, only in the transboundary river Minho (ICES, 2015; Almeida et al., 2021). Salmon and trout, however, have a larger expression on Spanish inland fisheries as a target for recreational fishermen, as their commercial capture is also only allowed in the river Minho (Alvarez et al., 2010).

Another problematic issue on commercial fishing is that the gears normally used are not selective for the target species, especially in rivers where endangered fish species occur (e.g., Atlantic salmon and sea trout). As migration periods coincide with the fishing season, these threatened species are usually caught by the nets targeting other species (e.g., shads), thus compromising their ability to complete their migratory routes. Fishing activities remain a major threat to many small and vulnerable populations of salmonids in Iberia, and exploitation rates are still under careful review and management (OSPAR, 2010).

Bycatch is also a serious problem for allis shad mortality in the marine environment. Although this species is not targeted in marine fisheries, there are reports of high numbers of landings, which significantly affect stocks (Trancart et al., 2014). It is extremely important to improve knowledge of the distribution of shads in the open sea to support the appropriate management of critical areas for the protection of shad populations (Trancart et al., 2014).

Increased fishing pressure could result in overexploitation of anadromous populations with some specific effects on population: decline in overall stock

abundance and average fish size, adverse genetic selection leading to loss of potential fecundity, reduced average spawning size and finally loss of genetic diversity (Smith et al., 1991; Pérez-Ruzafa et al., 2006). The pressure exerted by overfishing and illegal fisheries increases the vulnerability of anadromous fish populations, contributing to the decline of Atlantic salmon, sea trout, sea lamprey and shad populations, as well as the extinction of sturgeon, in Iberian rivers (OSPAR, 2010; Ludwig et al., 2011; Rougier et al., 2012; Almeida et al., 2018).

Poaching is still a common problem in Iberia (ICES, 2015; Mota et al., 2016). For lampreys, for instance, in years of decreasing stocks and inflating prices, illegal fishing increases (Almeida et al., 2021). Poachers may use different strategies to catch lampreys, such as removing the females from the nests, leaving only the males there to attract more females (pheromone cues), which are more appreciated for gastronomic purposes due to their gonads. Another approach used by poachers consists of attracting the sea lampreys to a refuge area (e.g., tree branches placed on the river bed) to catch them while they are resting during the day. For these strategies, poachers mostly use illegal gears (e.g., wounding gears, like *bicheiro/galheiro*) (Araújo et al., 2016).

Although local authorities set rules to control and manage fishing activities (see chapter 5), it is difficult to eradicate illegal practices directed to anadromous fish because of their high commercial value (Stratoudakis et al., 2016). In addition to the obvious impacts in anadromous fish populations, poaching also has negative effects on other habitats and fish species, mostly due to the habitual use of more destructive and less selective fishing gear (Braga et al., 2022).

Climate change

Climate change is a growing threat to anadromous fishes that have complex interactions and cumulative effects with other threats (e.g., Maitland et al., 2015; Clemens et al., 2021), and Iberia is located in a region particularly vulnerable to this threat (e.g., Andrade et al., 2021; Pereira et al., 2021). Physical changes in temperature, precipitation, groundwater discharge, and increased ice-free periods for lakes could affect community structure and the fecundity,

survival, growth, and distribution of anadromous species (Hittle et al., 2021). Since the life cycle of migratory species involves two habitats, they are particularly vulnerable to environmental change, which may affect either of these habitats as well as the journey between them (Chaparro-Pedraza & Roos., 2019).

The effects of environmental change on wild populations of Atlantic salmon, both in abundance (Ozgul et al., 2010; Lane et al., 2012) and in dynamics (Cornulier et al., 2013; Nelson & Yamanaka, 2013), have become increasingly documented over the years (Hittle et al., 2021). A recent study (Wang et al., 2021) reviewed the impacts of a changing climate on several lamprey species, from physiology (e.g., Baer et al., 2018; Whitesel et al., 2020), phenology (Kirillova et al., 2016; Wang et al., 2021), shifts in distribution range (Lassalle et al., 2008; Elliott et al., 2021), genetic adaptation (Close et al., 2002) to changes in species interactions and community structure (e.g., Boeker & Giest, 2016). In Central Portugal, it has been observed a clear effect of drought in the abundance of sea lamprey using the fish pass located at the Coimbra Dam (Fig. 7).

Increasing temperatures, persistent decreases of river flow caused by natural or artificial shifts in the hydrologic regime, and habitat disturbance caused by extreme events, may make habitats currently occupied by anadromous fishes uninhabitable in the nearby future, as their environmental preferences may no longer be met in the places where they currently live (Hughes, 2000). For example, climate change will increase thermal and hydrologic variability, including droughts and floods that will alter anadromous fish migration (Wang et al., 2021). The projected increase in extreme weather events may also escalate toxic runoff into watersheds that otherwise support anadromous fish diversity (Lassalle et al., 2009). On the other hand, the interactions between climate change and oceanographic regimes can limit the availability of host species (Clemens et al., 2019) and, thus, the ability of some anadromous fishes to complete their life cycle. Climate change issues may also lead to a significant change in the way river basins are managed to exploit and provide water resources for human and agriculture use, which usually are seen as priorities in comparison with the maintenance of environmental and ecological integrity (Allan et al., 2013). Hence the

Fig. 7 Number of sea lampreys *Petromyzon marinus* L. using the Coimbra Dam fish pass between 2013 and 2022. Dry years (medium rainfall below the national average; IPMA, 2022b) are identified in black. Count data was obtained through continuous recording and subsequent visual counts of fish using the vertical slot fish pass installed at the Coimbra Dam, the first unsurmountable dam in the Mondego River (Central Portugal)

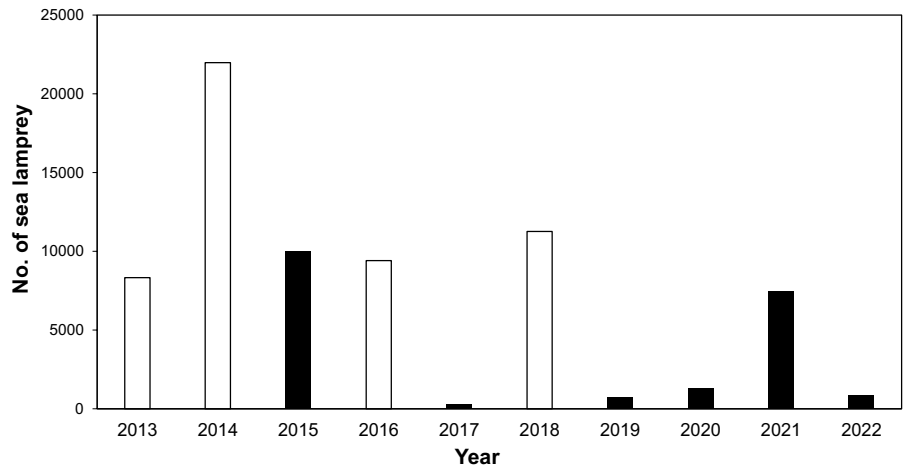
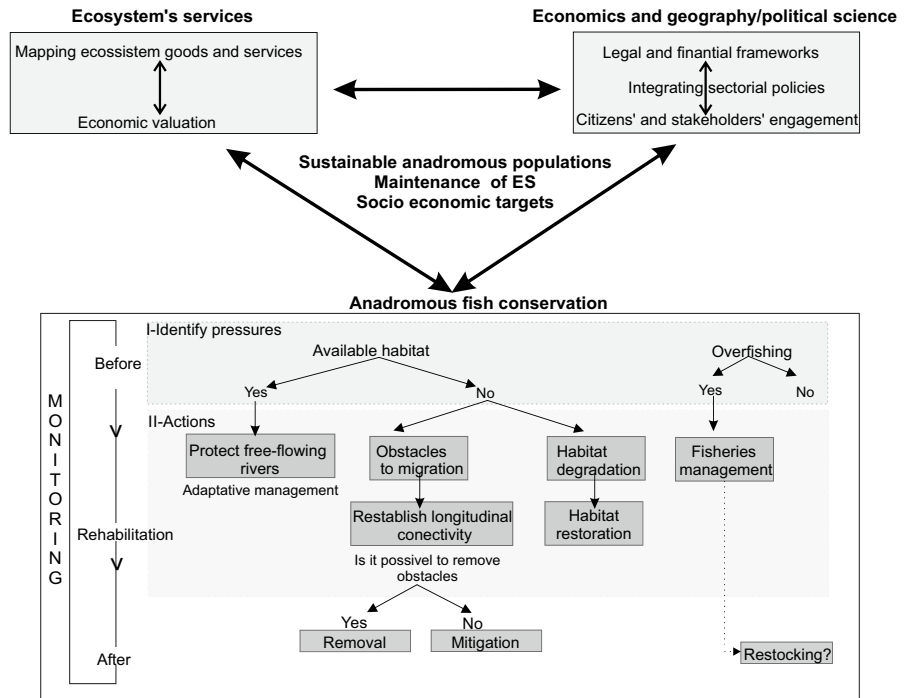


Fig. 8 Proposed multi-dimensional approach to move towards a more integrative management and achieve the sustainability of anadromous species' populations and respective Ecosystem Services (ES)



ultimate impacts of climate change to anadromous fishes are not completely understood at specific geographical locations and across life stages, nor the impacts on the ES they provide.

Present management efforts towards sustainability

Given the particularities of aquatic ecosystems functioning (Vannote et al, 1980; Amoros & Roux., 1988;

Arthington et al., 2010), as well as the complexity of the anadromous fish life cycles (Lucas & Baras 2001) and the threats affecting these species (see Sect. 4), the maintenance of the ES generated by these species requires an interdisciplinary and long-term integrated approach (see Fig. 8) (Garcia et al., 2003; Arthington et al., 2010; Gonzalez del Tánago et al., 2012). This should take into account different temporal and spatial scales, as well as different domains of knowledge, namely, governance and socioeconomics, but it also

requires stakeholders engagement. Related ES are highly dependent on healthy anadromous fish populations, that, in turn, can only be attained by reviving their natural reproductive cycle and ensuring that the available habitat still fulfil specie's needs. Additionally, due to the high economic value of these species, fishing pressure must be carefully managed (Arlinghaus et al., 2002; Stratoudakis et al., 2016; Brownson et al., 2019). Conflicts between environmental and ecological status, the sustainability of ES, the public policies, and local development projects, change among watersheds and in this sense, 'one size fits all' strategies do not work properly. Thus, compatibility between environmental and socioeconomic goals is crucial and requires, above all, the coordination between regional and national agencies and entities managing these resources, both in marine, brackish and freshwater environments (Grizzetti et al., 2016; Drouineau et al., 2018) (Fig. 8). In the present section, the multiple legal frameworks that were implemented over the last two decades in terms of fisheries and water management, habitat restoration, as well as the rising need to shift towards an ecosystem's services-based approach (Garcia et al., 2003; Bouwma et al., 2018; Souliotis & Voulvoulis, 2021) are explored in the context of the anadromous species.

Fisheries management and efforts for stock sustainability

Until recently, fisheries management was mostly focused on economic revenue, disregarding the sustainability of the practices and the preservation of the stocks (e.g., Garrido et al., 2005; Santos et al., 2012; Mota et al., 2016; Ferguson-Cradler, 2018). Despite all the focus on the global fisheries crisis at sea during the twentieth century, inland waters seemed to be less of a priority.

Throughout the twentieth century and at the beginning of the twenty-first century, Portuguese legislation on inland fisheries consisted of a practical approach which, depending on the river and local tradition, defined the target species, the allowed fishing gears, the maximum number of licences, the fishing season, the minimum size of capture and, in some cases, the maximum daily catch permitted (Stratoudakis et al., 2016; Almeida et al., 2021). No consistency among river basins or scientific support was

guaranteed, which hampered sustainability efforts and regulatory oversight while encouraging fishermen's complaints. Nowadays, anadromous fish are still the most valued inland fisheries (Antunes et al., 2015; Stratoudakis et al., 2016), although stocks can no longer sustain a market based on quantity. As these species are considered a delicacy, the provision services should be promoted based on the quality of the product, ensuring the sustainability of the fisheries and the local origin of the product to the consumer.

A *nouvelle* approach to fisheries management emerged at the end of the twentieth century entitled 'collaborative governance'. This approach seems especially effective on data poor small scale fisheries and combines the involvement of stakeholders in the decision-making process, promoting a rational approach that benefits all the parties and ensures sustainability and the compatibility of the different uses of the river (Ansell & Gash, 2008; Almeida et al., 2018; Stratoudakis et al., 2020). Local fishermen communities and stakeholders' engagement (e.g., scientists, governmental agencies, environmental NGO, municipalities), has been promoted to guarantee the commitment of users to a long-term conservation strategy and, simultaneously, reducing potential conflicts. This link has been strengthened by the proactive action of environmental NGO's and increasing number of environmental educational programs aiming to raise social awareness and public demonstrations. This managing scheme, coupled with fish-habitat restoration, might help preserve the existing artisanal fisheries while promoting the recovery of anadromous fish stocks. Very encouraging results were achieved in a pilot project in the Mondego River that focused on sea lamprey and shads (Almeida et al., 2018, 2021). The proximity to the fishing community allowed for a better understanding of the fisheries reality. This new management approach, grounded on the research dedicated to anadromous species and promoted by habitat restoration measures such as fish pass (e.g., Quintella et al., 2003; Andrade et al., 2007; Pereira et al., 2017, 2019; Belo et al., 2021), contributed to a significant increase in abundance of sea lamprey larvae in the Mondego river (Stratoudakis et al., 2020; Almeida et al., 2021). Another aspect of the modern view of fisheries management is focused on increasing fish value, while reducing the quantity of fish necessary for a fisherman to have a profitable season (Santos et al., 2012). This, however,

requires a coordinated strategy between fishermen and intermediaries to ensure they all benefit at the end. Another important measure to ensure the correct valuation of wild fish is to guarantee its origin and capture method, targeting the informed buyer, which prefers local fish captured through a sustainable fishery. The pilot implementation of a label of origin was recently introduced for anadromous fisheries in rivers Vouga and Mondego (Portugal), in the framework of the Life Águeda and An@adromos.PT projects, with positive responses from the fishermen community. A major result from this combined approach was the change in mind-set observed within this community. In river Mondego, some fishers voluntarily started moderating their fishing effort to avoid the consequent drop in prices, thus securing a higher revenue by killing fewer fish (Stratoudakis et al., 2020).

When stocks are too low, these measures are no longer suitable, and as a last resort restocking can be used to recover wild fish populations (Fig. 7). In Portugal, prolonged restocking programs were mostly employed for trout and Atlantic salmon. However, these measures failed either due to high mortality or dispersal (Teixeira et al., 2006). The use of specimens from other regions may also have promoted genetic introgression and produced less adaptable progeny (Lourenço, 2004). Efforts are currently being made to optimise and enhance the success of future restocking actions, through an experimental approach to the production of wild-reared trout, aiming to improve their survival rate in the wild, but related work is still in its beginning.

Water management and habitat restoration

In retrospect, the Natura 2000 Directive (92/43/EEC) was the first legal framework within the European Union that targeted the protection of rare, threatened, or endemic species and habitats (aquatic habitats and biodiversity) and focused on improving the ecological status of aquatic ecosystems (water quality). As part of the implementation of this Directive, each Member State identified a list of sites hosting natural habitats and wild fauna and flora of interest, including threatened anadromous species such as the Atlantic sturgeon, Atlantic salmon, sea trout, sea lamprey, river lamprey, and allis and twaite shads. These species were also protected under the Bern Convention (Conservation of European wildlife and natural

habitats), as well as the Bonn Convention (Conservation of Migratory Species of Wild Animals). Still under the EU's Nature Conservation Directives the indirect protection of anadromous fish was reinforced by the obligation to prevent deterioration of the designated sites within the Natura 2000 network. Later in 2000, the most relevant water policy initiative of the last 20 years, the EU Water Framework Directive (WFD), was implemented with the aim of ensuring the ecological and chemical improvement of surface water and groundwater while preventing deterioration. Among other biological quality elements included in the multimetric index for assessing the ecological quality of rivers, changes in the composition, abundance and age structure of the fish fauna were contemplated and anadromous species were included as an indicator of good ecological quality. In the perspective of the hydro-morphological quality elements, the hydrological regime and river continuity, which are fundamental for anadromous species, are also key components of good ecological status, but only indirectly regarded in the WFD through the support of "ecological flows" and the restoration of longitudinal connectivity of river networks. In this sense, relevant actions for the conservation of anadromous species and ES maintenance and sustainability (Larinier, 2001; Tickner et al., 2020), such as dam removal, fish pass installation and habitat restoration were only implicitly considered. Dam construction or hydropower development was not fully prohibited (Duarte et al., 2021), and the implementation of these legal provisions into each of the EU Member States has varied according to the national interests and proven insufficient to prevent further degradation of the natural characteristics and biodiversity of free-flowing rivers (Larinier, 2008; Segurado et al., 2015; Grill et al., 2019; Kagalu & Latinopoulos., 2020; EEA, 2021; Schäfer, 2021). Within the Iberian national legislation, the first generation of River Basin Management Plans—RBMPs (1997–2001) had different goals. The divergences between countries continued after the transposition of the WFD into the Iberian national legislation (Garrido & Llamas, 2009; Martínez-Fernández et al., 2020). Moreover, the hydraulic paradigm persisted over time, and hydroelectric production and agricultural water demands are currently growing pressures associated with EU energy targets for 2020–2030, the EU's Common Agricultural Policy (CAP) and the EU Landscape

Convention (Council of Europe, ETS No.176). In 2018, under the context of climate change adaptation, the new National Irrigation Plan foresees more than 90,000 ha of newly irrigated land and several new multipurpose dams, such as the Tagus project and an intertidal dam in Vouga estuary (EDIA, 2021).

Considering the previously identified shortcomings in the legislation, the attempt to integrate measures to promote the longitudinal connectivity of rivers in the framework of RBMP (2016–2021), failed to ensure the “good ecological status” of rivers due to lack of effective implementation. The environmental effect of barriers was identified as the major reason for only 40% of the EU’s surface water bodies have reached the “good ecological status” or “good ecological potential” (EEA, 2018; Feio et al., 2021) and the reason why the environmental objectives of the WFD were not met by 2015, being postponed for 2021 and lastly to 2027 (Bouwma et al., 2018). This is a particularly worrying scenario, as in Iberia, reduced flows resulting from water abstraction and water retention by dams, with consequences for longitudinal connectivity, are worsened by climate warming (Feio et al., 2021). This aspect is particularly relevant for anadromous species, since when key habitats are disconnected and environmental cues are disrupted (through natural and artificial changes in flow and water temperature regimes), species abundance is highly affected (Moser et al., 2021). Therefore, regarding habitat availability, despite the need to ensure the ecological quality of water and habitats through restoration measures, most of the efforts to support anadromous species conservation and ES maintenance must heavily focus on the reestablishment or improvement of longitudinal connectivity and habitat integrity (Fig. 8).

Among the mitigation efforts that support anadromous species conservation, obstacle removals are the only solution that truly restores river connectivity. In case of obsolete barriers and where water use permits expired, this measure was adopted by the Spanish National Strategy for River Restoration (NSRR), which removed more than 200 dams by 2017 and 108 obstacles in 2021 alone. When removal is not feasible, alternative mitigation measures can include fish pass installation or retrofitting existing ones, implementation of ecological flows and promotion of more coherent sustainable ES management (Gonzalez del Tánago et al., 2012;

Almeida et al., 2018; Van Puijenbroek et al., 2019). In Portugal, despite the existence of legislation since 1892 concerning river connectivity and the introduction, in 1962, of the obligation to install fish passes in dams and weirs as a mitigation measure (national Fishing inland law), only 46 fish passes were installed (RBMPs 2016–2021). Most of these devices have not been monitored and their efficiency is still unknown (Santo, 2005).

Nevertheless, the paradigm is shifting, and several investments have been done in terms of fish pass monitoring (Santos et al., 2012; Pereira et al., 2017; Bravo-Córdoba et al., 2021; Bravo-Córdoba et al., 2022) and retrofit of the original designs for the Iberian species (Fuentes-Pérez et al., 2021). Moreover, a movement towards an integrated approach and adaptive management has been conducted by Portuguese projects such as the pioneer and international awarded project “Habitat restoration for diadromous fish in river Mondego, Portugal” (PROMAR 31–03–02–FEP-5), as well as the recent LIFE Águeda—Conservation and Management Actions for Migratory Fish in the Vouga River Basin (LIFE16 ENV/PT/000411) and MigraMiño (0016_MIGRA_MINO_MINHO_1_E) in Minho basin. These projects promoted habitat recovery through the removal of small weirs, implementation of fish pass devices in previously identified obstacles, and long-term monitoring programs. The projects’ success is attributed to the existence of historical data which provided a suitable reference situation (Azeiteito et al., 2021), previous knowledge of all the obstacles present in the catchment, their impact on species behaviour (Quintella et al., 2009; Pereira et al., 2017) and also extensive before-after monitoring. This approach contributed to the acceptance and participation of the public, fisherman and governance entities enrolled within the catchment (Fig. 8). To justify the costs of protection and restoration embedded in the RBMP and prioritise the measures mentioned (Terêncio et al., 2021), the integration of ES in the economic valuation has also received great attention (e.g., Liu et al., 2010; Doherty et al., 2014; Pavanelli & Voulvoulis, 2019). The ES concept was first framed in 2008 on the Marine Strategy Framework Directive (MSFD), and posteriorly included in the revised environment-oriented policies, such as the Biodiversity Strategy and the second cycle of RBMPs. Nevertheless, no clear assessment methodologies were provided or

suggested (Arthington et al., 2010; Lamouroux et al., 2015; Bouwma et al., 2018) and in most cases, the operationalisation is only partial and/or questionable (Schäfer, 2021). The first review of the ESs linked to diadromous species and the respective economic assessment in the Atlantic Area is now being performed under the framework of the INTERREG AA DiadES Project (EAPA_18/2018) (Díaz et al., 2022). The output of this project will highlight the importance of anadromous species for ecosystem functions and services, and strengthen the rationale for protecting freshwater life under the increasing demand of basic human needs such as water and food. As such, the project represents a stepping stone towards the full integration of the ES at different spatiotemporal scales into WFD river basin planning (Grizzetti et al., 2019), thus reducing the potential conflict between policies and/or stakeholders (Islam & Repella, 2015).

Favourable developments towards the ES management concept have been made, particularly due to the strong support from academics, environmental organisations and population movement to a New Water Culture (Benarroch et al., 2021). These questioned the construction of new multipurpose dams, demanded the prioritisation of barrier removals and pushed for the adoption of alternative ideas on water and fisheries management (adaptive management, full cost allocation, appropriate science integration) (Arlinghaus et al., 2002; Suding, 2011). A strict protection scheme for non-impacted and restored rivers is also rising with the EU Commission's Green Deal, and its nature restoration law project, which are supported by the EU Biodiversity Strategy 2030 and EU strategy on Adaptation to Climate Change. The first one aims to restore and preserve ecological flows of at least 25,000 km free flowing rivers, and the second is set on the protection of 30% of EU land and sea (1/3 of which under 'strict protection'), the promotion of nature-based solutions and transition to a climate friendly power production system (trade-offs, funding and policy making).

Regarding the financial support available, several EU funds such as LIFE/Life + Programme (targeting environment and climate action—e.g., LIFE Segura Riverlink, LIFE Águeda), Horizon Europe (under the strategic orientations "Restoring Europe's ecosystems and biodiversity, and managing sustainably natural resources"), Invest EU ("Sustainable Infrastructure"), Cohesion policy funds (European Maritime,

Fisheries and Aquaculture Fund), and the EU Agricultural Fund for the Rural Development (EAFRD) as well as complementary national and regional funding mechanisms that incorporate the private sector, are available. Thus, the following years will be crucial to develop the tools required for the full integration of the ES management concept into the river basin management plans and join efforts to move towards the sustainability of the ecosystem services generated.

Future perspectives

The decline in abundance of diadromous fishes is closely associated with human activities, especially those affecting the more vulnerable riverine portions of their life cycles. Humans have influenced them in many ways, as shown in previous sections. However, for conservation efforts to succeed, restoration options must be available. That is, the identification and characterisation of drivers of decline must be accompanied by realistic and effective ways to reverse them. Return to a pristine status is almost impossible, but extant pressures should be reversed to a point that the quality and quantity of available habitat allow species to recover to a fully functional status, capable of being sustainably exploited.

As stated in the previous section, river restoration is the promise for many Iberian rivers, because it has the potential for resulting in considerable biodiversity gains to an extent not yet seen among the present generation. The removal of a dam will restore the natural dynamics of the river, protect and restore river habitats and banks, reconnect flood plains, restore natural flow patterns, sediment and energy flows, and open up fish migration routes. It will also improve resilience when faced with pressures such as the impact of climate change (Gough et al., 2018). A recent study on this by Portland State University, USA, found that billions of dollars could be saved if dams were removed rather than repaired. The study estimates that the cost of removing 36,000 dams by 2050 in the USA would be 10–30 times cheaper than repair and maintenance of these infrastructures (Grabowski et al., 2018). However, there remains a lot of uncertainty about where the dams are located, which are obsolete, and which are the most appropriate for removal. Therefore, mapping of all small and large dams in Iberia and elaboration of a priority list for their removal is

a vital step, in order to integrate these removals into regional RBMP.

On the other hand, even considering all the environmental costs related with dam construction and operation, these infrastructures can also play a vital role for human population development, specially within the current context of climate change and global warming (by storing water for human and agriculture consumption in drought periods), as well as considering the increasing demand towards more renewable energy sources. Therefore, it is unlikely that dams will be removed just to favour native anadromous fish and related ES. Thus, the best solution for this problem in the future may be to combine the economic interests of hydropower production with the maintenance of ecosystem integrity, in an “ecoregulation approach” (Jones, 2014). This can be done through the implementation of dam operation schemes and regulated discharges that benefit fish species of conservation, cultural and socioeconomic interest. However, practical application of this concept has had little or no development, mainly because the scientific knowledge needed for an integrated and successful implementation is almost non-existent and, currently, of the uttermost need to promote a sustainable exploitation of fish-related ES in regulated rivers (Moreira et al., 2019).

Co-management in fisheries allows for fishery sustainability to be achieved by involving fishermen, scientists, administration and authorities. Sustainability is achieved by the union of its three defining pillars: Environmental, Economic and Social. Integrated management in fisheries allows involvement of every person who represents each of these pillars, promoting a balanced resource exploitation at all levels. By sharing knowledge between fishermen and scientists, it is possible to establish policies that lead to the social-economic wellbeing of the sector, while maintaining a good environmental status of resources. This new “collaborative governance” is showing encouraging results in the pilot basin where it has been implemented (Almeida et al. 2018, 2021), so the replication of these strategies to other rivers, might be an effective way to enhance the ES provided by anadromous species.

Future climate-related changes are projected to beget shifts in the distribution range of aquatic species, changes in primary and secondary productivity, and shifts in timing of biological events (Lotze

et al., 2019). Species are gradually moving into cooler waters, and, as a result, species from warmer waters are replacing those traditionally caught in many fisheries worldwide. These shifts can lead to local extinction and colonisation events, resulting in changes in the pattern of species distributions and richness. Overall, changes in the pattern of species richness may disrupt aquatic biodiversity and ecosystems, and impact commercial fisheries (e.g., Boavida-Portugal et al., 2022). Evidence of climate change impacts on anadromous species are piling up, and Iberia aquatic ecosystems are amongst the most affected by this threat. So, it is vital to identify where and how these impacts might occur in order to mitigate the projected effects on these species. The comparison between potential distributions in the present and the future, allows assessing spatial dynamics of biodiversity and applying methodologies for the identification of refuges and priority areas for conservation (Alagador et al., 2016). The inclusion of these projections in integrated management plans, where different stakeholders participate, enables adaptive measures to be taken into account and the impacts on the ES provided by anadromous species minimised.

In conclusion, the future of anadromous fish, and the sustainability of associated ES, will depend on the way we deal with their potential, based on what we have learned from a legacy of past excesses. If we continue overexploiting their populations and reducing the habitat available for the completion of the life cycles, aggravated by present climate threats, anadromous fish in Iberia will tend to be reduced to residual populations with little or no use within human activities. The key to successfully manage anadromous fish species towards the sustainable promotion and exploitation of related ES, is the integration and compatibility of all legal uses associated with aquatic ecosystems, in a joint effort by interested stakeholders, fish scientists and governmental agencies, to protect and enhance the provisional, cultural, regulatory and support functions of these fishes, while mitigating existing threats.

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Data availability Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

Declarations

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

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