Limnetica, 43(1): 9-28 (2024). DOI: 10.23818/limn.43.02

Why and when do freshwater fish migrate? Observations of migration patterns of the native fishes from the Iberian Peninsula (SW Europe)

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Received: 21/07/21 Accepted: 20/01/23

ABSTRACT

Why and when do freshwater fish migrate? Observations of migration patterns of the native fishes from the Iberian Peninsula (SW Europe)

We reviewed information on Iberian freshwater fish to characterize their migratory status and identify migration reasons and periods. Most species migrate (87.3 %; 62 species from 15 families). A large number are potamodromous species (45 species from 6 families) but diadromous species (17 species from 11 families) also exist, including anadromous (9 species) and catadromous (8 species). The spawning period is a primary driver of fish migration but feeding and refuge-associated migrations also take place. Sexual maturity is the most important cue triggering fish migration, and other important factors include water temperature, river flow, currents, salinity and photoperiod. Spawning and migrating periods are in general prolonged and vary among years, as a response to the environmental variability of Mediterranean river systems, which are the most frequent in the Iberian Peninsula. Migratory movements of the various native species of each site cover almost the whole or the whole year. Therefore, to allow fish migration, Iberian freshwaters should always be connected, or their fish passes should be permanently, or practically always, in operation.

Key words: fish migration, freshwater, native species, migrating periods, Iberian Peninsula, Mediterranean rivers

RESUMEN

¿Por qué y cuándo migran los peces continentales? Observaciones de los patrones de migración de los peces autóctonos de la Península Ibérica (SO Europa)

Recopilamos información sobre los peces autóctonos ibéricos de aguas continentales para caracterizar su estatus migratorio e identificar las posibles razones y períodos de sus migraciones. La mayoría de las especies migran (87.3 %; 62 especies de 15 familias). Un gran número son especies potamódromas (45 especies de 6 familias) pero también existen especies diádromas (17 especies de 11 familias), incluyendo anádromas (9 sp.) y catádromas (8 sp.). El período de desove es uno de los principales impulsores de la migración de los peces, pero también se producen migraciones relacionadas con la alimentación y el refugio. La madurez sexual es la señal más importante que desencadena la migración de los peces, y otros importantes factores incluyen la temperatura del agua, el caudal de los ríos, las corrientes, la salinidad y el fotoperiodo. Los periodos de desove y migración son prolongados y cambiantes entre años, como respuesta a la variabilidad anual de los sistemas fluviales mediterráneos, que son los más frecuentes en la Península Ibérica. Los movimientos migratorios de las distintas especies autóctonas de cada tramo cubren prácticamente todo o todo el año. Por lo tanto, para permitir la migración de los peces, las aguas continentales ibéricas deberían estar siempre conectadas o sus dispositivos de paso para *peces tendrían que estar casi siempre o permanentemente en funcionamiento.*

Palabras clave: *migración piscícola, aguas continentales, especies autóctonas, períodos migratorios, Península Ibérica, ríos mediterráneos*

INTRODUCTION

Freshwater fish migration

Migration is a common phenomenon in many organisms, which has been defined as a specific mass behaviour that occurs a couple of times per year with a predetermined objective (Armstrong et al., 2010). Migration has been typically associated with reproduction or feeding. It can include the entire population (e.g., the European eel, *Anguilla anguilla*) or only part, which occurs when just a fraction of a population migrates and the remainder is resident (e.g., big-scale sand smelt, *Atherina boyeri*, and the European flounder, *Platichthys flesus*) (Morais & Daverat, 2016).

Migratory fish species can be classified as potamodromous or diadromous, with the former completing their life cycles in freshwaters and the later completed undertaking regular, seasonal, and life-stage-consistent migrations between marine and freshwater environments (McDowall, 1997; 2008). Diadromous fish can be further sub-divided into anadromous, when they migrate from marine environments to freshwater to spawn (e.g., salmonids and shads), catadromous, when adult fish move from freshwaters to the sea to spawn (e.g., anguillid and mullets), or amphidromous (just a few Pacific species).

Fish migrate for different reasons, including at least the following (Armstrong et al., 2010):

a) *Spawning*: to achieve reproductive success, spawning must be done with great accuracy in suitable areas at a time when other sexually mature fish are present (Wooton, 1990).

b) *Dispersion*: larvae, fry, and juveniles must move to disperse and colonise. For metapopulation conservation, drift is an indispensable natural phenomenon of fundamental biological importance (Baudoin et al., 2014).

c) *Feeding*: several fishes may make regular migrations, following seasonal patterns, moving to feeding areas at appropriate environments (Baudoin et al., 2014).

d) *Refuge*: fish undertake movements to escape threatening environments, to avoid acute adverse conditions, often seasonal in nature, including floods and seasonal drying of river sections, high water temperatures, low oxygen concentrations, pollution, or other unwelcome physiological challenges, such as evading predators (Feunteun et al., 2011).

e) *Displacement*: fish may get moved passively, being displaced downstream due to pollution, or being washed downstream by drift, floods, or other events. They then need to move to re-colonise areas once the event has passed (Baudoin et al., 2014).

Whatever the life stage, upstream and downstream migrations cues and triggers may be endogenous, linked to fish size and growth (Acolas et al., 2012), metabolism (Forseth et al., 1999) or sex (Ohms et al., 2014). They may also be exogenous, and linked to environmental conditions (e.g., water discharge, temperature, and photoperiod), density dependence, food abundance or even climate variability. Moreover, migration processes are often triggered by a combination of factors, the effects of which may interact and vary among populations, or among individuals within populations (Acolas & Lambert, 2016).

Iberian freshwater native fish species

Iberian freshwater native fish fauna comprises 19 families and 70 species (Table 1), with a high degree of endemicity (80 % of species; Doadrio et al., 2011). Iberian river basins flow either to the Atlantic Ocean (including the Cantabrian Sea) or to the Mediterranean Sea. Some fish species occur only in basins draining to the Atlantic (e.g., *Lampetra lampreys*; Atlantic salmon, *Salmo*

Table 1. List of the freshwater native fish species of the Iberian Peninsula, and their migration behaviour. It is indicated with an asterisk (*) the species for which no specific information is available and which is inferred from the behaviour of other species of the same genus. *Relación de las especies de peces continentales autóctonos de la Península Ibérica y su comportamiento migratorio. Se indican con un asterisco (*) las especies de las que no se dispone de información concreta y que se infiere a partir del comportamiento de las otras especies de su mismo género.*

Species	Migration behaviour
Syngnathidae	
Black-striped pipefish (*Syngnathus abaster*)	Diadromous (anadromous)
Petromyzontidae	
Costa de Plata lamprey (*Lampetra alavariensis*)	Potamodromous
Nabão lamprey (*Lampetra auremensis*)	Potamodromous
European river lamprey (*Lampetra fluviatilis*)	Potamodromous
Sado lamprey (*Lampetra lusitanica*)	Potamodromous
European brook lamprey (*Lampetra planeri*)	Potamodromous
Sea lamprey (*Petromyzon marinus*)	Diadromous (anadromous)
Cottidae	
Pyrenean sculpin (*Cottus hispaniolensis*)	Sedentary
Adour sculpin (*Cottus aturi*)	Sedentary
Acipenseridae	
European sturgeon (*Acipenser sturio*)	Diadromous (anadromous)
Clupeidae	
Allis shad (*Alosa alosa*)	Diadromous (anadromous)
Twaite shad (*Alosa fallax*)	Diadromous (anadromous)
Anguillidae	
European eel (*Anguilla anguilla*)	Diadromous (catadromous)
Atherinidae	
Big-scale sand smelt (*Atherina boyeri*)	Diadromous (anadromous)
Salmonidae	
Atlantic salmon (*Salmo salar*)	Diadromous (anadromous)
Brown trout, Sea trout (*Salmo trutta*)	Potamodromous & diadromous (anadromous)
Cyprinidae	
Bermejuela (*Achondrostoma arcasii*)	Potamodromous
Western ruivaco (*Achondrostoma occidentale*)	Potamodromous*
Ruivaco (*Achondrostoma oligolepis*)	Potamodromous
Sarda (*Achondrostoma salmantinum*)	Potamodromous
Jarabugo (*Anaecypris hispanica*)	Potamodromous
Iberian redfin barbel (*Barbus haasi*)	Potamodromous
Western Mediterranean barbel (*Barbus meridionalis*)	Potamodromous
Pyrenean gudgeon (*Gobio lozanoi*)	Potamodromous
Southwestern arched-mouth nase (*Iberochondrostoma almacai*)	Potamodromous
Iberian arched-mouth nase (*Iberochondrostoma lemmingii*)	Potamodromous
Portuguese arched-mouth nase (*Iberochondrostoma lusitanicum*)	Potamodromous*
Lisbon arched-mouth nase (*Iberochondrostoma olisiponensis*)	Potamodromous*
Oretanian arched-mouth nase (*Iberochondrostoma oretanum*)	Potamodromous*
Iberian barbel (*Luciobarbus bocagei*)	Potamodromous
Iberian long-snout barbel (*Luciobarbus comizo*)	Potamodromous
Ebro barbel (*Luciobarbus graellsii*)	Potamodromous
Eastern Iberian barbel (*Luciobarbus guiraonis*)	Potamodromous
Iberian small-head barbel (*Luciobarbus microcephalus*)	Potamodromous
Southern Iberian barbel (*Luciobarbus sclateri*)	Potamodromous
Steindachner barbel (*Luicobarbus steindachneri*)	Potamodromous
Jucar nase (*Parachondrostoma arrigonis*)	Potamodromous
Ebro nase (*Parachondrostoma miegii*)	Potamodromous
Turia nase (*Parachondrostoma turiense*)	Potamodromous
Pyrenean minnow (*Phoxinus bigerri*)	Potamodromous

Cont.

Table 1. (cont.)

Cyprinidae (cont.)	
Northern straight-mouth nase (*Pseudochondrostoma duriense*)	Potamodromous
Iberian straight-mouth nase (*Pseudochondrostoma polylepis*)	Potamodromous
Southern straight-mouth nase (*Pseudochondrostoma willkommii*)	Potamodromous
Calandino (*Squalius alburnoides*)	Potamodromous
Arade chub (*Squalius aradensis*)	Potamodromous
Northern Iberian chub (*Squalius carolitertii*)	Potamodromous
Gallo chub (*Squalius castellanus*)	Potamodromous*
Catalan chub (*Squalius laietanus*)	Potamodromous
Málaga chub (*Squalius malacitanus*)	Potamodromous*
Bogardilla (*Squalius palaciosi*)	Potamodromous*
Southern Iberian chub (*Squalius pyrenaicus*)	Potamodromous
Mira chub (*Squalius torgalensis*)	Potamodromous*
Eastern Iberian chub (*Squalius valentinus*)	Potamodromous
Cobitidae	
Northern Iberian spined-loach (*Cobitis calderoni*)	Sedentary
Southern Iberian spined-loach (*Cobitis paludica*)	Sedentary
Vettonian spined-loach (*Cobitis vettonica*)	Sedentary
Homalopteridae	
Pyrenean stone loach (*Barbatula quignardi*)	Potamodromous
Gasterosteidae	
Three-spined stickleback (*Gasterosteus aculeatus*)	Potamodromous
Aphaniidae	
Baetican toothcarp (*Aphanius baeticus*)	Sedentary
Iberian toothcarp (*Aphanius iberus*)	Sedentary
Valenciidae	
Samaruc (*Valencia hispanica*)	Sedentary
Blenniidae	
Freshwater blenny (*Salaria fluviatilis*)	Potamodromous
Gobiidae	
Common goby (*Pomatoschistus microps*)	Diadromous (anadromous)
Mugilidae	
Thicklip grey mullet (*Chelon labrosus*)	Diadromous (catadromous)
Thinlip grey mullet (*Chelon ramada*)	Diadromous (catadromous)
Flathead grey mullet (*Mugil cephalus*)	Diadromous (catadromous)
Leaping mullet (*Liza saliens*)	Diadromous (catadromous)
Golden grey mullet (*Liza aurata*)	Diadromous (catadromous)
Pleuronectidae	
European flounder (*Platichthys flesus*)	Diadromous (catadromous)
Moronidae	
European sea bass (*Dicentrarchus labrax*)	Diadromous (catadromous)

salar, or sculpins, Cottus spp), while others are more common in them than in those flowing to the Mediterranean (e.g., allis shad, *Alosa alosa*, or European flounder, *P. flesus*).

The Iberian Peninsula has a long history of anthropogenic disturbance that has led to the poor conservation status of its ichthyofauna, with 67 % of species catalogued as critically endangered, endangered, or vulnerable, according to UICN criteria (Doadrio et al., 2011). The main threats to Iberian ichthyofauna are similar to those affecting other Mediterranean regions (Darwall et al., 2014), and include hydrologic and habitat alterations, impacts of alien species and pollution and constraints associated with global warming (Doadrio, 2001, Cabral et al., 2005, Maceda-Veiga, 2012, Radinger & García-Berthou, 2020).

Information about migrating behaviours and patterns is scarce for most Iberian freshwater native fish. We present a thorough review of fish migration from the Iberian Peninsula, with the aim of providing basic information on fish migration that may be useful to conserve and restore native fish populations and their habitats in Iberian rivers, estuaries, lakes, and coastal lagoons.

METHODS

Study area

The Iberian Peninsula (Fig. 1) has 1794 known large dams. Within Spain there are 1538 large dams and at least 22 000 other migratory barriers. Portugal has 256 large dams and at least 8094 other migratory barriers (Ordeix et al., 2018). Although dam and weir removal has been increasingly used in the last few decades, only 254 river obstacles were eliminated across Spain over the past decades, whilst in Portugal only 5 river obstacles were removed (Ordeix et al., 2018). More than 500 fish passes had been constructed in Spain and more than 55 in Portugal by 2016 (Ordeix et al., 2018), and only a small percentage of them are functional (Santo, 2005, Elvira et al., 1988, Ordeix et al., 2011).

After the building of most weirs and dams during last centuries, mainly due to river fragmentation, there has been an estimated 80 % loss of accessible habitat for sea lamprey (*P. marinus*) (Mateus et al., 2012), and over 80 % loss of ac-

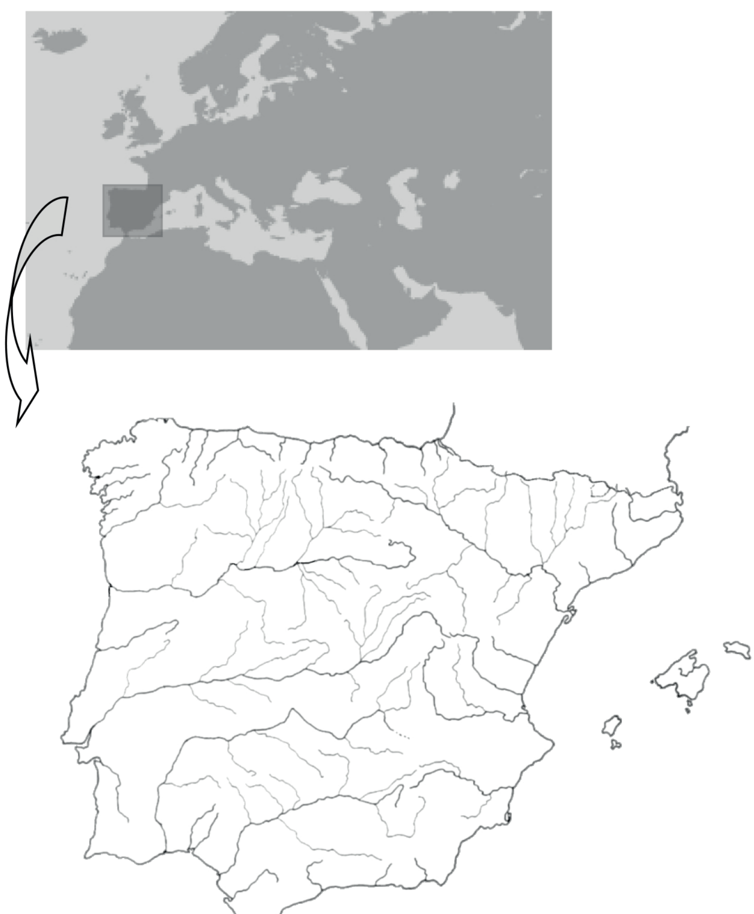

Figure 1. Study site: the Iberian Peninsula, in the Western Mediterranean and Western Palearctic, and its most important rivers. *Área de estudio: la Península Ibérica, en el Mediterráneo Occidental y el Paleártico Occidental y sus ríos más importantes.*

cessible habitat for the European eel (*A. anguilla*) (Clavero & Hermoso, 2015), historically widespread throughout the Iberian Peninsula. Likewise, species so typical of Iberian river ecosystems (chubs, barbels, loaches) have difficulties or are unable to develop their life cycle in reservoirs. To close their life cycle, they must migrate at least during the spawning period (Encina et al., 2006). Mostly the exotic species (such as the common carp) can reproduce in Iberian reservoirs.

Sources of information

We collected and updated information on all freshwater native fish species of the Iberian Peninsula (Kottelat & Freyhof, 2007, Doadrio et al., 2011; Table 1). The applied taxonomy is in accordance with Kottelat & Freyhof (2007), except for a few species described more recently. Several marine adventitious species and marine seasonal species that occur in the estuaries have also been included here.

We reviewed 376 books and articles on the biology and ecology of native Iberian freshwater fish, with especial attention to fish passage assessments, spawning and migrating periods, and other possible associated causes of the migrations. Google Scholar was used for general bibliographic search using general referencing such as the common and scientific names of the fish species; ScienceDirect, Scopus and PubMed were used for advanced searches, using keywords.

RESULTS

Most Iberian native freshwater fishes (87.3 %; 62 species from 15 families) migrate (Table 2), most of them being potamodromous species (45 species from 6 families). There are also 17 diadromous species from 11 families, 9 of them being anadromous and 8 being catadromous (Fig. 2). Amphidromous species (following McDowall, 1997) are absent. Only 2 families (Petromyzontidae and Salmonidae) include species with con-

Table 2. Migrating behaviour within families of the Iberian freshwater native fishes. *Comportamiento migratorio en las familias de peces continentales autóctonos ibéricos.*

Family and common name	Number of species	Number of potamodromous species	Number of diadromous species	% Migratory species
Syngnathidae (pipehorses)	1		1	100
Petromyzontidae (lampreys)	6	4	1	100
Cottidae (sculpins)	2			0
Acipenseridae (sturgeons)	1		1	100
Clupeidae (shads)	2		2	100
Anguillidae (eels)	1		1	100
Atherinidae (silversides)	1		1	100
Salmonidae (salmons and trouts)	2	1	2	100
Cyprinidae (barbels, chubs, etc)	37	37		100
Cobitidae (loaches)	3			0
Homalopteridae (river loaches)	1	1		100
Gasterosteidae (sticklebacks)	1	1		100
Aphaniidae (Oriental killifishes)	2			0
Valenciidae (toothcarps)	1			0
Blenniidae (blennies)	1	1		100
Gobiidae (gobies)	1		1	100
Mugilidae (mullets)	5		5	100
Pleuronectidae (flounders)	1		1	100
Moronidae (temperate basses)	1		1	100
TOTAL	70	**45**	**17**	**87.3**

trasting migratory behaviours, potamodromous –brook lampreys and brown trout- and anadromous –sea lamprey, the Atlantic salmon and sea trout- (Table 2). One species, brown trout (*S. trutta*), superimposes three different migratory patterns, depending on their populations: sedentary, potadromous and anadromous, namely sea trout.

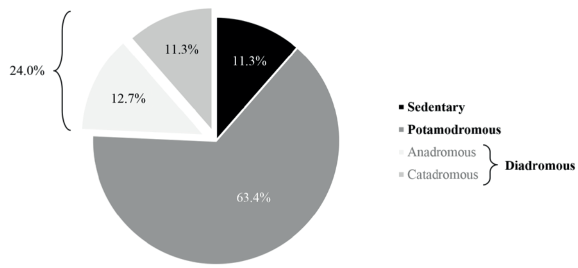

Figure 2. Migration behaviour of Iberian freshwater native fish, divided into two major groups: potamodromous and diadromous (subdivided into anadromous and catadromous) species. *Comportamiento migratorio de los peces continentales ibéricos autóctonos, divididos en dos grandes grupos: especies potamódromas y diádromas (subdivididas en anádromas y catádromas).*

Likewise, three-spined stickleback (*Gasterosteus aculeatus*) is potamodromous around the Iberian Peninsula, but catadromous behaviours, which are common in northern Europe, have not been reported (Fernández et al., 2015).

Few species (11.3 %; 8 species from 4 families) are considered sedentary (Kottelat & Freyhof, 2007, Doadrio et al., 2011).

Why

Few studies from the Iberian Peninsula contain information on fish migration associated with spawning periods, feeding and refuge. Dispersion and displacement have not been assessed (Table 3). Migration has been mostly associated with the spawning periods for salmonids, cyprinids, sturgeons, and shads, among others (Table 3). Information about fish migration related with feeding is available for some groups which spawn in marine environments and move to estuaries, rivers, or coastal lagoons in search of food to grow, such as the European eel (*A. anguilla*) and mullets. Associated with refuge, jarabugo (*Anaecypris*

Table 3. Summary of different drivers associated with the Iberian freshwater native fish migration (by families). *Resumen de los diferentes impulsores asociados a la migración de los peces continentales autóctonos ibéricos (por familias).*

Family and common name	Spawning	Feeding	Refuge	References
Syngnathidae (pipehorses)	X			Sostoa et al., 1990, Doadrio et al., 2011, López et al., 2015
Petromyzontidae (lampreys)	X			Salvador, 2003, Doadrio et al., 2011, Mateus et al., 2012, Silva et al., 2013, +5
Cottidae (sculpins)				
Acipenseridae (sturgeons)	X			Classen, 1944, Porres & Farnós, 1999
Clupeidae (shads)	X			López et al., 2007, Mota et al., 2015, Nachón et al., 2015, Life MigratoEbre, +5
Anguillidae (eels)		X		Lobón-Cerviá et al., 1995, Cobo et al., 2014, Santos et al., 2014, +15
Atherinidae (silversides)	X			Fernández-Delgado et al., 1988, Jiménez et al., 2002, López et al., 2015, +2
Salmonidae (salmons and trouts)	X			Utrilla & Lobón-Cerviá, 1999, Caballero et al., 2010, Santos et al., 2004, Larios-López et al., 2015, +14
Cyprinidae (barbels, chubs, etc)	X		X	Santos et al., 2002, Ordeix et al., 2011, Salvador, 2013, Santos et al., 2014: +110
Cobitidae (loaches)				
Homalopteridae (river loaches)	X			Sostoa et al., 1990, Doadrio et al., 2011, Ordeix et al., 2011, CERM data base
Gasterosteidae (sticklebacks)	X			Jiménez et al., 2002, Doadrio et al., 2011, López et al., 2015, Fernández-Delgado. et al., 2015, +1
Aphaniidae (Oriental killifishes)				
Valenciidae (toothcarps)				
Blenniidae (blennies)	X			Vila-Gisbert & Moreno-Amich, 1998, Rodríguez-Jiménez, 2001, Jiménez et al., 2002, Aparicio et al., 2012, +5
Gobiidae (gobies)	X	X		Sostoa et al., 1990, Fernández-Delgado et al., 2000, Doadrio et al., 2011, +1
Mugilidae (mullets)		X		Sostoa et al., 1990, Fernández-Delgado et al., 2000, Santos et al., 2004, +11
Pleuronectidae (flounders)		X		Martinho et al., 2008, Freitas et al., 2009, Sostoa et al., 1990, Doadrio et al., 2011
Moronidae (temperate basses)		X		Sostoa et al., 1990, Fernández-Delgado et al., 2000, Martinho et al., 2008, López et al., 2015

hispanica), an endemic cyprinid from small tributaries of the Guadiana River basin (SW Spain and S Portugal; Ribeiro et al., 2000), undertakes movements to avoid droughts of river sections. It looks for mean water temperatures of 25 ºC, resisting until 30 ºC (Salvador, 2009).

Sexual maturity and condition of fish is the most important cue used by Iberian freshwater native fishes for their migration, but others also play an important role (Table 4).

Sexual maturity of fish

For most of the Iberian native freshwater fish, reproductive period is long and variable from year to year. Most species have multiple spawning (Doadrio, 2001). Their spawning and ascending periods can also vary between years, depending on river discharge and water temperature. Thus, in northern Portugal (Santos et al., 2004), river discharge and water temperature explained 25 % of variation of Iberian straight-mouth nase (*P. polylepis*). Only temperature explained 21 % of variation of brown trout (*S. trutta*) and 17 % of sea lamprey (*P. marinus*). Water temperature (13 %) and rain (17 %) explained variation of flathead grey mullet (*M. cephalus*).

Following a quite general pattern in animal bi-

Table 4. Number of citations for each different cue or trigger associated with Iberian freshwater native fish migration (by families). *Número de citas para cada señal o detonante diferente asociado a la migración de los peces continentales autóctonos ibéricos (por familias).*

Family and common name	SMC	WT	RFM	TC	PH	MC	TU	SAL	References
Syngnathidae (pipehorses)	3							1	Sostoa et al., 1990, Doadrio et al., 2011, López et al., 2015
Petromyzontidae (lampreys)	8	2			1				Almeida et al., 2000, Rodríguez-Muñoz et al., 2001, Santos et al, 2004, Ferreira, 2011, Doadrio et al., 2011, Mateus et al., 2012, Silva et al., 2013, Silva, 2014
Cottidae (sculpins)									
Acipenseridae (sturgeons)	3		1						Classen, 1944, Porres & Farnós, 1999, Fernández-Pasquier, 2000
Clupeidae (shads)	7							1	Sostoa et al., 1990, López et al., 2007, Doadrio et al., 2011, López et al., 2015, Mota et al., 2015, Nachón et al., 2015, Life MigratoEbre data base
Anguillidae (eels)	5	2	5	1	2	1	1	1	Labar et al., 1987, Domingos, 1992, Lobón-Cerviá et al., 1995, Arribas et al., 2012, Gómez et al., 2012, Cobo et al., 2014, CERM data base, Life MigratoEbre data base
Atherinidae (silversides)	2						2	2	Sostoa et al., 1990, Pombo & Rebelo, 2002, Pombo et al., 2005, Aparicio et al., 2013; López et al., 2015
Salmonidae (salmons and trouts)	7	4	5		2				Sostoa et al., 1990, Utrilla & Lobón, 1999, Santos et al., 2002, Santos et al, 2004, Doadrio et al., 2011, Ordeix et al., 2011, Caballero et al., 2010, Caballero, 2013, Yécora et al., 2013, García-Vega et al., 2022
Cyprinidae (barbels, chubs, etc)	9	9	6		3	1			Santos et al., 2002, Ribeiro et al., 2003, Santos et al, 2004, Encina et al., 2006, Salvador, 2009, Salvador, 2009, Morán, 2010, Ordeix et al., 2011, Salvador, 2012, Sanz et al., 2013, Salvador, 2013, Ordeix, 2017, CERM data base, Sánchez-Pérez et al., 2022
Cobitidae (loaches)									
Homalopteridae (river loaches)	1	1	1						CERM data base
Gasterosteidae (sticklebacks)	1								López et al., 2015
Aphaniidae (Oriental killifishes)								1	Rodríguez-Climent et al., 2013
Valenciidae (toothcarps)									
Blenniidae (blennies)									
Gobiidae (gobies)		1						2	Sostoa et al., 1990, Rodríguez-Climent et al., 2013
Mugilidae (mullets)		4	1		3			3	Oliveira & Ferreira, 1997, Santos et al, 2004, Ordeix et al., 2011, Aparicio et al., 2012, Aparicio et al., 2013, Rodríguez-Climent et al., 2013, CERM data base, Life MigratoEbre data base
Pleuronectidae (flounders)	1							2	Sostoa et al., 1990, Morais et al., 2011
Moronidae (temperate basses)		1						2	Pombo & Rebelo, 2002, Baldó et al., 2005
TOTAL	**47**	**24**	**19**	**1**	**14**	**2**	**3**	**15**	

Legend: SMC: Sexual maturity and condition of fish; WT: Water temperature; RFM: River flow, currents, hydrology, and meteorology; TC: Tidal cycle; PH: Diurnal/nocturnal rhythm or photoperiod; MC: Moon cycle; TU: Turbidity; SAL: Salinity.

ology, in which males arrive to spawning places before females, in the lower Minho River in Portugal, more males of allis shad (*A. alosa*) than females were caught in March and April, and more females than males between May and July (Mota et al., 2015). Likewise, before becoming extinct in the lower Guadalquivir (SW Spain), more than half of the European sturgeon (*A. sturio*) going upstream were males (50-55 %) at the end of January and February. The ratio began to change in favour of females in the first days of March, comprising more than 90 % in May (Classen, 1944).

Water temperature

Water temperature is the most important factor stimulating upstream movements of cyprinids in spring. In the Touvedo fish lift, Lima River in northern Portugal (Santos et al., 2002), Iberian barbel (*L. bocagei*) and Northern straight-mouth nase (*P. duriense*) start to migrate at water temperatures above 15 ºC and 12-14 ºC, respectively. Iberian barbel and Iberian nase also move upstream of the Santa Teresa reservoir, in the Tormes River (Duero Basin, Spain; Sanz et al., 2013), when water temperature reaches 15 ºC and 17 ºC, respectively. In NE Catalonia (Ordeix et al., 2011), in the Llobregat river basin, Iberian redfin barbel (*B. haasi*) move upstream when water temperature rises up 7-10 ºC. In the Ter and Fluvià river basins (Ordeix et al., 2011, Ordeix, 2017), Western Mediterranean barbel (*B. meridionalis*) and Catalan chub (*Squalius laietanus*), when water temperature rises above 10 and 13 ºC, respectively, but high passage rates are associated with warmer water: 14-18 ºC.

Sea lamprey (*P. marinus*) migrate in northern Portugal (Santos et al., 2004) at temperatures above 11 ºC, showing pronounced activity at 12-16 ºC.

In the Lima River (northern Portugal; Santos et al., 2002), brown trout (*S. trutta*) migrate mainly when water temperature exceed 9-13 ºC. In the Bidasoa River (Navarre, N Spain), brown trout upstream movements occurred with 9.5-14.5 °C (García-Vega et al., 2022). In NE Catalonia (Ordeix et al., 2011), high passage rates are around 12 ºC.

Main seasonal activity of flathead grey mullet (*M. cephalus*) in N Portugal (Santos et al., 2004) begin in association with warmer water above 13 ºC, and the greatest increment is observed at temperatures above 21 ºC. Similar results have been found for thinlip grey mullet (*C. ramada*) in the River Tagus, Portugal (Oliveira & Ferreira, 1997), the Ter River (Ordeix et al., 2011) and the Ebre River (Aparicio et al., 2012), Catalonia.

In the coastal lagoons of the Ebre delta, Catalonia, a drop-in temperature to 3 ºC produces a massive migration of the common goby (*Pomatoschistus microps*) population towards the sea (Sostoa et al., 1990).

River flow, currents, hydrology, and meteorology

During flood periods, potamodoromous fish migrate upstream, hide or drift until they find shelter in zones down-river such as pools. Species associated with temporary or semi-permanent rivers may be forced to select those zones with more permanent water availability, usually found going downstream (Filipe et al., 2002); e.g., freshwater blenny (*S. fluviatilis*), whose spawning period extends from the end of May to the beginning of August (Vinyoles, 1993), coinciding with the driest period in the Iberian Peninsula. In summer, in many cases they remain concentrated in overcrowded pools. Survivors colonise upstream after subsequent rains (Casals, 2005).

Contrary to many other cyprinids, which migrate upstream mainly in spring, an Iberian fish of a Portuguese Mediterranean intermittent river, the ruivaco (*Achondrostoma oligolepis*), migrate upstream during autumn and winter, typically characterised by high flows (Silva et al., 2020).

The dynamics of diadromous fish are different. In the lower Guadalquivir River, Spain, the abundance of the European sturgeon (*A. sturio*) was directly correlated with the magnitude of river flow (Fernández-Pasquier, 2000). As observed elsewhere, in the Mondego estuary, Portugal, glass eel (*A. anguilla*) abundance is favoured by high river flows (Domingos, 1992).

Tidal cycle

Spatial changes in glass eel (*A. anguilla*) density within the Guadalquivir estuary, Andalucía, Spain (Arribas et al., 2012), depend on tidal and light situations, although maximum densities appear at diurnal and/or nocturnal flood tides. The European flounder (*P. flesus*) combines active migration strategies and selective tidal stream transport (Martinho et al., 2008).

Diurnal/nocturnal rhythm or photoperiod

Fish migration mostly occurs in the evening and at night: Iberian barbel (*L. bocagei*), Iberian straight-mouth nase (*P. polylepis*), Northern Iberian chub (*Squalius carolitertii*), brown trout (*S. trutta*) and sea lamprey (*P. marinus*) show significant nocturnal preferences in their upstream movements in the Lima River (Portugal; Santos et al., 2004), being also more active during rainy and cloudy days.

In the Bidasoa River (Navarre, N Spain), the most of upstream movements (81 %) of brown trout occurred when photoperiod was lower than 10.5 h (García-Vega et al., 2022).

However, some species have clear preferences to move during the day. Flathead grey mullet (*Mugil cephalus*), with hourly activity taking the form of a bimodal curve with its maxima in early morning (08.00–10.00 hours) and mid-afternoon (15.00–17.00 hours) in the Lima River (Portugal; Santos et al., 2004). Thinlip grey mullet (*C. ramada*) behaves in a similar way up to the Ter River, in Catalonia (Ordeix et al., 2011).

Moon cycle

The biggest catches of glass eel (*A. anguilla*) in the estuarine fisheries in Catalonia occur mostly during the new moon, also positively influenced by wind, big river flows and mild temperatures (Gómez et al., 2012). In the Fluvià River (NE Catalonia), during the breeding season, statistically significant differences between full moon and new moon crossing rates upstream of Western Mediterranean barbel (*B. meridionalis*) and Catalan chub (*S. laietanus*) were also observed (Ordeix, 2017).

Turbidity

Turbidity explains the emergence of several species: as the big-scale sand smelt (*A. boyeri*), which is also associated with high salinity (Sostoa et al., 1990), which appears related to high turbidity in the Ter and Daró estuaries, in Catalonia (Aparicio et al., 2013), and also in the Aveiro Estuary, in Portugal (Pombo et al., 2005). In addition, glass eel (*A. anguilla*) upstream migration is clearly associated with high turbidity in the Guadalquivir Estuary (Arribas et al., 2012).

Salinity

Several coastal strict catadromous species (e.g., big-scale sand smelt, *A. boyeri*, common goby, *P. microps*, black-striped pipefish, *Syngnathus abaster*, and the European flounder, *P. flesus*, among others), which spawn into the sea, enter the Ebre river sporadically in the period of minimum river flow, when the water is almost salted (40-60 %; Sostoa et al., 1990).

In the freshwater tidal area of the Minho estuary (northern Portugal; Morais et al., 2011), the European flounder (*P. flesus*) arrives from higher salinity to freshwater areas for spawning, contradicting the general assumption that the European flounder reproduces exclusively in marine waters (Martinho et al., 2008).

When

Most Iberian freshwater native fish migrate at specific times of the year, although some can migrate year-round (Table 5). Migration periods can be displayed in the following 3 groups:

a) *Late winter, spring and early summer for cyprinids, the European sturgeon and shads, among others*.

Although there is a latitudinal gradient in the Iberian Peninsula regarding the timing of migration, both potamodromous (cyprinids, with some exceptions, like the ruivaco (*A. oligolepis*; Silva et al., 2020), among others) and diadromous (such as sturgeons and shads) migrate upstream mainly in spring.

For example, around March-April, 51.9 % of the total observations of Iberian barbel (*L. bocagei*), and 77 % of Iberian straight-mouth nase (*P. polylepis*) going upstream are carried out in the Touvedo fish lift, in the Lima River, northern

Portugal (Santos et al., 2004). Also, in the upper basin of Tormes river (Salamanca, W Spain), Iberian barbel movements were concentrated between May and June; however, for Northern straight-mouth nase (*P. duriense*), the migration period extended until November (Pedescoll et al., 2019).

Before becoming extinct in the lower Guadalquivir (SW Spain), the European sturgeon (*A. sturio*) went upstream to spawn between the end of January and May (Classen, 1944). In the lower Ebre (Catalonia), they mainly appeared from March to July (Porres & Farnós, 1999).

Moreover, in the north-west of the Iberian Peninsula, catches of allis shad (*A. alosa*), first, and then twaite shad (*Alosa fallax*) decline from January at sea (Nachón et al., 2015). Twaite shad start their entry into the Ebre River estuary from February to March; it spawns upstream from May to June (López et al., 2015); adults go downstream in June (Life MigratoEbre database). Twaite shad young-of-the-year (YOY) seaward migration takes place in schools, during summer, autumn, and early winter (López et al., 2015; Nachón et al., 2019).

The European sea bass (*D. labrax*) and the European flounder (*P. flesus*) enter the estuaries in late winter and early spring (Martinho et al., 2008), respectively.

b) *Autumn, winter and spring for sea lamprey, the European eel, and brown trout*.

Despite the existing latitudinal gradient regarding the timing of migration, they migrate upstream mainly in winter.

Sea lamprey (*P. marinus*) initiate their upstream reproductive migration in Portuguese river basins in December, with a peak of reproductive migration between February and April, depending on the meteorological conditions (Almeida et al., 2000). Following the final stages of metamorphosis, the downstream migration typically occurs between November and April (Hardisty, 1986).

Although their recruitment occurs throughout the year, upstream migration for glass eel and elvers (*A. anguilla*) mostly happens in October-March (mainly in April) in northern Spain (Lara, 1994), October-April (mainly in May) in northern Portugal (Domingos, 1992, Antunes & Weber, 1996), October-May in southern Spain (Arribas et al., 2012), and October-March in Catalonia (Gómez et al., 2012), including a secondary peak in June in the Ebre Delta (López et al., 2015). Upstream movements of yellow (young) eels mostly take place in summer in the Ebre River, Catalonia (Aparicio et al., 2012), and in summer and early autumn in the Lima River, Portugal (Santos et al., 2004). Otherwise, downstream migration of silver (mature) eels occurs in September-October in the northern Costa Brava streams (Catalonia) (CERM database), between November and February in the Ebre river (Life MigratoEbre database) and until March in Cantabrian region (N Spain; Lobón-Cerviá & Carrascal, 1992).

The sooner brown trout (*S. trutta*) breeding population in the year is at the greatest latitude and altitude. A long-term (1995–2019) analysis in the lower River Bidasoa (Navarre, N Spain) showed that most upstream movements of potamodromous trout occurred in October–December (García-Vega et al., 2022). November-January, in the Pyrenees (Sostoa et al., 1995); December-February, in Asturias (N Spain; García & Braña, 1988); between October and early May, in the Baetican Mountains (SE Spain) (Larios-López et al., 2015). Brown trout mainly ascends in spring (57.9 %) in Lima River (N Portugal; Santos et al., 2004), although some seasonal activity persists in autumn (18.3 %).

c) *All year round for the Atlantic salmon, sea trout and mullets*.

In the Iberian Peninsula (Caballero et al., 2010), the Atlantic salmon's (*S. salar*) entry into rivers is gradual throughout the year. Young salmon go downstream between April and May. In the Ulla River (Galicia, N-W Spain), the Atlantic salmon starts to enter the river in March, but they do not go upstream to spawn until October (Caballero, 2013). Generally, adult salmon downstream migration occurred between December and April (Caballero et al., 2010).

In the Ulla River, sea trout (*S. trutta*) starts to enter the river in April and follows upstream in October (Caballero, 2013). In the lower River Bidasoa (Navarre, N Spain), despite entering it throughout the year, most upstream movements of sea trout occurred in June–July, but the largest individuals go upriver between October and De-

Table 5. Summary of spawning and migrating periods, up- and downstream, of Iberian freshwater native fish species. R = reproductive adults; Y = young; F = fry; · = few individuals; ? = probably. *Resumen de los periodos de desove y migración, aguas arriba y aguas abajo, de las especies de peces continentales autóctonos ibéricos. R = adultos reproductivos; Y = juveniles, F = alevines; · = pocos individuos; ? = probablemente.*

Family and common name	Month of **spawning** in freshwater												Month of **upstream migration**												Month of **downstream migration**												References
	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	J	F	M	A	My	Jn	Jl	Ag	S	O	N	D	
Syngnathidae (pipehorses)																																					Sostoa et al., 1990, Doadrio et al., 2011, López et al., 2015
Petromyzontidae (lampreys)		*																							Y	Y	Y	Y	Y	*			*	Y	Y	Y	Salvador, 2003, Doadrio et al., 2011, Mateus et al., 2012, Silva et al., 2013, +5
Cottidae (sculpins)																																					Sostoa et al., 1990, Sousa-Santos et al., 2014a
Acipenseridae (sturgeons)																			*	Y	Y																Classen, 1944, Porres & Farnós, 1999
Clupeidae (shads)													*	*					*						Y				R	R	Y	Y	Y	Y	Y	Y	López et al., 2007, Mota et al., 2015, Nachón et al., 2015, Life MigratoEbre, +5
Anguillidae (eels)													F	F	F	F	F	F	*	*	*	F	F	F	R	R	R	*	*	Y	Y	R	R	R	R	R	Lobón-Cerviá et al., 1995, Cobo et al., 2014, Santos et al., 2014, +15
Atherinidae (silversides)																	Y	Y																			Fernández-Delgado et al., 1988, Jiménez et al., 2002, López et al., 2015, +2
Salmonidae (salmons and trouts)																																					Utrilla & Lobón-Cerviá., 1999, Caballero et al., 2010, Santos et al., 2004, Larios-López et al., 2015, +14
Cyprinidae (barbels, chubs, etc)																														R		Y					Santos et al., 2002, Ordeix et al., 2011, Salvador, 2013, Santos et al., 2014, +110
Cobitidae (loaches)																																					Sostoa et al., 1990, Soriguer et al., 2000, Doadrio et al., 2011, Perdices, 2013, +6
Homalopteridae (river loaches)															?	?																					Sostoa et al., 1990, Doadrio et al., 2011, Ordeix et al., 2011, CERM data base
Gasterosteidae (sticklebacks)													?	?	?	?																					Jiménez et al., 2002, Doadrio et al., 2011, López et al., 2015, Fernández et al., 2015, +1
Aphaniidae (Oriental killifishes)																																					García-Berthou & Moreno-Amich, 1993, Fernández-Delgado et al., 1998, Clavero et al., 2004, +6
Valenciidae (toothcarps)																																					Sostoa et al., 1990, Jiménez et al., 2002, Caiola, 2011, López et al., 2015
Blenniidae (blennies)										*				?	?	*	*	?	*	?	*																Vila-Gisbert & Moreno-Amich, 1998, Rodríguez-Jiménez, 2001, Jiménez et al., 2002, Aparicio et al., 2012, +5
Gobiidae (gobies)																																					Sostoa et al., 1990, Fernández-Delgado et al., 2000, Doadrio et al., 2011, +1
Mugilidae (mullets)																									R	R	R	R	R	R	R	R					Sostoa et al., 1990, Fernández-Delgado et al., 2000, Santos et al., 2004, +11
Pleuronectidae (flounders)																										Y	Y										Martinho et al., 2008, Freitas et al., 2009, Sostoa et al., 1990, Doadrio et al., 2011
Moronidae (temperate basses)																																					Sostoa et al., 1990, Fernández-Delgado et al., 2000, Martinho et al., 2008, López et al., 2015
TOTAL																																					

Legend: R = reproductive adults; Y = young; F = fry; * = few individuals; ? = probably.

cember (García-Vega et al., 2022).

In spring, many adults and in summer, many juvenile mullet (thinlip grey mullet, *C. ramada*, flathead grey mullet, *M. cephalus* and thicklip grey mullet, *Chelon labrosus*) enter the estuaries and rivers (Ordeix et al., 2011, Aparicio et al., 2013). In the lower Ebre river (Catalonia), upstream migration of adults these three species was observed all year round, but specially in winter and spring. Downstream migration of adults was reported between November (also October for *C. labrosus*) and June (also in July for *C. ramada* and August for *M. cephalus*) (Life MigratoEbre database). In the Aveiro coastal lagoon, March corresponds to the seaward migration of some seasonal migrant species, namely golden grey mullet (*L. aurata*). A few weeks after each spawning period, mullet fry approach the shore in dense schools and enter lagoons, rivers, or even lakes (Pombo & Rebelo, 2002).

DISCUSSION

Potamodromous native fish species are globally predominant in the Iberian Peninsula, and diadromous are divided between catadromous and anadromous almost equally, as occurs in temperate regions (Lucas & Baras, 2001). The 17 diadromous native species (and 45 non-diadromous migrating ones) located are relatively equivalent to 17 diadromous species (and 24 non-diadromous migrating ones) located in New Zealand (McDowall, 2008), and 38 diadromous species (and 62 non-diadromous migrating ones) located in Canada (Scott & Crossman, 1973). Despite this, in general, the availability of information from the Iberian Peninsula is particularly associated with the commercial relevance in certain species (Mota et al., 2016); it is scarce for species that have very small distribution areas and for non-fishable species for anglers.

Why

Most drivers for Iberian freshwater native fish migration are associated to spawning and, for some species, to feeding and refuge (Table 3). However, some species or populations may not migrate; for example, if fish have good reproduction and feeding conditions in the area or section where they live. This could the case of the Mediterranean coastal lagoons occupied by toothcarps (Oliva-Paterna et al., 2008), and in the upper part of the Pyrenees, Catalonia, where adult brown trout (*S. trutta*) show a highly sedentary behaviour (Sostoa et al., 1995). But this is unclear for juveniles.

The differentiation of sexes during the migration may be related to the fact that males -in many cases, of smaller size and requiring less effort than females to produce their gametes- act as pioneers. For example, adult female lampreys are subsequently attracted to the spawning grounds by sexual pheromones (bile acids) released by mature males, who are the first to arrive and begin nesting activities (Hardisty, 1986).

For catadromous fish (e.g., European eel and mullets), the upstream passage –or their entry into coastal lagoons- associated to feeding could benefit their metapopulation by diminishing intraspecific competition in the downstream reaches. Better osmoregulation conditions in rivers and estuaries than in the sea can also favour them (Feunteun et al, 2011).

As has been indicated for the jarabugo (*A. hispanica*) in the Guadiana River basin, Spain and Portugal (Ribeiro et al., 2000), Mediterranean fishes can undertake migrations associated with refuge, to avoid seasonal drying of river sections, high water temperatures and low oxygen concentrations.

Contrary to some more northern European species (*S. salar*, *A. alosa* and *P. marinus*) (Travade & Larinier, 2002), endangered or already extinct in the Mediterranean basins, most of the Mediterranean freshwater native fish have multiple spawning. Including spawning periods extended and changing between years, they are probably adaptions to the Mediterranean climate (Cambray & Bruton, 1984).

There is a broad consensus that water temperature is an important factor-triggering up- and downstream migrations of several fish species. This is also relevant for estuaries (Aveiro, Guadalquivir, Ebre, Ter). Changes in river flow and water current influence migrating fish, which provide visual, tactile, and inertial cues. High water discharge stimulates the river ascent, also from lakes, estuaries, and coastal environments, often mixed with additional stimuli (temperature, photoperiod, etc), to concert movement in a single direction (Lucas & Baras, 2001). Likewise, an increase in rainfall, erosion and flow could change the composition of the dissolved or particulate water components and elicit the migratory response (Arribas et al., 2012). For example, intense rainfall reduces the salinity values, and glass eels swim driven by positive rheotaxis towards low salinity water (Tosi et al., 1989). This behaviour can be enhanced by the existence of an odoriferous cue in freshwater caused by the presence of other eels (Miles, 1968) or traces of geosmin (Tosi & Sola, 1993) in continental waters.

It is well known that estuarine fish colonize rivers, salt marshes and mudflats at each high tide (Feunteun et al., 2011). Likewise, most Iberian native cyprinids show significant nocturnal preferences in their upstream movements (Santos et al., 2004, Sanz et al., 2013). As has also been reported, for example, in Iberian estuaries (Guadalquivir, Ebre and Ter) for glass eel (*A. anguilla*) catches in the new moon, this is also assumed to be an adaptation to avoid visual predators (Jonnson, 1991).

When

Because of a latitudinal gradient regarding the timing of migration, in spring, southern populations start their upstream migration earlier than northern populations (Mennesson-Boisneau et al., 2000); and the southern spawn before the northern. For example, the Minho allis shad (*A. alosa*) population starts migration earlier in spring (in March, exceptionally in January) than northern European populations and later than Moroccan populations (Mota et al, 2015). Likewise, potamodromous populations of brown trout (*S. trutta*) generally go upstream to spawn much earlier in the year because of the higher latitude and altitude, due to low water temperatures and longer incubation periods (Gortázar et al., 2007).

Otherwise, in estuarine areas, fish diversity and density increase from spring with the appearance of fry mainly coming from the marine environment; they stay in the sea in winter, where temperature and salinity are more stable and warmer (Feunteun et al., 2011).

Seasonal migrations of Iberian fish are sometimes extensive but can be short: both can be manifested in irregular ways, as is typical in the Mediterranean climate. Coinciding with other areas of central and southern Europe, such as the United Kingdom (Armstrong et al., 2010) and France (Baudoin et al., 2014), Iberian freshwater native fish migration periods, both upstream and downstream, can occur the whole year round.

Migrations may be observed almost throughout the year if all the species are considered. Regarding obstacles, whatever the reason may be, free passage must be guaranteed as soon as migrators begin to arrive at an obstruction (Porcher & Travade, 2002). There are only very short periods, or no period, when fish passes should not be in operation. Attempts to pass obstructions without a fish pass (or with a badly designed one) can cause injuries or mortalities amongst migrating fish populations. The failure of just one fish pass on a migratory route is enough to totally ruin all other concerted efforts to maintain or develop stocks (Porcher & Travade, 2002).

CONCLUSIONS

We highlight that most of the Iberian freshwater native fishes migrate. Significant migrations have been mostly associated to the spawning periods. There is also information about feeding, for the groups that spawn in marine environments and come to the estuaries, rivers, or coastal lagoons to grow up, and associated with refuge.

Spawning periods are primary drivers of freshwater Iberian native fish migration. Their migrating periods are prolonged and change between years, adapting these periods to high year variability, which is characteristic of the Mediterranean climate. Sexual maturity is the most important cue which stimulate Iberian freshwater native fish migration. Water temperature, river flow, currents, hydrology and meteorology, salinity, and diurnal/nocturnal rhythm or photoperiod are also very important cues and triggers. Information is also available regarding tidal cycle, moon cycle and turbidity.

Although there is a latitudinal gradient in the Iberian Peninsula regarding the timing of migration, both potamodromous (cyprinids, among others) and diadromous (such as sturgeons and shads) migrate upstream in late winter, spring, and early summer. Other groups (sea lamprey, the European eel, and brown trout) migrate between autumn and spring, or all year round (the Atlantic salmon, sea trout and mullets).

These movements are quite extensive and vary between years. Migratory movements of the various native species of each site cover practically the whole or the whole year. Thus, to promote native fish species conservation, unrestricted movement is almost a permanent requirement: rivers, estuaries, lakes, and coastal lagoons should be always connected, without transversal obstacles, or their fish passes should practically always or always –all year round- be in operation.

ACKNOWLEDGMENTS

The authors thanks to Núria Sellarès, Quim Pou, Francesc Llach, Laia Jiménez and Èlia Bretxa, at some time, members of the Center for the Study of Mediterranean Rivers, for their commitment and full support for many years. To Antoni Munné, Carolina Solà, Mònica Bardina and Juanjo Villegas, among other members of the Catalan Water Agency, for their involvement in fish migration projects. To Nati Franch, Enric Gisbert, Josep Maria Queral, Karl Andree, and other colleagues of the Life MigratoEbre project. To our friends and families, for many, many reasons. Thanks also to Miguel Clavero and two anonymous reviewers, who greatly improved an early draft of this paper. This research was supported by the Government of Catalonia (CERCA Programme).

REFERENCES

Acolas, M. L., Rochard, E., Le Pichon, C. & Rouleau, E. (2012). Downstream migration patterns of one-year-old hatchery-reared European sturgeon (*Acipenser sturio*). *Journal of Experimental Marine Biology and Ecology*, 430–431. DOI: 10.1016/j.jembe.2012.06.026

Acolas, M. L. & Lambert, P. (2016). Life Histories of Anadromous Fishes. In: Morais, P., & Daverat, F. *An Introduction to Fish Migration*. (pp. 55-77). CRC Press, Boca Raton, Florida. United States of America. ISBN 9780367783068.

Almeida, P. R., Silva, H. T. & Quintella, B. R. (2000). The migratory behaviour of the sea lamprey *Petromyzon marinus* L., observed by acoustic telemetry in River Mondego (Portugal). In: Moore, A. & Russel, I. (eds.). *Advances in fish telemetry*. (pp 99–108). CEFAS: Lowestoft, Suffolk, England. United Kingdom.

Antunes, C. & Weber. M. (1996). The glass eel fishery and the by-catch in the Rio Minho after one decade (1981-1982 and 1991-1992). *Archives of Polish Fisheries*, 4, 131-139.

Aparicio, E., Pintor, C., Durán, C. & Carmona-Catot, G. (2012). Fish passage assessment at the most downstream barrier of the Ebro River (NE Iberian Peninsula). *Limnetica*, 31(1), 37-46. DOI: 10.1111/ 10.23818/limn.31.04

Aparicio, E., Carmona-Catot, G. & Alcaraz, C. (2013). *Les poblacions de peixos en els estuaris del Ter i el Daró*. (pp. 143-232). Col·lecció Recerca i Territori, 5. Museu de la Mediterrània & Parc Natural del Montgrí, les Illes Medes i el Baix Ter, Torroella de Montgrí. Catalonia. https://www.museudelamediterrania.cat/pujades/files/RIT5-ilovepdf-compressed.pdf

Armstrong, G. S., Aprahamian, M. W., Fewings, G. A., Gough, P. J., Reader, N. A. & Varallo, P. V. (2010). *Environment Agency Fish Pass Manual: Guidance Notes on the Legislation, Selection and Approval of Fish Passes in England and Wales*. Document – GEHO 0910 BTBP-E-E. Environment Agency, Bristol, England. United Kingdom.

Arribas, C., Fernández-Delgado, C., Oliva-Paterna, F. J. & Drake, P. (2012). Oceanic and local environmental conditions as forcing mechanisms of the glass eel recruitment to the southernmost European estuary. *Estuarine, Coastal and Shelf Science*, 107, 46-57. DOI: 10.1016/j.ecss.2012.04.024

Baudoin, J. M., Burgun, V., Chanseau, M., Larinier, M., Ovidio, M., Sremski, W., …. Voegtle, B. (2014). *Assessing the passage of obstacles by fish. Concepts, design and application*. Onema. France. ISBN: 979-10-91047-29-6.

Bruijs, M. C. M., Polman, H. J. G., Van M.Aerssen, G. H. F., Hadderingh, R. H., Winter, H. V. & Deerenberg, C. M. (2003). *Management of silver eel: human impact on downstream migrating eel in de river Meuse: impact assessment of hydroelectric power stations* *and commercial eel fisheries on the eel population in the river Meuse*. EU-Report Contract Q5RS-2000-31141 105. KEMA, RIVO (The Netherlands), IFÖ and FM (Germany). https://www.commissiemer.nl/docs/mer/p07/p0786/786-099silvereel.pdf

Caballero, J., Alvarez, J., Azpiroz, I., Baranda, A., Pedro, A., Eraso, E., ... Hervella, F. (2010). *Atlas de los Ríos Salmoneros de la Península Ibérica. Iberian Peninsula Salmon Rivers Atlas*. Publisher: Xunta de Galicia, Gobierno del Principado de Asturias, Gobierno de Cantabria, Diputación Foral de Bizcaia, Diputación Foral de Guipuzkoa and Gobierno de Navarra. Editor: Ekolur SL. Spain. ISBN: 978-84-613-9345-9.

Caballero, P. (2013). Biología y ecología del salmón atlántico (*Salmo salar*) y el reo o trucha de mar (*Salmo trutta*) en Galicia. *Mol*, 12. Galicia. Spain. ISBN: 978-84-613-9346-6

Cabral, M. J., Almeida, J., Almeida, P. R., Dellinger, T., De Almeida, N. F., Oliveira, M.E. .... Santos-Reis, M. (eds.). (2005). *Livro vermelho dos vertebrados de Portugal*. Instituto de Conservação da Natureza, Lisbon. Portugal. ISBN: 972-775-153-9.

Cambray, J. A. & Bruton, M. (1984). The reproductive strategy of a barb, *Barbus anoplus* (Pisces: Cyprinidae), colonizing a manmade lake in South Africa. *Journal of the Zoological Society of London*, 204, 143–168. DOI: 10.1111/j.1469-7998.1984.tb02367.x

Casals, F. (2005). *Les comunitats íctiques dels rius mediterranis: relacions amb les condicions ambientals*. (Ph.D. Thesis. University of Barcelona. Catalonia). Retrieved: https://tdx.cat/handle/10803/796#page=1

Classen, T. E. A. (1944). *Estudio bio-estadístico del esturión o sollo del Guadalquivir (Acipenser sturio* L.*)*. Ministerio de Marina. Instituto Español de Oceanografía. Trabajos, 19. Madrid. Spain.

Clavero, M. & Hermoso, V. (2015). Historical data to plan the recovery of the European eel. *Journal of Applied Ecology*, 52, 960–968. DOI: 10.1111/1365-2664.12446

Darwall, W., Carrizo, S., Numa, C., Barrios, V., Freyhof, J. & Smith, K. (2014). *Freshwater Key Biodiversity Areas in the Mediterranean Basin Hotspot: Informing species conservation and development planning in freshwater ecosystems*. IUCN. Cambridge, UK and Malaga, Spain.

Doadrio, I. (ed.). (2001). *Atlas y libro rojo de los peces continentales de España*. Consejo Superior de Investigaciones Científicas. Ministerio de Medio Ambiente. Madrid. Spain. ISBN 84-8014-313-5.

Doadrio, I., Perea, S., Garzón-Heydt, P. & González, J. L. (2011). *Ictiofauna continental española.* Bases para su seguimiento. DG Medio Natural y Política Forestal. MARM. Madrid. Spain. ISBN: 978-84-491-1158-7

Domingos, I. M. (1992). Fluctuation of glass eel migration in the Mondego Estuary (Portugal) in 1988 and 1989. *Irish Fisheries Investigation*, Series A 36, 1-4.

Elvira, B., Nicola, G. G. & Almodóvar, A. (1998). *Impacto de las obras hidráulicas en la ictiofauna. Dispositivos de paso para peces en las presas de España*. Colección técnica. Organismo Autónomo de Parques Naturales. Ministerio de Medio Ambiente. Madrid. Spain. ISBN: 84-8014-254-5.

Encina, L., Rodríguez, A. & Granado-Lorencio, C. (2006). The Iberian ichthyofauna: Ecological contributions. *Limnetica*, 25(1-2), 349-368. The ecology of the Iberian inland waters: Homage to Ramon Margalef. DOI: 10.23818/limn.25.24

Fernández, C., San Miguel, E., Amaro, R. & Hermida, M. (2015). Espinoso – *Gasterosteus aculeatus*. In: Salvador, A. & Elvira, B. (eds.). *Enciclopedia Virtual de los Vertebrados Españoles*. Sociedad de Amigos del MNCN - Museo Nacional de Ciencias Naturales - CSIC. Madrid. Spain. http://www.vertebradosibericos.org

Fernández-Pasquier, V. (2000). *Acipenser sturio* L. in the Guadalquivir river, Spain. Water regulation and fishery as factors in stock decline from 1932 to 1967. *Journal of Applied Ichthyology*, 15(4-5), 133-135. DOI: 10.1111/j.1439-0426.1999.tb00222.x

Feunteun, É., Ombredane, D. & Baglinière, J.-L. (2011). Variabilité des traits d'histoire de vie chez les poisons des hydrosystèmes continentaux. In: Keith, P., Persat, H., Feunteun, É. & Allardi, J. *Les poissons d'eau douce de*

France. (pp. 97-127). Collection Inventai¬res & biodiversité, Biotope Éditions, Mèze - Museum National d'Histoire Naturelle, Paris. France. ISBN: 978-2-914817-69-1

Filipe, A. F., Cowx, I. G. & Collarespereira, M. J. (2002). Spatial modelling of freshwater fish in semi-arid river systems: a tool for conservation. *River Research and Applications*, 18, 123-136. DOI: 10.1002/rra.638

Forseth, T., Naesje, T. F., Jonsson, B. & Harsaker, K. (1999). Juvenile migration in brown trout: a consequence of energetic state. *Journal of Animal Ecology*, 68, 783–793. DOI: 10.1046/j.1365-2656.1999.00329.x

García, A. & Braña, F. (1988). Reproductive biology of brown trout (*Salmo trutta* L) in the Aller river (Asturias; northern Spain). *Polskie Archiwum Hydrobiologii*, 35, 361–373.

García-Vega, A, Fuentes-Pérez, J. F., Leunda, P. M., Ardaiz, J. & Sanz-Ronda, F. J. (2022). Upstream migration of anadromous and potamodromous brown trout: patterns and triggers in a 25-year overview. *Hydrobiologia*, 849 (1), 197-213. DOI: 10.1007/s10750-021-04720-9

Gómez, J., Rodon, J. & Allué, R. (2012). Modelos cuantitativos de captura de angula (*Anguilla anguilla*) en diferentes cuencas catalanas. *Proceedings of the IV Jornadas Ibéricas de Ictiología* (pp. 30). Girona. Catalonia.

Gortázar, J., García De Jalón, D., Alonso-González, C., Vizcaíno, P., Baena, D. & Marchamalo, M. (2007). Spawning period of a southern brown trout population in a highly unpredictable stream. *Ecology of Freshwater Fish*, 16, 515–527. DOI: 10.1111/j.1600-0633.2007.00246.x

Granado-Lorencio, C. (1996). *Ecología de peces*. Secretariado de Publicaciones de la Universidad de Sevilla. Sevilla. Spain. ISBN 84-472-0242-9

Granado-Lorencio, C. 2000. *Ecología de comunidades. El paradigma de los peces de agua dulce*. Secretariado de Publicaciones de la Universidad de Sevilla. Sevilla. Spain. ISBN: 84-472-0600-9

Hardisty, M. W. (1986). General introduction to lampreys. In: HOLČÍK, J. (ed.). *The freshwater fishes of Europe*. Vol 1, Part I − Petromyzontiformes. (pp. 19−83). Aula-Verlag, Wiesbaden, Hessen. Germany.

Hasler, A. D. & Scholz, A. T. (1983). *Olfactory imprinting and homing in salmon*. Springer, Berlin. Germany. ISBN 978-3-642-82070-0.

Jacquin, L., Petitjean, Q., Cote, J., Laffaille, P. & Jean, S. (2020). Effects of Pollution on Fish Behavior, Personality, and Cognition: Some Research Perspectives. *Frontiers in Ecology and Evolution*, 8, 86. DOI: 10.3389/fevo.2020.00086

Jonsson, N. (1991). Influence of water flow, temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research*, 66, 20-35.

Kottelat, M. & Freyhof, J. (2007). *Handbook of European freshwater fishes*. Publications Kottelat, Cornol and Freyhof. Berlin. Germany. ISBN: 978-2-8399-0298-4.

Labar, G. W., Hernando-Casal, J. A. & Fernández-Delgado, C. (1987). Local movements and population size of European eels, *Anguilla anguilla*, in a small lake in southwestern Spain. *Environmental Biology of Fishes*, 19(2), 111-117.

Lara, M. J. (1994). Catch statistics, capture methods, size, and development stages of glass eels in Asturias (northern western Spain). *Bulletin of the Sea Fisheries Institute*, 1(131), 31-39.

Lennox, R. J., Paukert, C. P, Aarestrup, K., Auger-Methe, M., Baumgartner, L., Birnie-Gauvin. K., …. Cooke, S. J. (2019). One Hundred Pressing Questions on the Future of Global Fish Migration Science, Conservation, and Policy. *Frontiers in Ecology and Evolution*, 7, 286. DOI: 10.3389/fevo.2019.00286

Lobón-Cerviá, J. & Carrascal, M. (1992). Seasonal timing of silver eels (*Anguilla anguilla* L.) in a Cantabrian stream (North Spain). *Archiv für Hydrobiologie*, 125(1), 121-126.

López, V., Franch, N., Pou, Q., Clavero, M., Gaya, N. & Queral, J. M. (2015). *Atles dels peixos del Delta de l'Ebre*. Col·lecció tècnica, 3. Parc Natural del Delta de l'Ebre, Departament d'Agricultura, Ramaderia, Pesca, Alimentació i Medi Natural, Generalitat de Catalunya. Catalonia. ISBN: 9788439393733.

Lucas, M. C. & Baras, E. (2001). *Migration of Freshwater Fishes*. Blackwell Science. Oxford. United Kingdom. ISBN 0-632-05754-8.

Maceda-Veiga, A. (2012). Towards the conservation of freshwater fish: Iberian Rivers as an example of threats and management practices. *Reviews in Fish Biology and Fisheries*, 23, 1-22. DOI: 10.1007/s11160-012-9275-5

Martinho, F., Leitao, R., Neto, J. M., Cabral, H., Lagardère, F. & Pardal, M. Â. (2008). Estuarine colonization, population structure and nursery functioning for 0-group sea bass (*Dicentrarchus labrax*), flounder (*Platichthys flesus*) and sole (*Solea solea*) in a mesotidal temperate estuary. *Journal of Applied Ichthyology*, 24(3), 229-237. DOI: 10.1111/j.1439-0426.2007.01049.x

Mateus, C. S., Rodríguez-Muñoz, R., Quintella, B. R., Alves, M. J. & Almeida, P. R. (2012). Lampreys of the Iberian Peninsula: distribution, population status and conservation. *Endangered Species Research*, 16, 183–198. DOI: 10.3354/esr00405

McCleave, J. D. & Wipplehauser, G. S. (1987). Behavioral aspects of selective tidal transport in juvenile American eel. In: Dadswell, M. J., Klauda, R. J., Moffitt, C. M., Saunders, R. L., Rulifson, R. A. & Cooper, J. E. (eds.). *Common Strategies of Anadromous and Catadromous Fishes*. (pp. 138-150). American Fisheries Society, Symposium 1, Bethesda, Maryland. United States of America.

McDowall, R. M. (1997). The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. *Reviews in Fish Biology and Fisheries*, 7(4), 443-462.

McDowall, R. M. (2008). Diadromy, history and ecology: a question of scale. *Hydrobiologia*, 602, 5-14. DOI: 10.1007/s10750-008-9290-7.

Mennesson-Boisneau, C., Aprahamian, M. W., Sabatié, R. & Cassou-Leins, J. J. (2000). Remontée migratoire des adultes. In: Baglinière, J. L. & Elie, P. (Eds). *Les aloses (*Alosa alosa *et* Alosa fallax *spp.)*. Écobiologie et variabilité des populations. (pp. 55–72). CEMAGREF INRA Éditions, Paris. France. ISBN 2-7380-0906-9.

Miles, S. G. (1968). Rheotaxis of elvers of the American eel (*Anguilla rostrata*) in the laboratory to water from different streams in Nova Scotia. *Journal of Fisheries Research Board of Canada*, 25, 1591-1602.

Morais, P., & Daverat, F. (ed.). (2016). *An Introduction to Fish Migration*. CRC Press, Boca Raton, Florida, United States of America. ISBN 9780367783068.

Morais, P., Dias, E., Babaluk, J. & Antunes, C. (2011). The migration patterns of the European flounder *Platichthys flesus* (Linnaeus, 1758) (Pleuronectidae, Pisces) at the southern limit of its distribution range: Ecological implications and fishery management. *Journal of Sea Research*, 65, 235–246. DOI: 10.1016/j.seares.2010.11.001

Mota, M, Bio, A., Bao, M., Pascual, S., Rochard, E. & Antunes, C. (2015). New insights into biology and ecology of the Minho River Allis shad (*Alosa alosa* L.): contribution to the conservation of one of the last European shad populations. *Reviews in Fish Biology and Fisheries*, 25(1), 395-412. DOI: 10.1007/s11160-015-9383-0

Mota, M, Rochard, E. & Antunes, C. (2016). Status of the Diadromous Fish of the Iberian Peninsula: Past, Present and Trends. *Limnetica*, 35(1), 1-18. DOI: 10.23818/limn.35.01

Nachón, D. J., Mota, M., Antunes, C., Serviá, M. J. & Cobo, F. (2015). Marine and continental distribution and dynamic of the early spawning migration of twaite shad (*Alosa fallax* (Lacépède, 1803)) and allis shad (*Alosa alosa* (Linnaeus, 1758)) in the north-west of the Iberian Peninsula. *Marine and Freshwater Research*, 67(8), 1229-1240. DOI: 10.1071/MF14243

Nelson, T. C., Doukakis, P., Lindley, S. T., Schreier, A. D., Hightower, J. E., Hildebrand, L. R., …. Webb, M. A. H. (2013). Research Tools to Investigate Movements, Migrations, and Life History of Sturgeons (Acipenseridae), with an Emphasis on Marine-Oriented Populations. *PLoS One*, 8(8), e71552. DOI: 10.1371/journal.pone.0071552

Ohms, H. A., Sloat, M. R., Reeves, G. H., Jordan, C. E. & Dunham, J. B. (2014). Influence of sex, migration distance, and latitude on life history expression in steelhead and rainbow trout (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences*, 71, 70–80. DOI: 10.1139/cjfas-2013-0274

Oliva-Paterna, F. J., Ruiz-Navarro, A., Torralva,

M. M. & Fernández-Delgado, C. (2008). Biology of the endangered cyprinodontid *Aphanius iberus* in a saline wetland (SE Iberian Peninsula). *Italian Journal of Zoology*, 76(3), 316-329. DOI: 10.1080/11250000802488159

Oliveira, J. M. & Ferreira, M. T. (1997). Abundance, size composition and growth of a thinlipped grey mullet, *Liza ramada* (Pisces: Mugilidae) population in an Iberian River. *Folia Zoologica*, 46, 375–384.

Ordeix, M., Pou-Rovira, Q., Sellarès, N., Bardina, M., Casamitjana, A., Solà, C. & Munné A. (2011). Fish pass assessment in the Rivers of Catalonia (NE Iberian Peninsula). A case study of weirs associated with hydropower plants and gauging stations. *Limnetica*, 30(2), 405-426. DOI: 10.23818/limn.30.29

Ordeix, M. (2017). Fish migration and fish ramp assessment at a gauging station on a Mediterranean river (Catalonia, NE Iberian Peninsula). *Limnetica*, 36(2), 427-443. DOI: 10.23818/limn.36.13

Ordeix, M., González, G., Sanz-Ronda, F. J. & Santos, J. M. (2018). Restoring fish migration in the rivers of the Iberian Peninsula. In: Brink, K., Gough, P., Royte, J., Schollema, P. P. & Wanningen, H. *From Sea to Source 2.0. Protection and restoration of fish migration in rivers worldwide*. (pp. 174-177). World Fish Migration Foundation, Groningen. The Netherlands. ISBN 978-90-04-38964-9

Pedescoll, A., Aguado, Marcos, C., González, G. (2019). Performance of a Pool and Weir Fishway for Iberian Cyprinids Migration: A Case Study. *Fishes*, 4(3), 45. DOI: 10.3390/fishes4030045

Pombo, L. & Rebelo, J. E. (2002). Spatial and temporal organization of a coastal lagoon fish community - Ria de Averio, Portugal. *Cybium, the European Journal of Ichthyology*, 26(3), 185-196.

Pombo, L., Elliot, M., & Rebelo, J. E. (2005). Ecology, age and growth of *Atherina boyeri* and *Atherina presbyter* in the Ria de Aveiro, Portugal. *Cybium*, 29, 47-55.

Porcher, J. P. & Travade, F. (2002). Fishways. Biological basis, limits and legal considerations. *Bulletin Français de la Pêche et de la Pisciculture*, 364, 9-20.

Porres, A. & Farnós, À. (1999). Evolució al segle XX de les poblacions d'esturió (Acipenser sturio) al riu Ebre. In: Fernández, J. V. & Farnós, À. (eds.). *Els esturions (el cas del riu Ebre)*. (pp. 93-112). Direcció General de Pesca Marítima, Departament d'Agricultura, Ramaderia i Pesca, Generalitat de Catalunya, and Museu del Montsià. Catalonia. ISBN: 978-84-393-4840-5.

Prignon, C., Micha, J. C. & Gillet, A. (1998). Biological and environmental characteristics of fish passage at the Tailfer dam on the Meuse River Belgium. In: Jungwirth, M., Schmutz, S. & Weiss, S. (eds.). *Fish migration and Fish Bypasses*. (pp. 69–84). Fishing News Books, Blackwell Science Ltd. Cambridge. United Kingdom. ISBN: 0852382537.

Radinger, J. & García-Berthou, E. (2020). The role of connectivity in the interplay between climate change and the spread of alien fish in a large Mediterranean river. *Global Change Biology*, 26, 6383–6398. DOI: 10.1111/gcb.15320

Ribeiro, F., Cowx, I. G. & Collares-Pereira, M. J. (2000). Life history traits of the endangered Iberian cyprinid *Anaecypris hispanica* and their implications for conservation. *Archiv für Hydrobiologie*, 149, 569–586. DOI: 10.1127/archiv-hydrobiol/149/2000/569

Rodríguez-Climent, S., Caiola, N. & Ibáñez, C. (2013). Salinity as the main factor structuring small-bodied fish assemblages in hydrologically altered Mediterranean coastal lagoons. *Scientia Marina*, 77(1), 37-45. DOI: 10.3989/scimar

Salvador, A. (2009). Jarabugo – *Anacypris hispanica*. In: *Enciclopedia Virtual de los Vertebrados Españoles*. Carrascal, L. M. & Salvador, A. (eds.). Sociedad de Amigos del MNCN - Museo Nacional de Ciencias Naturales - CSIC. Madrid. Spain. http://www.vertebradosibericos.org

Santo, M. (2005). *Dispositivos de passagem para peixes em Portugal*. Direcçao-Geral dos Recursos Florestais. Editideias-Ediçao e Produçao, Lda., Lisboa. Portugal. ISBN: 972-8097-61-1.

Santos, J. M., Ferreira, M. T., Godinho, F. N. & Bochechas, J. (2002). Performance of fish lift recently built at the Touvedo dam on the

Lima river, Portugal. *Journal of Applied Ichthyology*, 18, 118–123. DOI: 10.1046/j.1439-0426.2002.00309.x

Santos, J. M., Ferreira, M. T., Godinho, F. N. & Bochechas, J. (2004). Efficacy of nature-like bypass channel in a Portuguese lowland River. *Journal of Applied Ichthyology*, 20, 1-8. DOI: 10.1111/j.1439-0426.2005.00616.x

Sanz, F. J., Bravo-Córdoba, F. J., García-Vega, A. & Martínez De Azagra, A. (2013). Pasos para peces: escalas y otros dispositivos de paso. *Notas técnicas del CIREF*, 7. Centro Ibérico de Restauración Fluvial.

Scott, W. B. & Crossman, E. J. (1973). Freshwater fishes of Canada. *Bulletin of the Fisheries Research Board of Canada*, 184, 1-966. DOI: 10.1002/iroh.19760610109

SIBIC 2017. *Carta Piscícola Española*. Electronic publication (version 02/2017). http://www.cartapiscicola.es

Silva, S., Alexandre, C. M. & Quintella, B. R. (2020). Seasonal environmental variability drives the swimming performance of a resident Iberian fish. *Ecology of Freshwater Fish*, 30(3), 366-374. DOI: 10.1111/eff.12587

Slavík, O., Horký, P., Randák, T., Balvín, P. & Bílý, M. (2012). Brown Trout Spawning Migration in Fragmented Central European Headwaters: Effect of Isolation by Artificial Obstacles and the Moon Phase. *Transactions of the American Fisheries Society*, 141(3), 673-680. DOI: 10.1080/00028487.2012.675897

Sostoa, A. de, Allué, R., Bas, C., Casals, F., Casaponsa, J., Castillo, M. & Doadrio, I. (1990). *Peixos. Història Natural dels Països Catalans*, 12. Enciclopèdia Catalana, SA, Barcelona. Catalonia. ISBN: 8477394563

Sostoa, A. de, Nadal, J., Casals, F., Aparicio, E., Vargas, M. J., Olmo, J. M., Puig, M. A. & Malo, J. (1995). *Caudales Ecológicos*. Proyecto PIE 121043 FECSA-UNESA. Barcelona. Catalonia.

Teeter, J. (1980). Pheromone communication in sea lampreys (Petromyzon marinus). *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 1635–1640. DOI: 10.1139/f80-254

Tosi, L., Sola, C., Spampanato, A. & Tongiorgi, P. (1989). The behavior of glass eel of *Anguilla anguilla* toward salinity: discrimination and preferences. *Rivista Italiana Acquacoltura*, 24, 219-223.

Tosi, L. & Sola, C. (1993). Role of geosmin, a typical inland water odour, in guiding glass eel *Anguilla anguilla* (L.) migration. *Ethology*, 95, 177-195. DOI: 10.1111/j.1439-0310.1993.tb00468.x

Travade, F. & Larinier, M. (2002). Monitoring techniques for fishways. *Bulletin Français de la Pêche et de la Pisciculture*, 346 suppl., 166–180.

Vinyoles, D. (1993). *Biologia i ecologia de* Blennius fluviatilis *(Pisces: Blennidae) al Riu Matarranya*. (PhD. Thesis, Barcelona University. Barcelona, Catalonia). Retrieved: https://www.tesisenred.net/handle/10803/833#page=1

Wooton, R. J. (1990). *Ecology of teleost fishes*. Ed. Chapman & Hall, London. United Kingdom. ISBN 978-94-009-0829-1.