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Energetic aspects of spawning migrations and their implications for the management of southern European diadromous fish populations

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ABSTRACT

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Migratory species display very important roles in aquatic ecosystem functioning. The journeys between different habitats throughout the lifetime increase survival and reproductive success; however, a large energetic investment is required. Most diadromous fish species cease feeding soon before they start the spawning migration; thus, the energy available for maintenance, gonadal development and migratory journeys is limited. Diadromous species spend up to 90 % of the total energy available, and in some cases, the entire population dies during migration. The energy consumption during this phase is critical and affects the spawning and post-spawning success.

Several diadromous species are endangered due to the increase in human activities that have negative effects on aquatic habitats. The southern distribution range of most of the European diadromous species is the Iberian Peninsula. Several threats to diadromous species are present in this region, and extra energy consumption is required during spawning migration which compromises their conservation. Consequently, management measures for such species should consider their energetic limitations.

This review presents the energetic implications of diadromous spawning migrations and discusses the anthropogenic factors that negatively affect the spawning journeys of native southern European species. The spawning energetics of the diadromous species should be considered by natural resource managers; however, the integration of this domain still requires additional studies to measure the effects of the anthropogenic activities on these species.

Key words: Energy balance, freshwater, life cycle, migration, nutrition.

RESUMEN

Aspectos energéticos de las migraciones reproductoras y sus implicaciones en la gestión de las poblaciones de especies diadromas del sudoeste europeo

Las especies migratorias poseen un papel muy importante en el funcionamiento de los ecosistemas. Los viajes entre los diferentes hábitats durante el ciclo de vida aumentan la supervivencia y el éxito reproductivo, sin embargo, es necesaria una gran inversión energética. La mayoría de las especies de peces migratorios dejan de alimentarse antes del inicio de la migración de desove, por consiguiente, la energía disponible para el mantenimiento, desarrollo gonadal y viajes migratorios que es acumulada en fases anteriores, es finita. Las especies diadromas gastan hasta un 90 % de la energía total disponible, y en algunos casos la totalidad de la población muere durante la migración. El consumo de energía durante esta fase es crítica y afecta el desove y el éxito post-desove.

Varias especies diadromas están en peligro debido al aumento de las actividades humanas que tienen un impacto negativo en los hábitats acuáticos. El límite sur de distribución de la mayoría de las especies diadromas europeas es la Península Ibérica. Varias amenazas están presentes sobre estas especies en este territorio, exigiendo un consumo extra de energía durante las

migraciones de desove y así comprometiendo su conservación. Por lo tanto, las medidas de gestión de dichas especies deben considerar la respectiva limitación de energía.

Este trabajo presenta las implicaciones energéticas de las migraciones reproductivas diadromas y discute algunos factores que afectan los viajes de desove de las especies nativas de Europa del sur. La energía de reproducción de las especies diádromas debe ser considerada por los gestores de recursos naturales, aunque para ello se requiere todavía más estudios para cuantificar efectivamente los impactos de las actividades humanas en estas especies.

Palabras clave: *Agua dulce, balance energético, ciclo de vida, migración, nutrición.*

INTRODUCTION

Fish migrations are triggered by external factors (e.g., feeding, escapement from predators, climate change) that affect fish physiology and metabolism (Lucas & Baras, 2001). Migratory fish species appear to have adjusted their life cycles and distribution according to environmental characteristics, which have changed over time. As a consequence, the migratory pattern might be different within the species, depending on their geographic position as well as on their population (Northcote, 1984; Schlosser, 1995; Lucas & Baras, 2001; McMahon & Matter, 2006).

Diadromy is a complex type of migration performed by fish that can involve journeys over many thousands of kilometres (Limburg & Waldman, 2009). Diadromous migrations provide better nutrition, higher growth rates and spawning success in most appropriate habitats (Gross, 1987; Gross *et al.*, 1988; McDowall, 1988). Two main migratory behaviours by fish were first described by Myers (1949). Anadromous species hatch in continental waters, migrate and grow at sea and then return to inland waters to spawn, while catadromous species hatch at sea, migrate and grow in rivers and then return downstream to spawn at sea (Myers, 1949; McDowall, 1988). In addition, Myers (1949) described amphidromous species as those that undertake limited migrations mainly for feeding.

Diadromous migrations are periods of great metabolic expenditure and nutritional stress (Tocher, 2003; McDowall, 2008; Limburg & Waldman, 2009). Diadromous species typically do not feed during migration (e.g., eels, salmonids) and all the required energy reserves are stored during previous life stages. Thus, spawning migrations are intrinsically related to the nutritional status of these species, as demonstrated in the sea lamprey (Beamish *et al.*, 1979; Araújo *et al.*, 2013). Using this method, they allocate nutrients to the spawning ecosystems, independent of whether they come from oceans or rivers (Ben-David *et al.*, 1998; Helfield & Naiman, 2001; Moore, 2006; Nislow & Kynard, 2009).

The Iberian Peninsula (IP, southwest Europe) is located between the Atlantic Ocean and the Mediterranean Sea, and functions as a biogeographical transition zone (Filipe, 2010). Thus, this region is a natural distribution limit of several diadromous species. In addition, during the last glaciation, the IP was a potential refugee, which led to evolutionary bottlenecks and a high genetic differentiation within autochthonous populations and endemicity of freshwater species occurring in this region (Clavero & García-Berthou, 2006; Filipe, 2010). Consequently, several native fish species from the IP streams, such as sea lampreys or salmon, have shown unique genetic backgrounds in this section of their European distribution range (Rodriguez-Muñoz *et al.*, 2004; Verspoor *et al.*, 2007; Almada *et al.*, 2008).

Abiotic environmental variables are factors that strongly affect the diadromous fish species distribution ranges (Béguer *et al.*, 2007), and these are predicted to be particularly vulnerable to future climate changes (Lassalle *et al.*, 2009a). Thus, diadromous species of the IP are expected to suffer from potential contractions of their

distribution ranges and several species might disappear from this region (Lassalle *et al.*, 2008, 2009a; Lassalle & Rochard, 2009).

In the present work, we aimed to: (i) discuss the implications of spawning migrations on the energy balances of the diadromous species; and (ii) debate the main factors that threaten spawning journeys of this species, which may potentially compromise their fragile energetic equilibrium. A particular focus was made on European populations inhabiting the southern distribution range.

ENERGY CONSUMPTION AND SPAWNING MIGRATIONS

The energy available to fuel metabolic activities is dependent on the adequate balance between nutrient intake (crude lipid, protein and carbohydrates) and catabolism (Smith, 1989; Choat & Clements, 1998). The ability to use dietary energy for basic physiological functions, such as spawning migrations, is essential for fish (Hinch *et al.*, 2005; Tseng & Hwang, 2008). The performance of migratory journeys itself varies greatly among species and is dependent on swimming speed, journey distance, morphology and locomotion (Lindsey, 1978; Bernatchez & Dodson, 1987; Lauder, 2005). These parameters affect the cost of the migration per unit of distance. In addition, there are physiological differences within the same fish species and energy requirements and reserves between individuals of the same populations (Jonsson *et al.*, 1991). According to Durif *et al.* (2009), individuals of a larger size have an advantage because of greater energy stores and a higher swimming capacity and fecundity.

Energetic efficiency of fish

In general, migratory behaviour involves extra energy consumption and physiological adaptation (Crisp, 2000; Yaron & Sivan, 2005; Ramenofsky & Wingfield, 2007). However, the energy requirement in fish is significantly lower compared to mammals and birds (Smith, 1989).

First, the body temperature can be similar to the temperature of the environment, and thus, they are referred to as poikilothermic or ectothermic. In contrast, endothermic animals increase their energy demands when the temperature decreases below the "thermoneutral" due to increased oxygen inhalation (Joyce & Blaxter, 1965). Second, the movements of fish in water can consume small amounts of energy. The aquatic environment provides a greater ease of travelling compared to land or air. The density of water is approximately 800 times greater than air and the buoyancy and density of fish bodies is controlled innately (Lindsey, 1978). In addition, fish have managed to develop methods of appropriate propulsion and position in response to different environmental conditions (Lauder, 2005). In addition, fish excrete nitrogenous metabolites in the form of ammonia, whereas mammals convert these nitrogenous metabolites into urea and uric acid. These molecules are less toxic and more easily stored compared to ammonia, however, they are more complex compounds and the processes of synthesis of urea and uric acid require more energy (Martin & Blaxter, 1965; Smith, 1989). Only a minority of fish species is viviparous (Wourms *et al.*, 1988). In mammals, the synthesis of milk proteins is costly, and the efficiency of fat formation is relatively low (e.g., the content of fat in the milk of aquatic mammals reaches over 50 %) (Kielanowski, 1965; Hashizume *et al.*, 1965; Shahidi & Zhong). Finally, fish metabolise fatty acids more readily and efficiently, and thus, fish can exist for longer periods of time under conditions of food deprivation (Tseng & Hwang, 2008).

However, fish are less energy efficient in other functions. Depending on the temperature and salinity, water contains 20 to 40 times less oxygen compared to air per unit volume, and oxygen diffuses 10,000 times slower in water than in air (Graham, 1990). Under these circumstances, fish require 10 % of their oxygen intake for the production of the energy used in making water pass through the gills, while humans only require between 1-2 % of the oxygen of each inhalation to produce the energy for each breath.

Iteroparity and semelparity

The diadromous fish species can be classified on the basis of their iter- or semelparity. Most fish are iteroparous, which means that they spawn more than once during their lifetime (Narum *et al.*, 2008) and consume small amounts of energy in each migration and spawning event (Glebe & Leggett, 1981; Jonsson *et al.*, 1997; Yaron & Sivan, 2005). Iteroparous species allocate less energy reserves for gonadal development compared to post-spawning migration to ensure migration success. In some cases, such as trout *Salmo trutta*, most of the individuals of the same population are iteroparous, and provide little investment for spawning (Berg *et al.*, 1998). Conversely, the semelparous species only complete one spawning cycle in their lifetime (McDowall, 2008).

According to Glebe & Leggett (1981), the anadromous fish species are semelparous if more than 60% of the total energy is consumed during migration. As a consequence, these species will not have sufficient energy to return to the ocean. Thus, the iteroparous fish species have at least 40 % of total energy available to return to the ocean. Typically, anadromous salmonids use 50 to 70 % of their somatic energy reserves on migration (Brett, 1995) and it is assumed that factors such as the egg size and gonadosomatic index are related to semelparity (Yaron & Sivan, 2005) because these factors can affect the organismic energy balance. However, all individuals of some diadromous species, such as *A. anguilla* or *P. marinus*, perish after spawning, which is independent of the remain energy (Beamish *et al.*, 1979; Hardisty, 1986; van Ginneken & van den Thillart, 2000; Tesch, 2003; van Ginneken *et al.*, 2005).

Long temporal gaps can also occur between the start of the migration and spawning. Spawning adults of Atlantic salmon, *Salmo salar*, enter freshwater ecosystems year-round. The spawning season of *S. salar* occurs between November and January, and despite the short length of the available habitat in Iberian rivers (over 70 km in the case of Minho River), individuals might have to wait several months before spawning can occur (authors' observations). Thus, in some cases, *S. salar* are already at the spawning grounds long before they spawn. Longer waiting periods imply less energy available for returning to the ma-

Table 1. Native diadromous fish species of the Iberian Peninsula. FAO Code = species code from the Food and Agriculture Organisation; Types: Amp = amphydromous species; An = anadromous species; Cat = catadromous species; Conservation status: IUCN = conservation status according to IUCN (2012); Portugal = conservation status in Portugal according to Cabral *et al*. (2005); Spain = conservation status in Spain according to Doadrio (2001); CR = Critically Endangered; DD = Data Deficient; EN = Endangered; LC = Least Concern; LR = Lower Risk; VU = Vulnerable; – = No data available/not included in the Red Book; RE = Regionally Extinct. *Especies nativas de peces diadromos de la Península Ibérica. FAO Code = código de especies de la Organización de las Naciones Unidas para la Alimentación y la Agricultura; Types: Amp = especies amphidromas; An = especies anadromas; Cat = especies catadromas; Conservation status: IUCN = estado de conservación de acuerdo con IUCN (2012); Portugal = estado de conservación en Portugal de acuerdo con Cabral et al. (2005); Spain = estado de conservación en España de acuerdo con Doadrio (2001). CR = En Peligro Crítico; DD = Datos Insuficientes; EN = En Peligro; LC = Preocupación Menor; LR = Bajo Riesgo; VU = Vulnerable; – = No Hay Datos/No Incluido en el Libro Rojo; RE = Extinto Regionalmente.*

Scientific name	Common name	FAO Code	Type	Conservation status		
				IUCN	Portugal	Spain
Acipenser sturio	European sturgeon	APU	An	CR	RE	CR
Alosa alosa	Allis shad	ASD	An	LC	EN	VU
Alosa fallax	Twaite shad	SHA	An	LC	VU	VU
Anguilla anguilla	European eel	ELE	Cat	CR	EN	VU
Lampetra fluviatilis	European River lamprey	LAR	An	LC	CR	RE
Liza ramada	Thin-lipped grey mullet	MGC	Amph / Cat	LC	LC	—
Petromyzon marinus	Sea lamprey	LAU	An	LC	VU	VU
Platichthys flesus	European Flounder	FLE	Amph / Cat	LC	DD	—
Salmo salar	Atlantic salmon	SAL	An	LR/LC	CR	EN
Salmo trutta	Sea Trout	TRS	An	LC	CR	VU

rine ecosystems. Thus, the iter- and semelparity can result from a number of factors, such as the journey length and duration, habitat features, and waiting period energy cost, among many others.

Modelling energy balance

According to the first law of thermodynamics, all of the energy must be conserved across the systems. Thus, the study of energy balance in living beings concerns the transformation of energy within the individual, the population or the ecosystems. However, not all of the energy ingested is used by the fish due to losses that occur from intake to metabolism (Lovell, 1998). Thus, the digestible energy includes the fraction ingested and the fraction that is partly lost in faeces. The metabolised fraction represents the digestible energy corrected for the metabolic losses through the gills and urine. Finally, the net energy is equal to the metabolised energy excluding the energy lost by heat dissipation. Heat loss occurs by the energy cost of digestion, metabolism and excretion, and maintenance, i.e., the loss of energy due to basal metabolism (functioning of vital organs, response to disease) and the completion of basic functions (e.g., escape from predators, foraging). According to Odum & Barrett (2005), the universal model can be applied to any living component. The energy cost of spawning requires consideration of all the energetic balance. After the energy intake through nutrients by ingestion, part of the energy is used in respiration or excreted after metabolism or assimilation. Although one part of the energy is directed for growth and spawning, another part is stored for use when needed. However, there are situations where one part of the energy is excreted without being completely or partially metabolised. Thus, in the beginning of the migration, the net energy (or the total migration energy) can be represented by the sum of the maintenance energy intended for use in their vital functions, the energy for gonadal development, the energy for travelling to the spawning grounds, and the energy required for the spawning associated rituals, such as nest building (Moore *et al.*, 2004; van den Thillart *et al.*, 2009; Sousa *et al.*, 2012).

The dynamic energy budget (DEB) and bioenergetics models simulate energy acquisition and use, and can serve as a link between different levels of biological organisation using differential equations (Kooijman, 2010; Nisbet *et al.*, 2000, 2012; Hansen *et al.*, 2003). These models have been applied in the research and management of fish stocks, populations, food webs and ecosystems, and include the estimation of fish growth, intensity and dynamics of predator-prey interactions, nutrient cycling within aquatic food webs of varying trophic structure, and food requirements of single animals, whole populations, and communities of fish (Kitchell *et al.*, 1977; Hansen *et al.*, 2003). DEB relates metabolic organisation within organisms to physiological performance that affects higher levels of biological organisation, particularly in population dynamics and ecosystem processes. While the DEB models are more abstract, bioenergetic models consider individual scale differences or sex-specific conditions (Nisbet *et al.,* 2000). However, the knowledge on bioenergetics for migratory species is underrepresented in the literature (Stevens, 2006) despite its potential ecological importance (Souza *et al.*, 2013). Indeed, all semelparous species are critical in such models during spawning periods in freshwater streams, taking into account its full contribution to the ecosystem nutrient balance.

Energy sources

Energy balance is particularly critical for migratory species that stop feeding during spawning migration, which is dependent on the capacity of the liver to mobilise lipid reserves (Tseng & Hwang, 2008). Anadromous organisms commonly store resources at the ocean, while catadromous organisms store resources at estuarine and freshwater ecosystems (Tesch, 2003; Crossin *et al.*, 2004; Nislow & Kynard, 2009). Fasting behaviour is common during spawning migration and can result in the unsuccessful reproduction of individuals due to the lack of energy, because they can die before reaching the spawning grounds (Hardisty, 1986; Kadri *et al.*, 1995, 1997; Jonsson *et al.*1997; Baglinière

et al., 2003; Tesch, 2003). Thus, the energy required for metabolic functions and for the migratory journey of these species must be stored prior to the start of migration. Energy is predominantly stored as proteins and lipids in vertebrates (Kielanowski, 1965; Smith, 1989; Lovell, 1998). In fish, the lipids are stored in the form of visceral and somatic reserves (Beamish *et al*., 1979; Bird & Potter, 1983; Mesa & Magie, 2006; Boran & Karaçam, 2011). However, the concentration of energy in the *soma* is greater than in the *viscera* of *Salmo salar* and *Salmo trutta* (Jonsson *et al*., 1997; Berg *et al*., 1998) while in sea lampreys, visceral energy appears to be highly important (Araújo *et al*., 2013). The fatty acids are a specific group of lipids that are used as membrane components and also play an essential role as the major source of metabolic energy for spawning (particularly the $n-3$ polyunsaturated fatty acids; Beamish *et al*., 1979; Sargent *et al*., 1989; Tocher, 2003; Tseng & Hwang, 2008; Araújo *et al*., 2013). For successful spawning, the stored nutrients must support both the immediate energy needs as well as future requirements of the progeny; thus, some oils are selectively catalysed (lipogenesis) producing the required energy for gonadogenesis (Tocher, 2003). In the case of *P. marinus* and *S. salar*, there was an evident decrease in lipid levels during spawning migration, and at the end of the journey, there was also a high energy investment in nest building (Beamish *et al*., 1979; Jonsson *et al*., 1997; Sousa *et al*., 2012). Moreover, the fat stores of *A. anguilla* and *Salmo trutta* also include an important energy contribution for gonadal development during or after migration (Jonsson & Jonsson, 1997; van den Thillart *et al*., 2009).

Carbohydrates as an energy source are used primarily for digestion and metabolism; however, the contribution of carbohydrates in the energy budget is negligible in fish and is often ignored in the analysis of body composition (Beamish *et al*., 1979; Jonsson *et al*., 1997; Hendry & Berg, 1999; Ozório, 2008).

SPAWNING ENERGETICS OF IBERIAN SPECIES

There is a total of fourteen autochthonous diadromous fish species in Western Europe, where ten of which inhabit the freshwaters of the IP (Béguer *et al*., 2007; Lassalle *et al*., 2009b) (Table 1). In this region, both anadromous and catadromous species are present (Myers, 1949; McDowall, 1988). The season of the year as well as the environmental and physiological conditions affect their spawning migration, which in turn affects their nutritional condition (Lovern, 1958; Kao *et al.,* 2002; Bruijs & Durif, 2009; Boran & Karaçam, 2011). Studies on the energetic cost of spawning migrations are rare and have been performed in various regions of the world, which hinders their comparison (Table 2). In addition, there is a current lack of nutritional information regarding the energy and nutritional content during the migratory journeys of *A. sturio*, *Liza ramada* and *P. flesus*.

Shads

The Allis shad *Alosa alosa*, is particularly vulnerable to the disappearance in the IP following habitat fragmentation (Alexandrino, 1996, Bagliniére *et al*., 2003). *A. alosa* is an anadromous species and spawning normally occurs in higher sections of rivers with well-oxygenated waters. *A. alosa* distribution in the IP includes the main riverine systems, namely the Minho, Lima, Guadiana and northern basins (Bagliniére *et al*., 2003, Mota & Antunes, 2011). The anadromous Twaite shad *Alosa fallax* is present in every Atlantic and Mediterranean basins of the IP (Alexandrino, 1996). These spawning habitats consist of medium and higher stretches of rivers. However, hybridisation with *Alosa alosa* due to river fragmentation was reported in some major rivers (Alexandrino, 1996).

The maximum weight of juvenile *A. alosa* captured in the estuary of the Minho river is approximately 20 g, and the minimum weight at

Table 2. Existing information regarding the spawning energetics of the Iberian Peninsula diadromous species. Type: I, iteroparous; S, semelparous; ♀– female loss; ♂ – male loss; * Laboratory trials on marine migration; NA – not available or unknown information; bl – body length. *Información existente en relación con la energía de desove de las especies diadromas de la Península Ibérica. SW. Tipo: I, Iteróparo, S Semélparos; ♀– femenina; ♂– masculina; * Ensayos sobre la migración marina en laboratorio; NA – Información no disponible o desconocida; bl – longitud del cuerpo.*

Species	Type	Mean adult weight (g)	Mean length (cm)	Swimming speed (bl s⁻¹)	Energetic losses	Consumption (kJ km⁻¹ kg⁻¹)	System	Migration length (km)	References
Acipenser sturio					NA				
Alosa alosa					NA				
Alosa fallax					NA				
Anguilla anguilla	S	1,500	90	0.40–0.50	40 % (120 g of initial fat reserve)	0.42–0.62	*	5000–6000	Svedäng & Wickström, 1997; van Ginneken & van den Thillart, 2000; van Ginneken et al., 2005; Palstra et al., 2008; Durif et al., 2009; van den Thillart et al., 2009
Lampetra fluviatilis	S	55	30	0.33	(5 g of initial fat reserves)	51.1	Severn (UK)	100	Claridge & Potter, 1975; Moore & Potter, 1976
Liza ramada									
Petromyzon marinus	S	868	72	0.09	68 % ♂	15.5	St John (USA)	140	Beamish, 1979; Beamish et al., 1979
		885	73	0.10	62 % ♀	28.9			
	S	1,275	86	0.22	> 24 % (28 g of initial somatic lipids)	25.5	Minho (IP)	65	Araújo et al., 2013; MJA unpublished data
Platichthys flesus					NA				
Salmo salar	I	1,000–15,000	52–115	NA	60–70 %	1–2	Drammen (NO)	1000	Jonsson et al.,1991, 1997
Salmo trutta	I	NA	NA	NA	+20 % ♂ < 40 % ♀	2.73	Humla (NO)	NA	Berg et al., 1998

the river mouth in the beginning of the upstream spawning migration is 590 g (Mota & Antunes, 2011, 2012). This indicates that the increase in *A. alosa* weight during the marine phase is at least twenty-fold. However, the energetic cost of migration is unknown thus far for both shad species.

European eel

The European eel *Anguilla anguilla* is present all over the European coast. Although the main ecological features of the diadromous species are well defined, there are still uncertainties regarding spawning conditions (Tesch, 2003; van den Thillart *et al*., 2009; Avise, 2011). It is assumed with some reservations that mature silver eels spawn in the deep of the Sargasso. Small larvae (*leptocephalii*) were found near the region, whereas larger larvae were identified along the European coasts (Schmidt, 1923; Antunes & Tesch, 1997). However, only two studies have reported silver eel catches in the Sargasso Sea (Ernst, 1977 and Bast & Klinkhardt, 1988). At the riverine ecosystems, yellow European eel grow until they reach sexual maturation and store sufficient nutrients for the Sargasso Sea spawning journey.

Because the migratory species are difficult to follow in their natural ecosystem, several laboratory studies have been conducted (Svedang & Wickstrom, 1997; van Ginneken & van den Thillart, 2000; van Ginneken *et al*., 2005; Palstra *et al*., 2008) using *A. anguilla* to estimate the energy and lipid consumption during spawning oceanic migration. Some of these studies applied bioenergetics and biochemical tools under simulated migration conditions (van den Thillart *et al*., 2009; Ozório, 2008). Fish migration energetics have shown that eels are highly efficient at converting energy stores into mechanical work. In fact, they are four times more efficient than salmonids and tunas (van Ginneken *et al*., 2005; Sepulveda & Dickson, 2000). Such efficiency makes it possible for eels to perform a non-stop migration under fasting conditions with the available body energy depots (van den Thillart & Dufour, 2009). The anguilliform morphology appears to contribute to their high swimming efficiency (Palstra *et al*., 2008).

Lampreys

Two species of anadromous lampreys occur in the IP, the River Lamprey *Lampetra fluviatilis* and the Sea Lamprey *Petromyzon marinus* (Mateus *et al*., 2012). The *Lampetra* genus also includes the potamodromous European brook lamprey *L. planeri* and three other cryptic species native to Portuguese streams (see in Mateus *et al*., 2013). Different feeding habits occur within the anadromous lamprey species. While the greatest of all lampreys *P. marinus* feeds parasitically during the adult marine phase, *L. fluviatilis* spend a non-trophic period until spawning migration starts. Commercial fishermen target the sea lamprey in the IP.

One hematophagous post-metamorphic sea lamprey of 20 g was marked in the River Ulla and recaptured one year later during spawning migration at the estuary of the same river (Silva *et al*., 2013). After the marine stage, that sea lamprey returned at more than 1200 g, which represents an increase of more than sixty times its original weight. Sea lampreys apparently consume between approximately 15 and 30 kJ km^{-1} during upstream freshwater migration and the total consumed energy (and lipid stored) appears to be dependent on the migration length. While smaller *L. fluviatilis* require lower lipid reserves as an energy source for swimming, they also appear to be less energy efficient during the spawning run (Heikkala *et al*., 1984).

Flounder

The Flounder *Platichthys flesus* (order Pleuronectiformes) is present all over the coastal and estuarine habitats in the IP, and this species migration has long been assumed as catadromous (Summers, 1979). Technological developments can now investigate the migratory patterns of this species. According to Summers (1979), *P. flesus* spawning occurs in coastal areas, where the tides transport larvae inland which then return as adults to the coastal areas for spawning. However, the analysis of otolith microchemistry has shown that this species can develop different migration patterns, i.e., not strictly catadromous,

namely hatching and migrating inland followed by downstream spawning migration to coastal areas (Morais *et al.*, 2011; Daverat *et al.,* 2012). Thus, *P. flesus* physiological adaptations might not occur as spawning preparation for coastal, estuarine and freshwater habitats. Indeed, the inland journeys of some individuals of this species from the sea, or vice versa, may not occur exclusively for breeding and may occur regularly at some point in their life cycle.

Mullet

The Thin-lipped Grey Mullet *Liza ramada* is also considered catadromous, and the occurrence of this species in estuaries is frequent, where it uses selective tidal transport during juvenile stages (Almeida, 1996; Trancart *et al.*, 2012). In this case, this species does not always migrate inland and grows in tidal areas. In addition, short catadromous migrations appear be not strictly related to spawning but instead follow ecological factors, such as a reduction in predatory pressure (Trancart *et al.*, 2012).

Salmoniforms

Several *Salmoniforms* occur in the IP, however, the Atlantic Salmon *Salmo salar* and Sea Trout *Salmo trutta* are the only autochthonous species that perform anadromous migrations (Cabral *et al.*, 2005; Doadrio, 2001). Salmonids are amongst the faster and more effective swimming species, however, they have low metabolic efficiency compared to anguiliforms (van Ginneken *et al.*, 2005; Ozório, 2008). Moreover, larger *Salmo salar* have higher energy losses in adipose tissues, which indicate a lower post-spawning survival rate (Jonsson *et al.*, 1991; Jonsson *et al.*, 1997).

Sturgeon

The abundance of European Sturgeon *Acipenser sturio* is very low in the wild due to overfishing, pollution and hydro-construction (Gessner, 2000; Kirschbaum & Gessner, 2000). The economic importance of *A. sturio* arises from their use in caviar production (OSPAR, 2009) and

historical records of catches indicate that this long-life and slow-growing species can weigh more than 200 kg during spawning runs (Almaça & Elvira, 2000). The species originally reproduced in Iberian largest rivers (namely Guadiana, Guadalquivir and Ebro); however the only remaining European population originates from the Gironde-Garonne-Dordogne system in France (Nicola *et al.*, 1996; Lassalle *et al.*, 2011) and scientific research on wild individuals is very limited.

ENERGY-RELATED THREATS TO SUCCESSFUL SPAWNING OF THE DIADROMOUS SPECIES IN IBERIAN ECOSYSTEMS

Over the past decades, many diadromous species have suffered from significant decreases due to several factors that affect all stages of their life cycle (growth, development and spawning) (Ringuet *et al.*, 2002; Baglinière *et al.*, 2003; Limburg & Waldman, 2009). Human activities, such as damming, dredging and channelisation have been identified as the main reasons for the depletion of migratory species populations following the negative effects that may cause short-term stresses, increases in immune system activity and consequently endogenous energy consumption, which may affect breeding success (Nicola *et al.*, 1996; Larinier, 2001; Gehrke *et al.*, 2002; Kotusz *et al.*, 2006; Wilcove & Wikelski, 2008) (Fig. 1). The interruption of the migratory cycles of these species can result in severe consequences for the services provided by the ecosystems (MEA, 2005; Humphries & Winemiller, 2009).

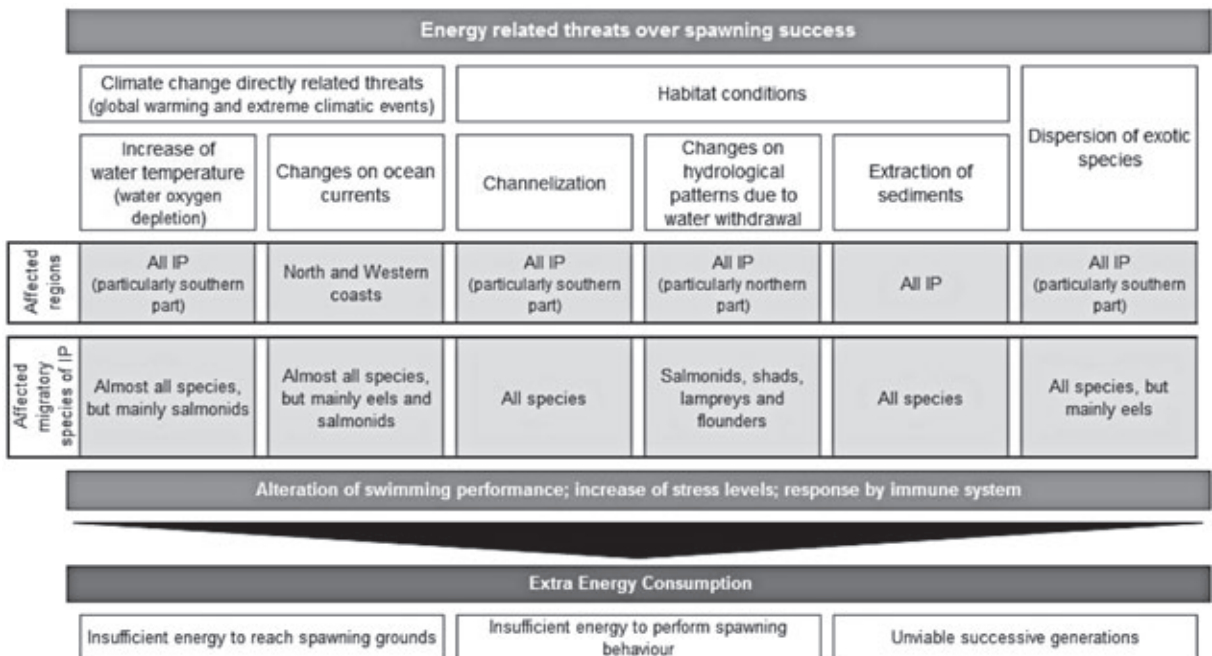### Climate change and global warming

Poikilothermic species, such as fish, are particularly vulnerable to climate change (Hinch *et al.,* 1996; 2005). Fish require a minimum temperature to activate the physiological mechanisms associated with spawning. In the case of *P. marinus*, spawning only occurs when temperatures rise above 15 °C (Hardisty, 1986; Sou-

sa *et al*., 2012). However, water temperature above the optimal threshold may also inhibit migration (Prignon *et al*., 1998; Kotusz *et al*., 2006; Jonsson & Jonsson, 2009). Furthermore, sea lamprey spawning grounds are located in shallow waters (Hardisty *et al*., 1986; Sousa *et al*., 2012). Therefore reduction of river-run-off and the alteration of hydrological patterns due to climate change may make it impossible to access adequate spawning grounds for several anadromous species.

Water temperature and other specific environmental factors, such as the oxygen level and photoperiod, are also used by *A. anguilla* (Bruijs & Durif, 2009) to "trigger" spawning migrations. The heating of water indicates a decrease in the solubility of oxygen, which results in an accelerated metabolism via an increases in respiration rates and energy consumption (Diaz & Breitburg, 2009). Moreover, changes in ocean currents can increase the energy required by species that perform extensive migratory journeys to reach their spawning grounds, such as *A. anguilla*, which migrates to the Sargasso Sea (Palstra *et al*., 2008).

Habitat conditions

The spawning grounds of anadromous species are selected following specific abiotic conditions, such as water current, oxygen levels, shadow and granulometry. Furthermore, spawning success is also dependent on habitat conditions, namely the length of the river available, as well as the mean slope and obstacles along the water course (Glebe & Leggett, 1981; Mesa & Magie, 2006; Bjornn *et al*., 1999; Leonard & McCormick, 1999), among other factors. High flow rates affect the swimming speed and increase energy losses and stress. In addition, the presence of obstacles may prevent fish from reaching the spawning grounds (Lundqvist *et al*., 2008), because extra efforts will pose migration delays and increase energy consumption (Bjornn *et al*., 1999; Mesa & Magie, 2006). Several intrinsic factors such as fish species, size, body energy depot, swimming speed and gonadal development may influence the success in passing these obstacles. The failure to minimise energy waste during spawning migration might also involve the overlap of

Figure 1. Energy related threats over spawning success based on an extensive literature review. This figure summarises what is known from the literature and as such, should not be considered exhaustive. *Amenazas relacionadas con la energía para el éxito reproductivo. Esta figura resume lo que se conoce de la literatura y, como tal, no debe considerarse como exhaustiva.*

physiological capacities (Bernatchez & Dodson, 1987). These factors affect the spawning success of diadromous populations and their abundance in the intermediate and long-term periods.

There are many examples throughout the native ranges of the Iberian diadromous species, where habitat fragmentation, combined with pollution and overfishing, result in the local extinction of migratory species (Béguer *et al.*, 2007). Many Iberian rivers are affected by the presence of structures that interrupt their natural course, and most of these obstacles are not equipped with the means to allow fish and other aquatic beings to move freely and safely downstream and upstream (Nicola *et al.*, 1996; Baglinière *et al.*, 2003; Limburg & Waldman, 2009). The Minho river is one of the less affected rivers of the IP with regards to anthropogenic influence, and in the best case scenario, only 39.3 % of the streams within the catchment are available for salmonids (CPTIRM, 2011). In addition, commercial fishing of diadromous species in Iberian estuaries is an important activity for riverine livelihoods (Dill, 1993; Souto, 2001). The fishing effort over shads by professional fishermen was affected in the mid 1990's in the IP following the construction of major dams for hydroelectric power generation (such as those in Minho and Tagus) (Alexandrino, 1996; Mota & Antunes, 2011). The spawning success of fishing escapees was also theoretically affected by their wounding level.

The scarcity of water is higher in the South IP (Sabater *et al.*, 2009) and channelisation is fairly frequent in this part of the Peninsula, which affect the spawning of migratory species (Maceda-Veiga, 2013). Since the 20th century, several diadromous fish species have declined considerably in the IP (such as eels and shads in Douro/Duero, Guadiana, Tagus or Minho/Miño catchments) and have even disappeared from the heavily-modified rivers of the region (Alexandrino, 1996; Nicola *et al.*, 1996; Mota & Antunes, 2011). Some of these alterations affect the natural flows and access to spawning grounds by the diadromous species, which will require an increase of stress and higher energy consumption.

Most diadromous fish species that are present in the IP perform *homing* behaviour, which means that the organisms return to the natal streams during spawning migrations (Hansen *et al.*, 1993; Alexandrino, 1996; Klemetsen *et al.*, 2003). In addition, seabed topography also appears to contribute to the geographical isolation of some species that usually do not perform *homing* migrations, such as the sea lamprey (Bergstedt & Seelye, 1995; Rodrigues-Muñoz *et al.*, 2004; Pinela *et al.*, 2009; Almeida P. R., personal communication). Thus, threats over natal inland ecosystems, such as habitat fragmentation, extraction of riverbed materials and pollution, which increase the energetic cost of migration, might compromise the conservation of such species.

Exotic threats

Several exotic species occur in the IP, and negative interactions with diadromous species might occur in several ways (e.g., predation on eggs; Leunda *et al.*, 2008). In addition, exotic species might affect the spawning success of diadromous species. One of the parasites found in Iberian streams is the nematode *Anguilicoloides crassus*. *A. anguilla* is deeply affected by this organism and infection rates have been increasing in recent years (Neto *et al.*, 2010; authors' unpublished data). This pathogenic nematode parasite lives in the swim bladder of *A. anguilla* during the freshwater stage and infection impairs the organ. This might affect not only buoyancy control but also the capacity to arrive in good condition at the Sargasso Sea because it "drains" eel energy via sanguivorous feeding (Székely *et al.*, 2009; van den Thillart *et al.*, 2009). The optimum swimming speed of infected eels is significantly lower compared with that of healthy eels (Székely *et al.*, 2009).

CONCLUSIONS AND PERSPECTIVES

Anthropogenic activities negatively affect diadromous populations via the perturbation of their fragile energy balance, particularly in the IP region, where this species are already stressed

by characteristic extreme conditions in this southern edge. However, currently this review underlines the scarce information available regarding energy balance both at the species level and at the ecosystem level. Thus, further studies should be undertaken to associate the threats, abundance of migratory species, and energy requirements at various ecological integration levels. One method may be to build ecosystem models considering the migratory species' contribution in the near future, because it would allow an evaluation of the energy fluxes between functional groups within aquatic food webs.

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