The haematophagous feeding stage of anadromous populations of sea lamprey *Petromyzon marinus*: low host selectivity and wide range of habitats

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Abstract Limited information is available regarding habitat use and host species of the haematophagous feeding stage of the anadromous sea lamprey *Petromyzon marinus* Linnaeus, 1758, due to the difficulties in capturing feeding lampreys and wounded hosts. The aim of this study is to provide new records of *P. marinus* feeding on host species and to review the available information in this regard to better know the ecology and distribution of sea lamprey during this stage. Thus, new records of *P. marinus* individuals or wounds on 23 species of fishes and cetaceans are provided. Nineteen of these species were described for the first time as hosts of *P. marinus*. As a result, an updated list of 54 host species is provided. They belong to diverse taxonomic groups and exhibit different morphological, physiological and ecological patterns. The attacks were located from fresh and brackish waters to open sea. The results suggest that the marine distribution of *P. marinus* is mainly related to coastal areas with part of the population widely dispersed in offshore areas. This remarkable capacity of inhabiting a broad range of aquatic ecosystems and exploiting different host species could have favoured the dispersal ability and evolutionary success of sea lamprey.

Keywords: Parasite-host interaction; distribution; trophic ecology; North Atlantic Ocean; fisheries; sea.

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Introduction

The sea lamprey *Petromyzon marinus* Linnaeus, 1758 is typically an anadromous species that spends the larval stages in streams and the adult-feeding stages in open sea waters. The larvae burrow in fine sediment and feed by filtration (Quintella et al., 2003). After metamorphosis, the juveniles migrate to the sea and begin feeding on blood and fluids of several species of Chondrichthyes, Osteichthyes and cetaceans (Beamish, 1980; Halliday, 1991; Kelly & King, 2001). In some cases, as in the Upper Laurentian Great Lakes of North America, postmetamorphic individuals can also complete the haematophagous feeding stage without migrating to the sea (Bergstedt & Swink, 1995); yet, even within rivers inside their natural range, evidence is increasing that haematophagous feeding can begin in freshwater (Silva et al., 2013b; c). After one to two years of haematophagous feeding (Halliday, 1991; Silva et al., 2013a) sea lamprey adults return to fresh water to spawn and die.

The freshwater phase of the *P. marinus* life cycle is well known, but as for the other anadromous lamprey species, very little information has been gathered during the oceanic phase (Renaud et al., 2009; Lança et al., 2013). Thus, due to inherent difficulties for capturing adult sea lampreys in the sea, available information is restricted to occasional captures of some species with wounds caused by *P. marinus* or, in some cases, with the lamprey attached (Halliday, 1991; Hardisty, 2006; Lança et al., 2013).

So far, most detailed studies on the haematophagous phase of *P. marinus* have been made for the landlocked populations of the Great Lakes of North America (Clemens et al., 2010). This is because the non-native landlocked form is considered a pest due to the high economic impact in terms of damage to fish stocks and the resultant expenditure of large sums of money on its control (Hardisty, 2006). Nonetheless, studies on the haematophagous stage of native anadromous *P. marinus* populations, threatened and economically important in some regions, have been increasing during recent years (Clemens et al., 2010). Therefore, the aim of this paper is to provide new findings on *P. marinus* host species obtained from several sources and in different aquatic habitats, as well as to review the available information on this regard in order to better know the ecology and distribution of sea lamprey during this stage.

Materials and methods

New records of *P. marinus* feeding on host species were obtained from inland and coastal commercial fisheries; inland and marine sport fishing; offshore surveys (scientific expeditions and mark-recapture campaigns); stranded individuals and personal communications from other researchers. The presence of wounds caused by *P. marinus* in those species was determined following King & Edsall (1979) and Ebener et al. (2006) and wounds were sorted into pierced (indicative of active feeding) and non-pierced wounds (cannot confirm active feeding) (Silva et al., 2013c).

Species captured with wounds caused by *P. marinus* were obtained from commercial fisheries (trammels and seines) operating off the NW Iberian Peninsula in 2012 and 2013 as well as one record from sport marine fishing in 2008 (Fig. 1). In adidition, information on species with sea lamprey wounds collected by monitoring surveys of

UTPB/Sp (Technical Unity of Coastal Fishing) during 2005 and 2006 was also included.

Data on sea lamprey hosts were also generated from a scientific expedition on the research vessel Vizconde de Eza in international waters of the Grand Banks of Newfoundland, in NAFO (Northwest Atlantic Fisheries Organization) regulatory areas 3N, 3O, 3L and 3M (43-48ºN; 46-52ºW; Fig. 1) from June to August 2013 (González-Costas et al., 2013). Important fisheries for the European fishing fleet are located in this region (García-Orellán, 2010). Information from a mark-recapture campaign of pelagic sharks captured by surface longline in the North West Atlantic (42°N; 45°W; Fig. 1) in 2009 and 2010 was also used. This study area is located in a very productive zone due to the confluence of the warm Gulf Stream and the cold Labrador Current (Hurrell et al., 2003).

Information on sea lamprey attachment and feeding was also obtained from four species of stranded cetaceans in the NW Iberian Peninsula. This information was collected from 2005 to 2013 by the CEMMA association (Coordinadora para o Estudio dos Mamíferos Mariños) and CEPESMA (Coordinadora para el Estudio y Protección de las Especies Marinas).

A species captured with postmetamorphic *P. marinus* still attached or wounds caused by them was obtained from commercial fishing in the River Miño estuary (NW Iberian Peninsula; Fig. 1). Several anadromous and euryhaline species are captured in this river mainly by trammel nets (BOPDEPO, 2013). Dr. John B. Hume provided information on newly metamorphosed *P. marinus* feeding on freshwater fish species in Lake Derg

(River Shannon, Ireland). The host individuals were collected by sport fishing between 2006 and 2012. Dr. Richard Sabatié provided information on host species of *P. marinus* observed in the French Brittany region (rivers, estuaries and coastal zone).

Results

In total, 27 new records of attachments of *P. marinus* on 23 different species are provided (Table 1), comprising two species of Chondrichthyes, 17 of Osteichthyes and four cetaceans belonging to 13 orders and 21 different families. These belong to two orders and two families of Chondrichthyes, 10 orders and 15 families of Osteichthyes, and four families of cetaceans belonging to the order Cetartiodactyla. Regarding the species ecology, 16 of them are marine, four are freshwater species and three are diadromous (Tables 1-2). Of these, 48% (11 of 23) are demersal and 52% are pelagic (Tables 1-2). All individuals showed pierced wounds (indicative of active feeding) with exception of *Reinhardtius hippoglossoides* (Walbaum, 1792).

Records are provided from fresh, brackish and marine waters (Table 1, Fig. 1). All host species from the coastal marine areas were captured up to 40 km from the coast. In that area, the species *Myliobatis aquila* (Linnaeus, 1758), *Belone belone* (Linnaeus, 1761) and *Merluccius merluccius* (Linnaeus, 1758) (the individual captured in 2007) were captured with a sea lamprey (total length of 20, 22 and 23 cm respectively) still attached to them. Moreover, a postmetamorphic sea lamprey (total length of 32.5 cm and weight of 65.8 g) was captured feeding on *Alosa alosa* (Linnaeus, 1758) (the individual captured in 2014) in the river Miño estuary. Coastal fishermen from the NW Iberian Peninsula confirmed that captures of *P. marinus* (both adults and newly transformed) as by-catch occur sporadically in this region with the main capture period situated between January and April.

Host species of *P. marinus* obtained in offshore surveys, *Sebastes mentella* Travin, 1951, *Anarhinchas lupus* Linnaeus, 1758 and *R. hippoglossoides* (Table 1) were caught by bottom trawl 430, 490 and 400 km from the nearest coast (Newfoundland) and at 200, 300 and 900 m deep respectively. Blue shark *Prionace glauca* (Linnaeus, 1758) was caught in two consecutive years with a sea lamprey still attached (Online Resource 1) 815 km from the nearest coast (Newfoundland).

On fusiform bony fishes, *P. marinus* wounds consistently occurred below the lateral line and usually close to the pectoral fins (Fig. 2). By contrast, *P. marinus* sucker marks on flatfish, sharks and cetaceans were spread along the lateral or dorsal regions (Fig. 3; Online Resource 1). Non-pierced scars were observed on different parts of the body of *P. glauca*, *Balaenoptera acutorostrata* Lacépède, 1804 and *Mesoplodon bidens* (Sowerby, 1804), which appeared to have been caused by drag and displacement of *P. marinus* (Fig. 3).

Following combination of our new records with a detailed review of the existing literature-based records, an updated list of host species described for anadromous *P. marinus* in its native range is presented (Table 2). A total of 54 confirmed host species: 6 chondrichthyans, 38 osteichthyans, and 10 cetaceans belonging to 12 orders and 28 different families are now listed. Moreover, in five species, non-pierced wounds were observed, so active feeding was not confirmed (Table 2). As shown in Table 3, fifty six percent of confirmed host species are at least near threatened, and 9% were not evaluated or current data are deficient. They also exhibit diverse distribution ranges and migratory patterns (Table 3). Most host species (91%) are carnivorous or planktivorous. Fifty two percent of host species were pelagic, and the 48% were demersal (Table 3).

Discussion

This study confirms the haematophagous feeding of anadromous *P. marinus* on 23 host species, 19 of which had not been described before as part of the diet of *P. marinus* (Table 1). These species are included in one superorder, five orders, and twelve families which were not referred as hosts of anadromous sea lampreys so far: *M. aquila* is the first species of superorder Batoidea; *Esox lucius* Linnaeus, 1758 is the first species of order Esociformes; *Solea solea* (Linnaeus, 1758) and *R. hippoglossoides* are the first species of the order Pleuronectiformes; *S. mentella* is the first species of order Scorpaeniformes; *B. belone* of order Beloniformes; *M. merluccius* of family Merluccidae; *Trichiurus lepturus* Linnaeus, 1758 of family Trichiuridae; *Trachurus trachurus* (Linnaeus, 1758) of family Carangidae; *A. lupus* of the family Anarhichadidae; *Boops boops* (Linnaeus, 1758) of family Sparidae; and finally *Physeter macrocephalus* Linnaeus, 1758 is the first record in the family Physeteridae. In the case of *P. glauca*, the presence of *P. marinus* attached to this species was described earlier by Benz & Bullard (2004); nonetheless, the active feeding on this species only now is confirmed.

The records of several demersal host species (Table 3) are in accordance with findings provided by Lança et al. (2013) from muscle fatty acid analysis of adult *P. marinus*, which point to the important role of these species in the diet of anadromous sea lamprey populations, at least during their marine stage. Besides, several demersal species have also been described by Orlov et al. (2009) as an important part of Pacific lamprey *Entosphenus tridentatus* (Richardson, 1836) diet. Pacific lamprey and sea lamprey are rather similar in their ecology, in that they both range widely during their parasitic phase (Kelly & King, 2001; Orlov et al., 2008; Clemens et al., 2010).

The ecological, morphological, physiological and taxonomical differences among host species of *P. marinus* are in accordance with a low degree of host selection as previously suggested by Silva et al. (2013c) for anadromous populations and by Hardisty & Potter (1971) and Bence et al. (2003) for landlocked populations. Indeed, the main selection factor seems to be the host size with larger individuals or species being the preferred hosts (Bence et al., 2003). Therefore, larger hosts provide to *P. marinus* a more nutritional feeding during more time (Farmer, 1980; Hardisty, 2006). Some small hosts were described for newly transformed *P. marinus* in freshwater (Araújo et al., 2013a; Silva et al., 2013b, c). However, as the haematophagous phase progresses, lampreys increase their size and consumption rate (Farmer, 1980). As a consequence, it has been suggested that they tend to progressively move away from the river of origin to the sea looking for larger hosts (Holčík, 1986; Halliday, 1991).

Kelly & King (2001) based on earlier works of Beamish (1980) and Farmer (1980) reported a total of 12 host species of *P. marinus*. But Lança et al. (2013) listed a total of 30 host species of *P. marinus* at sea, and this paper has increased that list to a total of 54 confirmed and five nonconfirmed host species from different taxonomic groups in fresh water, marine and brackish habitats within the natural range of *P. marinus*. The low selectivity of sea lamprey suggests that they could also feed on these non-confirmed host species.

Most listed host species are present along *P. marinus'* distribution range (Froese & Pauly, 2011; Renaud, 2011) and for sea lamprey as well; most of them are or were targeted by fishing activity (Froese & Pauly, 2011; IUCN, 2013). As a result of overfishing and other factors, populations of targeted fishes have been declining over decades (Pauly et al., 1998; Jackson et al., 2001). Although the role of targeted species in the diet of *P. marinus* may be overestimated because fisheries are often the source of information, this decline may directly affect populations of anadromous sea lamprey as host abundance can be the principal factor in predicting adult lamprey returns to the rivers (Murauskas et al., 2013).

This paper also records haematophagous feeding of *P. marinus* in freshwater in Ireland and in French Britanny (Table 1). Such evidence, together with recent observations in Iberian Peninsula streams (Araújo et al., 2013a; Silva et al., 2013b; c) and previously in North America (Beamish, 1980; Powell et al., 1999), suggest that freshwater feeding by early postmetamorphic sea lamprey is a widespread behaviour in anadromous populations of *P. marinus* in their native range. Feeding on exotic species was confirmed with the observation of *P. marinus* feeding on *E. lucius* in the Lake Derg. Both the freshwater feeding and the ability of feeding on exotic species have also been described for other anadromous species as European river lamprey *Lampetra fluviatilis* (Linnaeus, 1758) (Inger et al., 2010; Hume et al., 2013).

The downstream migration of *P. marinus* usually occurs between autumn and spring (Beamish, 1980; Kelly & King, 2001; Silva et al., 2013b) and partially overlaps with upstream migration of spawners, which takes place between winter and spring (Quintella et al., 2004; Hardisty, 2006; Cobo et al., 2010; Araújo et al., 2013b). Thus, both in East and West Atlantic (Beamish, 1980; Halliday, 1991; Dempson & Porter, 1993; Powell et al., 1999; Igoe et al., 2004; this paper) catches or observations of parasitic-phase sea lampreys in rivers, estuaries and coastal areas occur more often from autumn to spring and for the newly transformed individuals of small size or individuals of adult size. By contrast, records in more remote areas occur mainly in summer and for lampreys of medium size. This is in accordance with the suggested short duration of the haematophagous stage of *P. marinus* of close to one year, as recently described by Silva et al. (2013a).

Several *P. marinus* have been caught up to 350-450 km away from the nearest coast (Lelek, 1973; Dempson & Porter, 1993; Kelly & King, 2001) and at up to 985-1000 m deep (Hardisty & Potter, 1971; Beamish, 1980). Also, the occurrence of sea lampreys feeding in Icelandic waters has been reported (Pereira et al., 2012; Ólafsdóttir & Shinn, 2013), the rivers in which the existence of reproduction or larval populations of *P. marinus* has not been described so far (Pereira et al., 2012). Haedrich (1977) reported a bottom trawl-caught specimen at 4099 m deep, 400 km off southern New England, but acknowledged the possibility that capture occurred in midwater upon net retrieval. Our results (captures at up to 815 km from the nearest coast) confirm that at least part of the sea lamprey population can be widely dispersed at sea. In addition, some listed host species are oceanodromous, and they present wide habitat ranges reaching deep waters and areas located far from the coast as is the case with *P. glauca*, *Scomber scombrus*

Linnaeus, 1758, *Urophycis chuss* (Walbaum, 1792), *M. merluccius*, *T. trachurus*, *S. mentella*, *Grampus griseus* (Cuvier, 1812) and *P. macrocephalus* that can reach 1000 m depth (Froese & Pauly, 2011; IUCN, 2013). In the case of *C. maximus*, *Somniosus microcephalus* (Bloch & Schneider, 1801) and *R. hippoglossoides,* their habitats at depths greater than 2000 m are reported (Froese & Pauly, 2011).

Nonetheless, several factors suggest that *P. marinus* distribution range at sea is partially restricted. Silva et al. (2013a) showed that *P. marinus* can reach the adult size in approximately 1 year of haematophagous feeding. Moreover, part of the postmetamorphic population can spend several months, feeding in rivers and estuaries, before migrating to sea (Silva et al., 2013b, c). Genetic differences suggest that little exchange of individuals exists between European and North American sea lamprey populations (Rodríguez-Muñoz et al., 2004; Genner et al., 2012); although some individuals may cross the Atlantic Ocean attached to their hosts, it will, therefore, not be a common pattern. *Petromyzon marinus* as well as *E. tridentatus* do not home to natal streams (Waldman et al., 2008; Spice et al., 2012). They are widely dispersed at sea, and then they look for suitable spawning streams based on different factors as the presence of larval pheromones (Meckley et al., 2014). However, the genetic differences recorded by Spice et al. (2012) for *E. tridentatus* between locations, which are inconsistent with philopatry, show also the absence of panmixia, which those authors consider as being due to a limited dispersal at sea.

Besides, most catches and observations of *P. marinus* have occurred in coastal and shallow regions, corresponding to the continental slope and shelf area (Beamish, 1980; Halliday, 1991; Dempson & Porter, 1993; Hardisty, 2006) as also described for *E.*

tridentatus (Orlov et al., 2008, 2009). Thus, Orlov et al. (2008) provide catches of *E. tridentatus* widely dispersed at sea and at depths up to 1485 m but with over 80% of individuals captured at depths less than 500 m when using bottom trawls and less than 200 m in pelagic surveys. Therefore, as also suggested by Lança et al. (2013) marine distribution of *P. marinus* seems to occur mainly in the continental shelf and slope regions until the mesopelagic level, with a small part of the population reaching more remote areas. Distribution of anadromous lampreys at sea seems to be linked to the abundance of hosts and their mobility (Johnson & Anderson, 1980; Orlov et al., 2008; Lança et al., 2013; Murauskas et al., 2013). Individuals attached to large hosts with wide dispersion patterns could get constant and highly nutritive food but that strategy could also increase the risk of not returning to fresh waters to reproduce (Lança et al., 2013).

Finally, related to the selection of feeding sites on the host body by *P. marinus*, our data in accordance with previous findings have shown a preference for feeding under the lateral line and in the vicinity of the pectoral fin for most host species (Farmer & Beamish, 1973; Beamish, 1980; Cochran, 1986), and preference for the dorsal and lateral regions for flatfishes, cetaceans and some shark species (Nichols & Hamilton, 2004; Wilkie et al., 2004; Nichols & Tscherter, 2011; Samarra et al., 2012; Ólafsdóttir & Shinn, 2013). It seems to be related to a thinner muscular layer, less dense scaling and the presence of relatively large blood vessels (Farmer & Beamish, 1973; Farmer, 1980; Cochran & Lyons, 2010; Nichols & Tscherter, 2011). Besides, in larger host species as cetaceans, it seems to be related also to areas exposed to low water flows (Nichols & Tscherter, 2011). These preferences appear to combine low costs in terms of handling time before feeding with greater rates of energy intake once feeding has been initiated (Farmer, 1980; Cochran, 1986).

The great number of non-pierced wounds in cetaceans and chondrichthyans might be caused by the search of sea lamprey for more suitable feeding areas (Nichols & Tscherter, 2011). Related to the ability of *P. marinus* to feed on sharks (urea-rich species), Wilkie et al. (2004) confirmed the ability of sea lamprey to penetrate the dermal denticle armour of sharks, to rapidly excrete large volumes of urea and a high capacity to deaminate amino acids. These authors concluded that these abilities may represent adaptations that have contributed to the evolutionary success of lampreys.

In conclusion, this study demonstrates that in its natural range, the haematophagous feeding stage of *P. marinus* exhibits a low selectivity of host species, as shown for landlocked populations and a wide range of habitats (from rivers and estuaries to coastal and offshore areas) that they can use during this stage. This plasticity in the haematophagous stage related to habitat and host species could have favoured the dispersal ability and evolutionary success of sea lamprey.

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Tables

Table 1 New records of host species of anadromous *Petromyzon marinus* during the haematophagous feeding phase. In bold host species described for the first time as part of the diet of *P. marinus*. For *S. trutta* (R): resident form. NWAO: North West Atlantic Ocean; NWIP: North West Iberian Peninsula; FB: French Brittany; MR: mark-recapture campaign; CF: commercial fishing; SF: sport fishing; UPT: upstream permanent trap; SCE: scientific expedition; STR: stranded individual

Species	Location of capture	Method	Habitat	Date
Chondrichthyes				
***Prionace glauca* (Linnaeus, 1758)**	NWAO (42ºN; 45ºW)	MR	Ocean	27/04/2009
***Prionace glauca* (Linnaeus, 1758)**	NWAO (42ºN; 45ºW)	MR	Ocean	05/07/2010
***Myliobatis aquila* (Linnaeus, 1758)**	Ría de Vigo, NWIP	CF	Ocean	June 2013
Osteichthyes				
***Belone belone* (Linnaeus, 1761)**	Cies Islands, NWIP	SF	Coast	09/02/2008
***Alosa alosa* (Linnaeus, 1758)**	River Miño estuary, NWIP	CF	Estuary	10/05/2011
***Alosa alosa* (Linnaeus, 1758)**	River Miño estuary, NWIP	CF	Estuary	25/03/2014
***Alosa alosa* (Linnaeus, 1758)**[c]	Pont-Scorff, FB	UPT	Freshwater	01/05/2010
***Abramis brama* (Linnaeus, 1758)**[b]	Lough Derg, Ireland	SF	Freshwater	2006-2012
***Rutilus rutilus* (Linnaeus, 1758)**[b]	Lough Derg, Ireland	SF	Freshwater	2006-2012
***Esox lucius* Linnaeus, 1758**[b]	Lough Derg, Ireland	SF	Freshwater	2006-2012
***Merluccius merluccius* (Linnaeus, 1758)**	Portonovo, NWIP	SCE	Coast	14/03/2007
***Merluccius merluccius* (Linnaeus, 1758)**	Portonovo, NWIP	SCE	Coast	25/05/2005
***Liza ramada* (Risso, 1810)**[c]	Saint-Nazaire Port, FB	CF	Estuary	April 2009
***Anarhichas lupus* Linnaeus, 1758**	NWAO (47ºN; 47ºW)	SCE	Ocean	01/07/2013
***Trachurus trachurus* Linnaeus, 1758**	Ría de Vigo, NWIP	CF	Coast	01/05/2012
Scomber scombrus Linnaeus, 1758[c]	Bay of Vilaine, FB	CF	Coast	April 2009
***Boops boops* (Linnaeus, 1758)**	Ría de Pontevedra, NWIP	CF	Coast	04/10/2013
***Trichiurus lepturus* Linnaeus, 1758**	Ancora, NWIP	CF	Coast	April 2012
***Reinhardtius hippoglossoides* (Walbaum, 1792)**[a]	NWAO (43ºN; 52ºW)	SCE	Ocean	01/07/2013
***Solea solea* (Linnaeus, 1758)**[c]	Bay of Vilaine, FB	CF	Coast	April 2009
Salmo salar Linnaeus, 1758[c]	Pont-Scorff, FB	UPT	Freshwater	May 2010
Salmo trutta Linnaeus, 1758 (R)[b]	Lough Derg, Ireland	SF	Freshwater	2006-2012

***Sebastes mentella* Travin, 1951**	NWAO (48ºN; 46ºW)	SCE	Ocean	01/07/2013
Cetaceans				
Balaenoptera acutorostrata Lacépède, 1804	Camariñas, NWIP	STR	Coast	14/03/2005
***Grampus griseus* (Cuvier, 1812)**	Baiona Estuary, NWIP	STR	Coast	17/10/1998
***Physeter macrocephalus* Linnaeus, 1758**	Ribadesella, NWIP	STR	Coast	01/05/2013
***Mesoplodon bidens* (Sowerby, 1804)**	Ribeira, NWIP	STR	Coast	26/11/2012

[a] Only non-pierced wounds were recorded (confirmation of active feeding was not accomplished)
[b] Hume pers comm
[c] Sabatié pers comm

Table 2 List of host species described for the haematophagous stage of anadromous *Petromyzon marinus.* D: demersal; P-O: pelagic-oceanic; P-N: pelagic-neritic; B: bathypelagic; Po: potamodromous; Di: diadromous; O: oceanodromous; NM: non migratory

Order	Family	Species	Ecology	Reference
Chondrichthyes				
Carcharhiniformes	Carcharhinidae	*Carcharhinus obscurus* (Lesueur, 1818)	D, O	Jensen & Schwartz (1994)
Carcharhiniformes	Carcharhinidae	*Carcharhinus plumbeus* (Nardo, 1827)	D, O	Jensen & Schwartz (1994)
Carcharhiniformes	Carcharhinidae	*Galeocerdo cuvier* (Péron and Lesueur, 1822)	D, O	Jensen et al. (1998)
Carcharhiniformes	Carcharhinidae	*Prionace glauca* (Linnaeus, 1758)	P-O, O	This paper
Lamniformes	Cetorhinidae	*Cetorhinus maximus* (Gunnerus, 1765)	P-O, O	Beamish (1980); Wilkie et al. (2004)
Myliobatiformes	Myliobatidae	*Myliobatis aquila* (Linnaeus, 1758)	D, O	This paper
Squaliformes	Somniosidae	*Somniosus microcephalus* (Bloch and Schneider, 1801)[a]	D, O	Gallant et al. (2006)
Osteichthyes				
Acipenseriformes	Acipenseridae	*Acipenser oxyrinchus* Mitchill, 1815	D, Di	Renaud (2011)
Acipenseriformes	Acipenseridae	*Acipenser sturio* Linnaeus, 1758	D, Di	Hardisty (1986)
Beloniformes	Belonidae	*Belone belone* (Linnaeus, 1761)	P-O, O	This paper
Clupeiformes	Clupeidae	*Alosa aestivalis* (Mitchill, 1814)	P-N, Di	Beamish (1980)
Clupeiformes	Clupeidae	*Alosa alosa* (Linnaeus, 1758)	P-N, Di	This paper
Clupeiformes	Clupeidae	*Alosa fallax* (Lacépède, 1803)	P-N, Di	Silva et al. (2013b)
Clupeiformes	Clupeidae	*Alosa pseudoharengus* (Wilson, 1811)	P-N, Di	Beamish (1980)
Clupeiformes	Clupeidae	*Alosa sapidissima* (Wilson, 1811)	P-N, Di	Beamish (1980)
Clupeiformes	Clupeidae	*Brevoortia tyrannus* (Latrobe, 1802)	P-N, O	Mansuetti (1962)
Clupeiformes	Clupeidae	*Clupea harengus* Linnaeus, 1758	D, O	Farmer (1980)
Cypriniformes	Catostomidae	*Catostomus commersonii* (Lacepède, 1803)	D, Di	Potter & Beamish (1977)
Cypriniformes	Cyprinidae	*Abramis brama* (Linnaeus, 1758)	D, Po	Hume pers comm
Cypriniformes	Cyprinidae	*Luciobarbus bocagei* (Steindachner, 1864)[a]	D, Po	Araújo et al. (2013a)
Cypriniformes	Cyprinidae	*Pseudochondrostoma duriense* (Coelho, 1985)	D, Po	Silva et al. (2013c)
Cypriniformes	Cyprinidae	*Rutilus rutilus* (Linnaeus, 1758)	D, Po	Hume pers comm
Esociformes	Esocidae	*Esox lucius* Linnaeus, 1758	D, Po	Hume pers comm
Gadiformes	Gadidae	*Gadus morhua* Linnaeus, 1758	D, O	Beamish (1980)
Gadiformes	Gadidae	*Melanogrammus aeglefinus* (Linnaeus, 1758)	D, O	Beamish (1980)
Gadiformes	Gadidae	*Pollachius virens* (Linnaeus, 1758)	D, O	Beamish (1980)
Gadiformes	Phycidae	*Urophycis chuss* (Walbaum, 1792)	D, O	Farmer (1980)

Gadiformes	Merlucciidae	*Merluccius merluccius* (Linnaeus, 1758)	D, O	This paper
Mugiliformes	Mugilidae	*Liza aurata* (Risso, 1810)	P-N, Di	Silva et al. (2013b)
Mugiliformes	Mugilidae	*Liza ramada* (Risso, 1810)	P-N, Di	Sabatié pers comm
Perciformes	Anarhichadidae	*Anarhichas lupus* Linnaeus, 1758	D, O	This paper
Perciformes	Carangidae	*Trachurus trachurus* (Linnaeus, 1758)	P-N, O	This paper
Perciformes	Moronidae	*Dicentrarchus labrax* (Linnaeus, 1758)	D, Di	Taverny & Elie (2010)
Perciformes	Moronidae	*Morone saxatilis* (Walbaum, 1792)	D, Di	Beamish (1980)
Perciformes	Pomatomidae	*Pomatomus saltatrix* (Linnaeus, 1766)	P-O, O	Beamish (1980)
Perciformes	Sciaenidae	*Cynoscion regalis* (Bloch and Schneider, 1801)	D, O	Beamish (1980)
Perciformes	Scombridae	*Scomber scombrus* Linnaeus, 1758	P-N, O	Farmer (1980); Sabatié pers comm
Perciformes	Scombridae	*Thunnus thynnus* (Linnaeus, 1758)	P-O, O	Halliday (1991)
Perciformes	Sparidae	*Boops boops* (Linnaeus, 1758)	D, O	This paper
Perciformes	Trichiuridae	*Trichiurus lepturus* Linnaeus, 1758	D, Di	This paper
Perciformes	Xiphiidae	*Xiphias gladius* Linnaeus, 1758	P-O, O	Beamish (1980)
Pleuronectiformes	Pleuronectidae	*Reinhardtius hippoglossoides* (Walbaum, 1792)[a]	D, O	This paper
Pleuronectiformes	Soleidae	*Solea solea* (Linnaeus, 1758)	D, O	Sabatié pers comm
Salmoniformes	Salmonidae	*Salmo salar* Linnaeus, 1758	D, Di	Beamish (1980); Silva et al. (2013b)
Salmoniformes	Salmonidae	*Salmo trutta* Linnaeus, 1758[b]	P-N, Di	Silva et al. (2013b, in press); Hume pers comm
Salmoniformes	Salmonidae	*Salvelinus fontinalis* (Mitchill, 1814)	D, Di	Beamish (1980)
Scorpaeniformes	Sebastidae	*Sebastes mentella* Travin, 1951	B, O	This paper
Cetaceans				
Cetartiodactyla	Balaenidae	*Eubalaena glacialis* (Müller, 1776)[a]	P-O, O	Nichols & Hamilton (2004)
Cetartiodactyla	Balaenopteridae	*Balaenoptera acutorostrata* Lacépède, 1804	P-O, O	Nichols & Tscherter (2011); this paper
Cetartiodactyla	Balaenopteridae	*Balaenoptera borealis* Lesson, 1828	P-O, O	Japha (1910)
Cetartiodactyla	Balaenopteridae	*Balaenoptera physalus* (Linnaeus, 1758)	P-O, O	Japha (1910)
Cetartiodactyla	Delphinidae	*Grampus griseus* (Cuvier, 1812)	P-O, O	This paper
Cetartiodactyla	Delphinidae	*Orcinus orca* (Linnaeus, 1758)[a]	P-O, O	Samarra et al. (2012)
Cetartiodactyla	Phocoenidae	*Phocoena phocoena* (Linnaeus, 1758)	P-O, O	van Utrecht (1959)
Cetartiodactyla	Physeteridae	*Kogia breviceps* (Blainville, 1838)	P-O, NM	McAlpine (2003)
Cetartiodactyla	Physeteridae	*Kogia sima* (Owen, 1866)	P-O, NM	McAlpine (2003)
Cetartiodactyla	Physeteridae	*Physeter macrocephalus* Linnaeus, 1758	P-O, O	This paper
Cetartiodactyla	Ziphidae	*Mesoplodon bidens* (Sowerby, 1804)	P-O, NM	This paper
Cetartiodactyla	Ziphidae	*Ziphius cavirostris* Cuvier, 1823	P-O, NM	Heyning (2003)

[a] Only non-pierced wounds were recorded (confirmation of active feeding was not accomplished)
[b] Both resident and anadromous forms

Table 3 Ecological classification of host species described for the haematophagous stage of anadromous *Petromyzon marinus.*

Distribution range (migratory pattern)	**n**	**%**	**Habitat in the water column**	**n**	**%**
Freshwater (potamodromous)	4	7			
Freshwater (non-migratory)	0	0	Demersal	26	48
Diadromous	16	30	Pelagic (neritic)	11	20
Marine (oceanodromous)	30	56	Pelagic (oceanic)	16	30
Marine (non-migratory)	4	7	Bathypelagic	1	2
Total	54	100	Total	54	100
Trophic guild	**n**	**%**	**Conservation status (IUCN)**	**n**	**%**
			Critically endangered	1	2
Carnivorous	28	52	Endangered	3	6
Detritivorous	1	2	Vulnerable	7	13
Grazers	0	0	Near threatened	20	37
Omnivorous	4	7	Least concern	18	33
Planktivorous	21	39	Not Evaluated and Deficient Data	5	9
Total	54	100	Total	54	100

Figure captions

Fig. 1 Location of areas where species wounded by *Petromyzon marinus* were found. A: Coast and estuaries of NW Iberian Peninsula (commercial fishing, sport fishing and strandings); B: Rivers, estuaries and coast of French Brittany (R. Sabatié pers comm); C: Lough Derg, Ireland (J. B. Hume pers comm); D: North West Atlantic Ocean (mark-recapture campaign); E: North West Atlantic Ocean (scientific expedition)

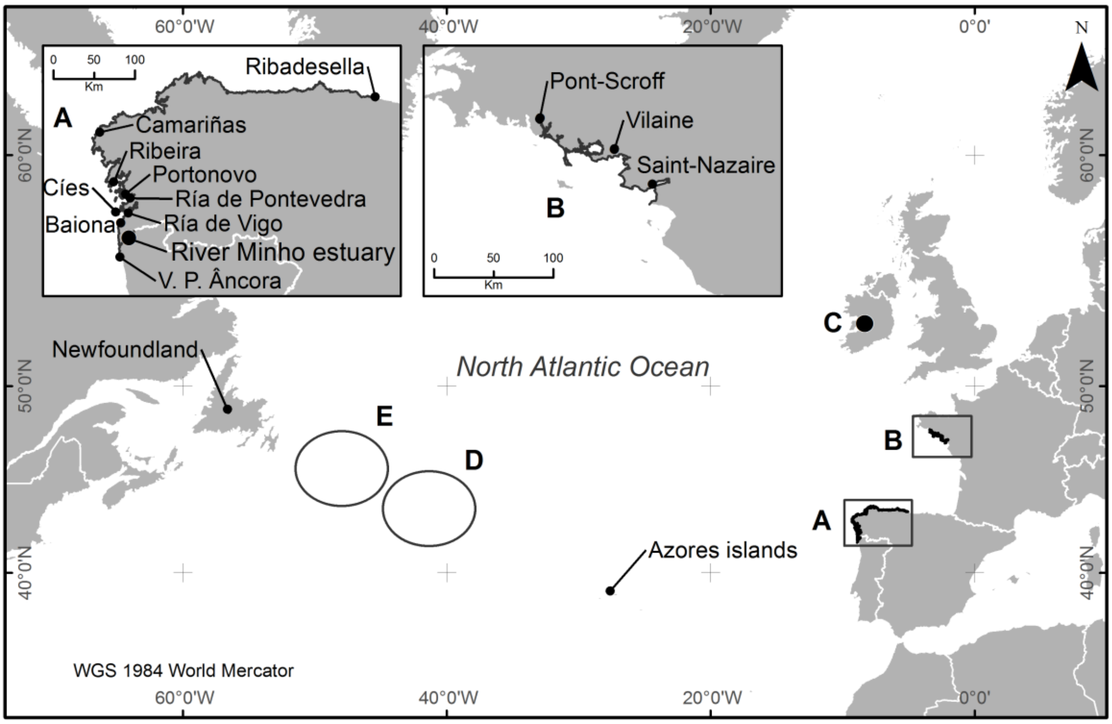


Fig. 2 *Alosa alosa* (**a**), *Liza ramada* (**b**), *Scomber scombrus* (**c**), *Trachurus trachurus* (**d**), *Merluccius merluccius* (**e**) and *Sebates metella* (**f**) attacked by *Petromyzon marinus*

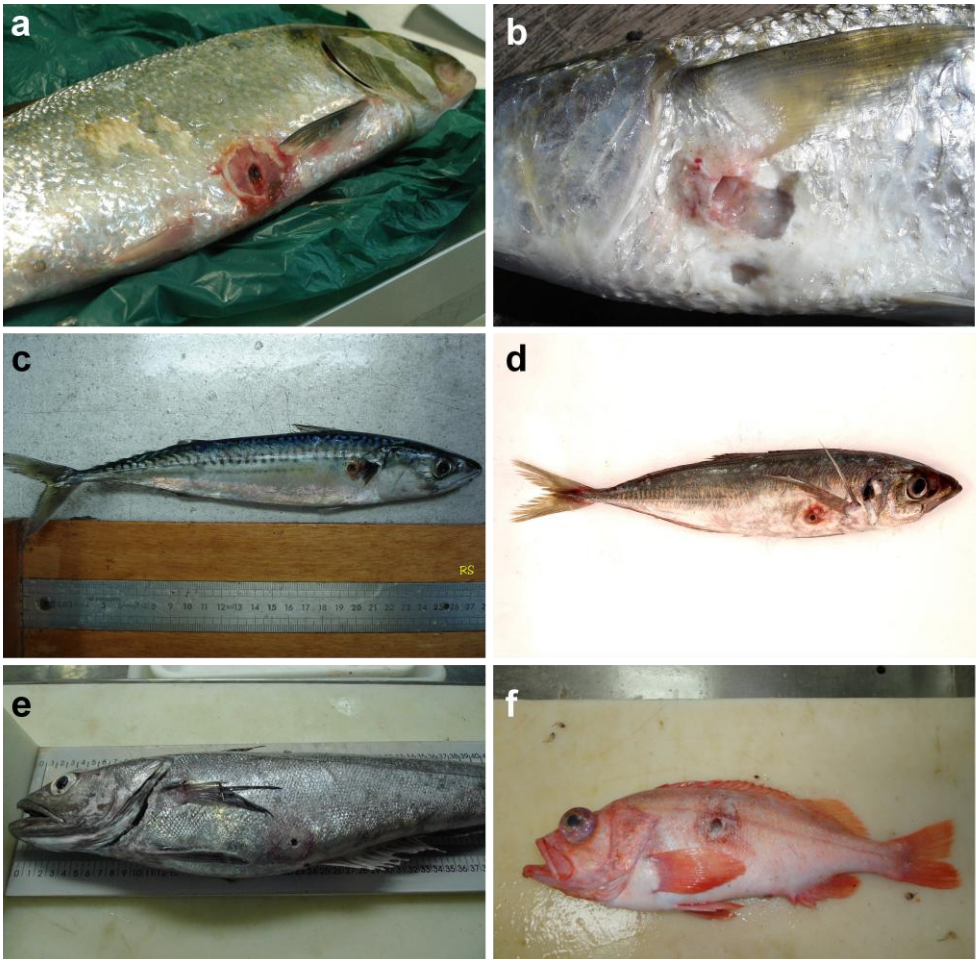
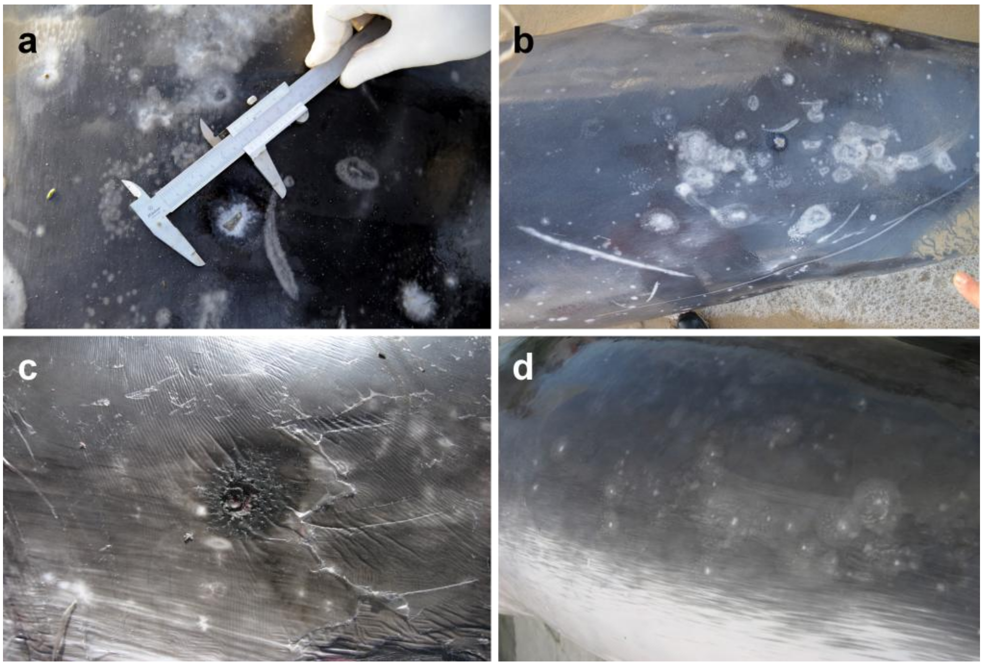


Fig. 3 Pierced (**a**) and non-pierced (**b**) wounds caused by *Petromyzon marinus* on *Mesoplodon bidens*. Pierced (**c**) and non-pierced (**d**) wounds caused by *P. marinus* on *Balaenoptera acutorostrata*



Online resource 1 First evidence of *Petromyzon marinus* feeding on *Prionace glauca*