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Report on the ecology of diadromous fish at sea

Sophie a M Elliott, Noémie Deleys, Etienne Rivot, Anthony Acou, Elodie Reveillac, Laurent Beaulaton

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Synthèse sur les connaissances disponibles sur les migrateurs en mer

Report on the ecology of diadromous fish at sea

Rapport d'étape 1

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- **REPORT ON THE ECOLOGY OF DIADROMOUS FISH AT SEA**

- **ABSTRACT**

Very little is known about diadromous fish distribution at sea. Twelve diadromous fish have been found to occur in France. However, numerous species have declined in recent years. Here, we collated a database of 168 904 hauls from 42 fisheries dependent and independent surveys between 1965 and 2019 and analyse data containing information on diadromous fish known to occur within French marine waters.

The aim of this study is to 1) evaluate the use of the existing databases to study diadromous fish, 2) improve understanding of diadromous fish ecology at sea, 3) assess the value of marine protected areas for diadromous fish, and 4) evaluate the risk of capture of diadromous fish from the different surveys and gear types.

- **MOTS CLES**

Diadromous fish, IUCN red listed species, Species distribution, Europe, Fisheries dependent data, Fisheries independent data, Bycatch, Marine Protected Areas.

• **SOMMAIRE**

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I. Introduction

Diadromous fish migrate between sea and fresh water during their life cycle. Some spend most of their lives at sea and reproduce in fresh water (anadromous species) while other spend most of their time in freshwater and reproduce at sea (catadromous species) (Lassalle et al., 2009, 2008). Twelve diadromous fish have been found to occur in France (Table 1). They have been of economic importance for centuries. However, numerous species have declined in recent years (Béguer et al., 2007; Lassalle et al., 2008). Reasons for their decline has been related to increased demand, increased river pollution, the construction of dams and anthropogenically induced climate change (Lassalle et al., 2009, 2008; Lassalle and Rochard, 2009; Limburg and Waldman, 2009). To date (2020), insufficient information exists to evaluate mortality at sea.

As a consequence of their decline, all 12 species are red listed under the International Union for the Conservation of Nature (IUCN). Numerous species have also been listed under various conventions for their protection: the convention for international trade of endangered species (CITES); the Habitats Directive's annexes; the Bern convention; and the convention for the protection of the marine environment of the North-East Atlantic (OSPAR) (Table 1).

Although the biology and ecology of diadromous fish has been well studied in freshwater (e.g. Béguer et al., 2007; Lassalle et al., 2009, 2008), surprisingly very little is known about the distribution and lives of diadromous fish at sea. Here we analyse existing data containing information on diadromous fish known to occur in French marine waters, with the aim to:

- 1) evaluate the use of the existing databases analysed to study diadromous fish at sea.
- 2) assess their spatial distribution according to different life history stage at sea and analyse long-term temporal trends in relative abundance;
- 3) assess the value of Marine Protected Areas for diadromous fish;
- 4) evaluate the risk of capture of diadromous fish from the different surveys and gear types.

II. Methods

- 1) Fisheries independent (International Scientific Bottom Trawl Surveys and French scientific surveys) and French fisheries dependent observer data (ObsMer) were collated from Institut Français pour l'Exploitation de la Mer (IFREMER) and the International Council for the Exploration of the Sea (ICES) the Database of Trawl Surveys (DATRAS) portal (<https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx>). To gather French scientific surveys, surveys that had information on diadromous fish (<https://campagnes.flotteoceanographique.fr/campaign>; Table S1 in Appendix) were requested, taking information provided within Regimbart et al, (2018) (Table 2.1).
- 2) The three datasets were compiled, analysed and diadromous fish distributions mapped in R CRAN free software (version 3.3, <http://cran.r-project.org>; Table 2.2).

- 3) Literature reviews on diadromous fish distribution, habitat, their size ranges, maturity and timing of migrations, are being undertaken to match against diadromous fish recordings from the database. Using the literature reviews and expert knowledge, data cleaning is being undertaken, correcting potential mis-identified species and any other obvious errors (Table 2.3-11).
- 4) Summary reports on species distribution, length, migration, abundance, bycatch and the value of the database are being developed for each species or group of species. Where sufficient data existed species distribution models will be undertaken (i.e. shads, the European eel, the flounder, mullet and smelt; Table 2.3-11).
- 5) The value of existing Marine Protected Areas (MPAs) for diadromous fish will be analysed from the cleaned data (points iii-iv; Table 2.12).
- 6) An analysis of diadromous fish catchability will be estimated from information on survey effort and fish capture over the course of the year. The latter will build upon work undertaken by Drogou et al. (2008) (Table 2.13).
- 7) Finally, there will be an evaluation on the use of the surveys analysed for diadromous fish distribution (Table 2.14).

Refer to Table 2 for estimated timing of delivery.

Table 1. Diadromous fish observed within French marine waters and their conservation status. A = Anadromous, C = Catadromous, - = not listed.




| Latin name | EN name | FR name | Type | IUCN FR 2019 ¹ | IUCN EU 2011 ² | IUCN world ⁴ | CITES | Habitat Directive | Bern | OSPAR |
|-----------------------------|---------------------------------|------------------------------|------|---------------------------|---------------------------|-------------------------|-------|-------------------|------|-------|
| <i>Acipenser sturio</i> | European sea sturgeon | Esturgeon européen | A | CR | CR | CR | AI | All, AIV* | III | Y |
| <i>Alosa alosa</i> | Allis shad | Grande alose | A | CR | LC | LC | - | II, V | III | - |
| <i>Alosa fallax</i> | (Atlantic)Twait shad | Alose feinte atlantique | A | NT | LC | LC | - | II, V | III | - |
| <i>Alosa agone</i> | Mediterranean twaite shad | Alose feinte méditerranéenne | A | NT | LC | LC | - | II, V | III | - |
| <i>Anguilla anguilla</i> | European eel | Anguille européenne | C | CR | CR | CR | AII | - | - | Y |
| <i>Lampetra fluviatilis</i> | European river lamprey /Lampern | Lamproie fluviatile | A | VU | LC | LC | NA | II, V | III | - |
| <i>Petromyzon marinus</i> | Sea lamprey | Lamproie marine | A | EN | LC | LC | - | II | III | Y |
| <i>Liza/Chelon ramada</i> | Thinlip mullet | Mulet porc | C | LC | LC | LC | - | - | - | - |
| <i>Osmerus eperlanus</i> | Smelt | Eperlan | A | NT | LC | LC | - | - | - | - |
| <i>Platichthys flesus</i> | European flounder | Flet | C | DD | LC | LC | - | - | - | - |
| <i>Salmo salar</i> | Atlantic salmon | Saumon Atlantique | A | NT | VU ³ | LC | - | II, V | III | Y |
| <i>Salmo trutta</i> | Sea trout | Truite de mer | A | LC | LC | LC | - | - | - | - |

¹ UICN et al, 2019; ² Freyhof and Brooks, 2011; ³ Nieto et al, 2015; ⁴ <https://www.iucnredlist.org/>.

Table 2. Estimated timeline for diadromous fish at sea deliverables.

| | | Contract 1 | | | | | Contract 2 | | | | | Proposed extra | | | | | | | | | | | | | | | | | |
|-------|---|------------|---|---|---|---|------------|---|---|---|---|----------------|---|---|---|------|----|----|----|---|---|---|---|---|---|---|---|---|--|
| | | 2019 | | | | | 2020 | | | | | 2021 | | | | 2022 | | | | | | | | | | | | | |
| Topic | Detail | 1 | 2 | 3 | 4 | 5 | 6 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | |
| 1 | Data collation | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 2 | Database compilation | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 3 | Lamprey | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | R script | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Literature research | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions (from team + external - paper) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 4 | Salmonids | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | R script (as per lamprey + catchability + external data) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Literature research | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions (from team) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 5 | Shads | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | R script (as per Salmonid + SDM - FI+FD data. + abundance) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Literature research | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions (from team + external) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 6 | Eel | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | R script (as per Shad + SDM - FI) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Literature research | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions (from team + external) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 7 | Sturgeon | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | R script (as per lamprey) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Literature research | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions (from team + Bordeaux team) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 8 | Mullet | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | R script (as per Shad + SDM - FI+FD) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Literature research | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions (from team + external) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 9 | Smelt | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | R script (as per Salmon +SDM - FI data) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Literature research | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions (from team + external) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 10 | Flounder | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | R script (as per salmon + SDM - FI+FD) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Literature research | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions (from team + external) | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 11 | DF distribution paper | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Compiling all the above with seasonal and stage distribution. | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 12 | MPAs | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Mapping DF and migration within French MPAs - M1 support | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Modelling DF presence in MPA -M2 support | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 13 | Catchability of diadromous fish | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Analyse DF catchability in space and time | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Literature research | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Writing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Revisions | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 14 | Value of the database | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | What's missing | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | What could be done to improve | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| | Collecting more recent data & DF update | | | | | | | | | | | | | | | | | | | | | | | | | | | | |

Table 1 key

| | |
|---|----------------------------|
| DF | Diadromous fish |
| FD | Fisheries dependent data |
| FI | Fisheries independent data |
| MPA | Marine Protected Area |
| SDM | Species Distribution Model |
|  | Reporting |
|  | Completed |
|  | To complete |

III. Results

III.1. Survey data

From the 168 904 hauls out with transitional waters, 10 0617 hauls came from ObsMer data from 2003 to 2019 (Fig. 1.a), 54 865 hauls came from fisheries independent data submitted to ICES DATRAS (Fig. 1.b) between 1965 and 2018 and 13,422 hauls were collected from IFREMER from French scientific surveys (1976 to 2018; Fig. 1.c; Table S1 in Appendix A1). The spatial and temporal coverage for the three different datasets can be found within Appendix A1.

Note, through working with colleagues from French National Institute of Environmental Research and Technology (IRSTEA; Bordeaux) on shad, differences were observed in shad presence and the numbers caught within the ObsMer dataset. Following communication with IFREMER, a new extraction of ObsMer data was provided (31/07/20; Table 2.1-2).

III.2. Species distribution

Varying distributions can be observed from the different datasets (Fig. 2). From analyses of diadromous fish distribution individually, error in species identification and length has been observed (learnt through existing literature on the species and expert knowledge). Due to varying spatial effort (haul duration, vessel size and power, and sampling effort; Fig. 3), precise measures of abundance cannot be performed. To date (04/08/2020) analysis and cleaning of lamprey presence, abundance and length has been completed to the best of our knowledge (Appendix A). However the new ObsMer dataset has not yet been incorporated into Appendix A.

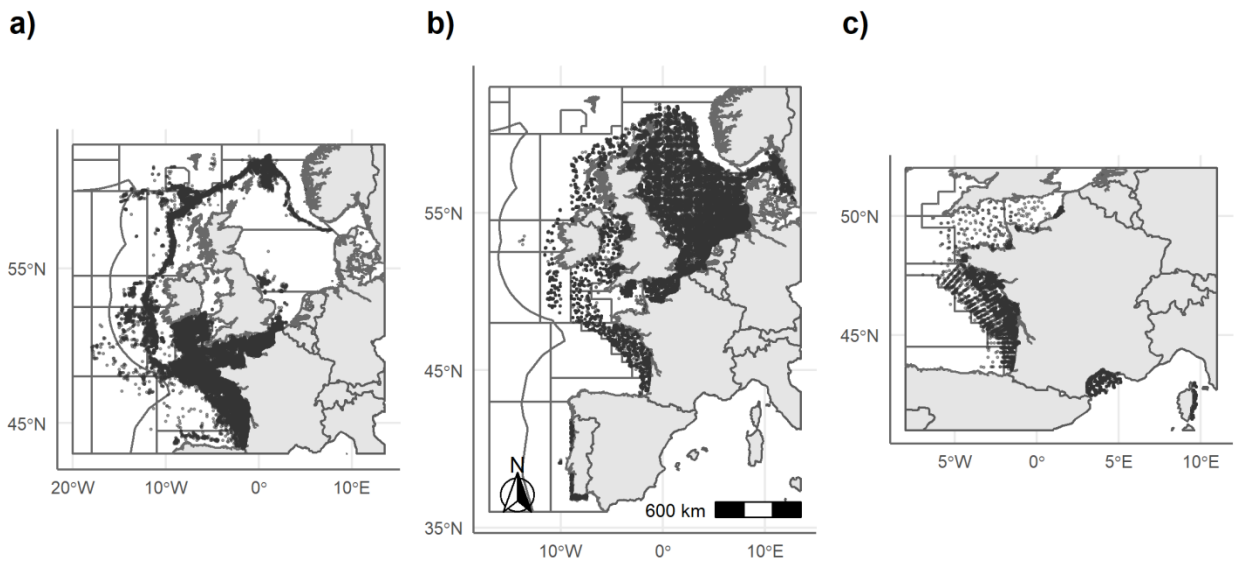


Fig. 1. Haul locations for a) fisheries dependent ObsMer surveys b) fisheries independent ICES DATRAS and c) French national scientific surveys. Black solid lines delineate ICES statistical divisions.

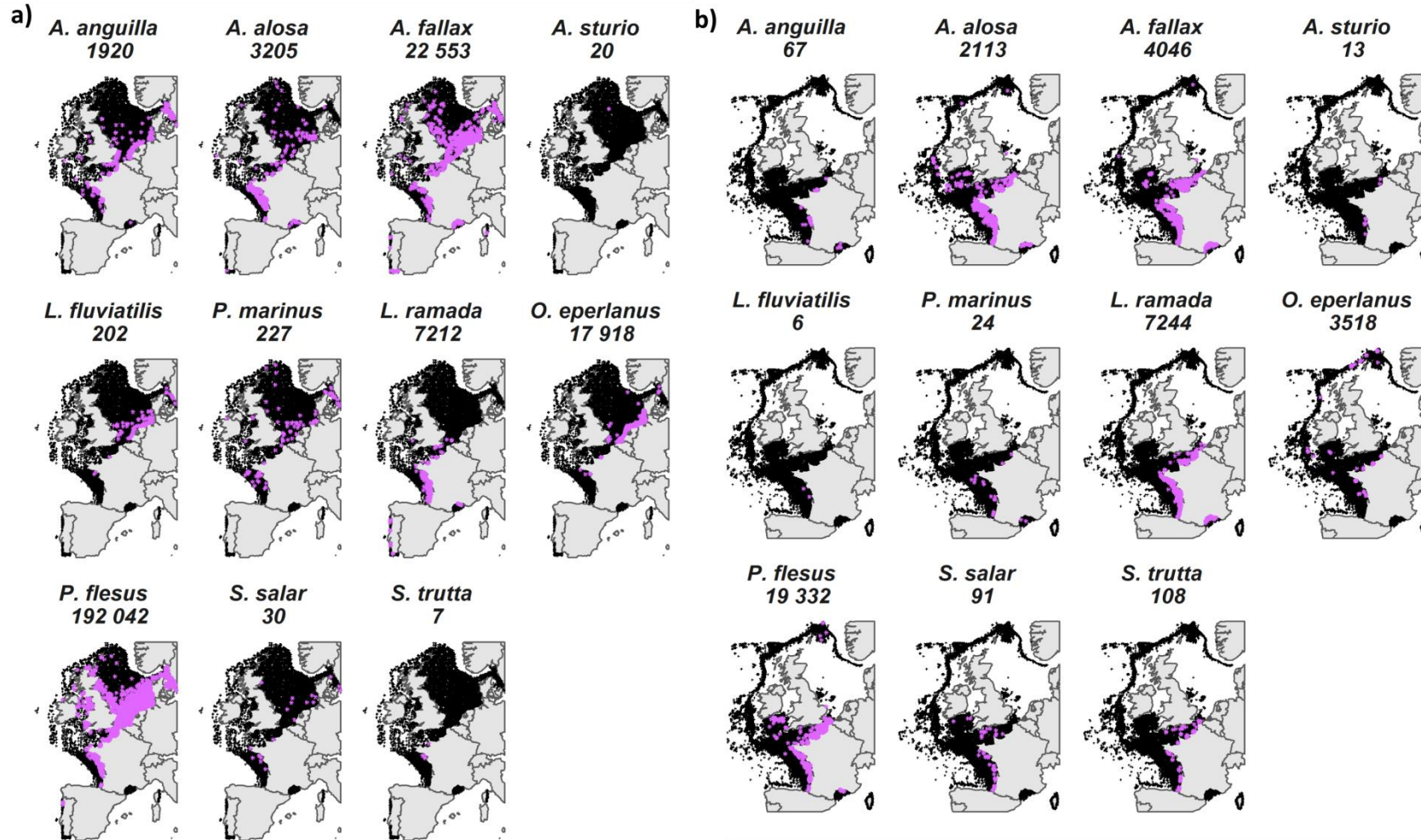


Fig. 2. Presence (violet points) absence (black points) map of diadromous fish using a) Fisheries independent data and b) fisheries dependent data. The numbers under the species names indicate the total number of individuals recorded. **Note, these results have not been verified for errors.**

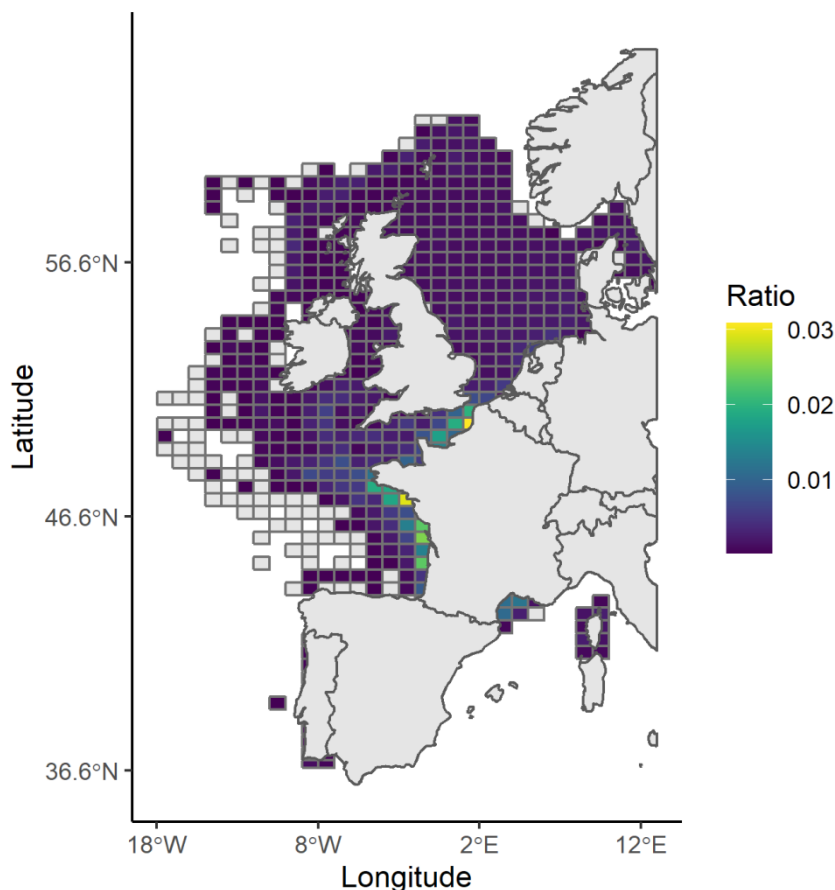


Fig. 3. Proportions of total hauls per ICES rectangle combining ObsMer data (2003-2019), scientific bottom trawl survey data submitted to DATRAS (1965-2018) and French scientific survey data (1976-2018). Grey cells indicate where <0.0001 hauls were undertaken.

IV. Next steps

At present analysis is being undertaken one group of species at a time (Table 2). During species analysis, the data is corrected for species miss-identification and error in lengths. Following the process of data cleaning, species distribution models and relative abundance tendencies will be undertaken where sufficient data exists.

It is planned for a first- and second-year master's student (November 2020 – February 2021 and February – August 2021) to support the project (Table 2) and help forward diadromous fish distribution within MPAs.

Accurate estimations of abundance are not possible with the data provided due to insufficient information on effort. Given the vulnerability of diadromous fish (Table 1) and the lack of information of their migrations at sea and mortality, it is hoped to calculate catchability of each species over the course of the year. The latter will give an indication of their vulnerability to different gear types, in addition to providing information on datasets which may be more useful to continue collating information on

diadromous fish from. An evaluation of the use of fisheries independent and dependent data to inform us on diadromous fish distribution and abundance is being undertaken.

V. Acknowledgements

We are extremely grateful to all those who were involved in collecting and compiling the fisheries dependent and independent surveys. We are also grateful to the French Research Institute for Exploitation of the Sea (IFREMER) and the French marine fisheries and aquaculture administration (DPMA) to have given us access to their data.

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VII. Appendix A¹

Shedding light on the distribution of lampreys at sea

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Running page head: Lamprey at sea distribution

¹ **Note:** This manuscript was submitted to the Journal of Endangered Species for publication as a short note (25/05/20) and is now (04/08/20) being revised to be submitted as a full length paper within the same journal.

ABSTRACT

Almost nothing is known about lamprey distribution at sea. In this paper, we collated a database of 150,758 hauls from fisheries dependent and independent surveys between 1965 and 2018. A total of 238 sea lamprey *Petromyzon marinus* and 208 European river lamprey *Lampetra fluviatilis* were identified. Sizes ranged from 13 cm to 80 cm and 14 cm to 42 cm (respectively). Presences were recorded throughout the greater North Sea, the Bay of Biscay and the Celtic sea. The largest proportion of lampreys were observed within the Skagerrak and North Sea (ICES divisions 3.b, 4.b and 4.c), from North Sea International Bottom Trawl Surveys. For both lampreys, there was an increase in size with depth of capture. A higher proportion of lamprey was detected in spring and autumn. Seasonal length variations were observed for *L. marinus* but not for *L. fluviatilis*. These new observations provide unprecedented information about lamprey at sea, and highlight study locations and surveys within north western European waters, which may be more pertinent for lamprey observations at sea.

KEY WORDS: Endangered species, Lamprey, *Lampetra fluviatilis*, *Petromyzon marinus*, Distribution, Ecology, Growth, Surveys

1. INTRODUCTION

Lampreys are primitive jawless vertebrates with particularly complex life histories (Kelly and King, 2001). They occur within temperate waters of both the northern and southern hemisphere (Kelly and King, 2001; Renaud, 1997). Three semelparous anadromous lamprey species have been identified in north western European waters: the sea lamprey *Petromyzon marinus*; the Artic lamprey *Lethentron japonicum* (only observed in Sweden) (Maitland, 1980); the European river lamprey *Lampetra fluviatilis*. Very little is known on the distribution at sea of *P. marinus* and *L. fluviatilis*.

The population status of *P. marinus* and *L. fluviatilis* is of major concern. During the late twentieth century, the culmination of both increased demand for lamprey, increased river pollution, and the construction of dams led to their decline (Kelly and King, 2001; Mateus et al., 2012). Both *P. marinus* and *L. fluviatilis* are listed under the Habitat Directive (92/43/EEC), the Bern convention (Appendix III) and the Barcelona convention. *P. marinus* is also listed under the OSPAR

convention. While considered as 'least concern' in the international union for conservation of nature (IUCN) red list in Europe (Freyhoff and Brooks, 2011), both species are threatened in many countries (Mateus et al., 2012).

Life cycles of *P. marinus* and *L. fluviatilis* are only partially known. The marine phase remains largely a black box (ICES, 2015). Improving knowledge on the biology and ecology of lamprey at sea is critical. Adults *P. marinus* and *L. fluviatilis* migrate upstream to spawn around April May (Beamish, 1980; Farmer, 1980; Maitland, 1980). The young larvae begin to swim downstream and between three and eight years later, where they metamorphosize, mature and migrate to marine waters (11-16 cm) during late autumn winter (Beamish, 1980; Beamish and Potter, 1978; Youson and Potter, 1979). During their marine phase they become parasitic adults for 18 to 28 months (Beamish, 1980; Farmer, 1980). Lamprey parasitize a range of hosts from bony fish, elasmobranchs to mammals (Halliday, 1991; Kelly and King, 2001; Lança et al., 2013; Maitland, 1980). Adults of *L. fluviatilis* range between 20 and 50 cm (Kelly and King, 2001), whereas the larger *P. marinus* ranges between 60 and 90 cm (Beaulaton et al., 2008).

Given their recent declines in population status, a better understanding of their ecology at sea is essential. To improve our knowledge on lamprey distribution at sea, we collated an unprecedented database of 150 758 hauls from fisheries independent and French fisheries dependent data taking place throughout Northern European waters. From this database, we analysed the distribution of *P. marinus* and *L. fluviatilis* between 1965 and 2018, seasonal and depth length relationships, and survey and gear type capture rate.

2. METHOD

Fisheries independent data are available from International Council for the Exploration of the Sea (ICES) the Database of Trawl Surveys (DATRAS) portal (<https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx>), French scientific surveys (excluding data available through DATRAS) and French fisheries dependent observer data (ObsMer; more details in Fauconnet et al., (2015)) were analysed (Fig. 1; Table S1). To gather French scientific surveys, surveys undertaken by Institut Français pour l'Exploitation de la Mer (IFREMER) that may have information on diadromous fish (<https://campagnes.flotteoceanographique.fr/campaign; Table S1>)

were requested, taking information provided within Regimbart et al, (2018). Only hauls downstream of transitional waters were taken into account.

Lampreys were only present in a very small minority of hauls (0.003 % presence). Biological information containing the fish captured, their number and lengths were recorded. Due to the limited number of presence observations and difficulties in taking into account spatio-temporal heterogeneity, only simple robust statistical analysis was performed to avoid over-interpretation of the data. All mapping and length frequency analysis was undertaken within R CRAN free software (version 3.3, <http://cran.r-project.org>). Within this study, we also compared our data to Halliday's (1991) data (1979-1990) on *P. marinus* length in relation to depth and month, off the coast of northeast America.

3. RESULTS

From the 150,758 hauls out with transitional waters which were analysed, a lamprey presence of 0.16 % was observed. A total of 446 lampreys were identified between 1965 and 2018 (Table 1; Table S1) from 68,287 hauls from scientific trawl surveys and 82,471 hauls from French fishing vessels (Fig. 1). From both the fisheries dependent and independent data, *Petromyzon marinus* was recorded more frequently (11 and 227 respectively) than *Lampetra fluviatilis* (6 and 202 respectively) (Table 1). Both species had an overlapping distribution in space and depth (Fig. 2, Table 1-2). Excluding ICES divisions which had relatively few hauls (3.b and 7.b), highest lamprey presence was within 3.a, 4.b, 4.c (the Skagerrak Sea and the North Sea along the Dutch and western German coasts; Table 2; Fig. 2). 2252 hauls took place within the Mediterranean Sea, albeit no lampreys were observed (Fig. 1 and 2, Table S1).

From the fisheries independent data, relatively more lampreys were identified within North Sea International Bottom Trawl Surveys (NS-IBTS; Table 1; Fig. 2). From the ObsMer dataset a higher capture rate of both species was recorded from set longline gear type (Table 1).

P. marinus length range was between 13 and 80 cm (mean 26.56 cm, Standard error (SE) \pm 2.35 cm), whereas *L. fluviatilis* length range was between 14 and 42 cm (mean 29.89 cm, SE \pm 0.89 cm) (Fig. 3). An increase in *P. marinus* and *L. fluviatilis* length with depth was detected ($P < 0.001$, DF = 3, LL = -1023.16, deviance explained 26%; $P < 0.01$, DF = 3, LL = -603.22, deviance explained = 8.99%

respectively; Fig. 4.a). From the survey data collected in this study, no lamprey was identified deeper than 170 m (Fig. 4.a-c).

Indications of two length modes were detected for *P. marinus* over the course of the year (Fig. 5.i.a and b.). Growth of smaller individuals can be observed from winter to autumn for *P. marinus* ($P < 0.001$, $DF = 3$, $LL = -1080.03$, deviance explained 8.88 %; Fig. 5.i.a-b.). Results suggested a bimodal distribution of length (Fig. 3.b.) for *L. fluviatilis*. No evidence of growth over the course of the year (Fig 5.ii.a and b). For both lampreys, there was a higher proportion of presence in spring and autumn (Fig. 5.c.).

4. DISCUSSION

Presence of lamprey was reported in only 0.16 % of hauls, which confirms the rarity of lampreys at sea. More *Petromyzon marinus* were observed than *Lampetra fluviatilis*. This result is inconsistent with Maitland, (1980) and Thiel et al., (2009), who reported more abundant *L. fluviatilis*. However, their analysis was based on a greater proportion of coastal surveys than in our database. Both species were found to have overlapping distributions. Nonetheless due to similar morphological characteristics miss-identification may have taken place (Renaud, 1997). A higher proportion of both species was found within ICES divisions 3.a and 4.b-c, within the Skagerrak Sea and the North Sea along the Dutch and German coast. No lampreys were recorded in the Mediterranean Sea, where they are known to inhabit (Bianco, 2014).

A greater proportion of lampreys were observed from the fisheries independent data than the dependent data. It is thought that lampreys may detach themselves from their hosts at the time of capture (Halliday, 1991). Longer hauls from fisheries dependent data, may therefore report less observations as a result of a higher detachment rate. In addition, fisheries dependent observations were scarce within the North Sea and absent within the Baltic Sea where presence was greater. Thiel et al., (2009) analysed lamprey catch from commercial and published records and also recorded high numbers of *P. marinus* and *L. fluviatilis* within the Baltic Sea.

More lampreys were recorded from NS-IBTSs, likely due to the higher presence of lampreys within this ICES division 3.a and 4.b-c. Lamprey observations from the fisheries dependent data were mainly from set long lines. Insufficient survey information was available to calculate Catch Per Unit Effort (CPUE) for each gear

type. It should be noted that none of the surveys were designed to target lamprey species.

Length ranges within our dataset were in line with previous literature (Beamish, 1980; Kelly and King, 2001; Maitland, 1980). However, smaller *P. marinus* were measured than expected (Beaulaton et al., 2008). The latter may be because of a large number of small individuals in shallow waters. The increase in length with depth corroborates with Beamish (1980) and Halliday (1991).

Recently metamorphosed lampreys are supposed to migrate to their marine habitat late autumn winter. Mature adults return to freshwater habitats to reproduce around April May (Beamish, 1980; Farmer, 1980; Stratoudakis et al., 2016). We observed two presence peaks in line with this literature. Nonetheless, smaller individuals had a higher presence in spring than autumn. The latter maybe due to the few large lamprey caught. It is thought that larger lamprey parasitize larger fish (e.g. cetaceans and larger elasmobranchs) (Halliday, 1991), which are rarely caught in fisheries dependent and independent surveys. Furthermore, cetaceans and elasmobranchs often migrate long distances and into deeper waters, which our data does not cover. Alternatively, the lower number of large individuals may be because of high natural death rate of lampreys at sea. Mortality from fishing activity is thought to be low (Stratoudakis et al., 2016).

P. marinus appeared to have a bimodal length tendency, with an increase in size of juvenile lampreys over the course of the year, and another mode of larger individuals. Various hypotheses exist for the length of time that lamprey are supposed to inhabit marine waters (1-2.5 years) (Halliday, 1991; Silva et al., 2013). Our results suggest the existence of two length modes which corroborates with Silva et al. (2013) hypothesis, that sea lamprey occupy marine waters for approximately one year.

4.1. CONCLUSION

Our analysis synthesises an unprecedented database of fisheries dependent and independent data and provides insight into the mystery of lamprey at sea. This study highlights regions of higher lamprey presence at sea within north western European waters, indicates survey and gear type capture rate, and provides seasonal, depth and length relationships. Conservation measures have been set up across the globe to try and restore populations (e.g. rebuilding programs, improved river connectivity,

removal of barriers and weirs etc.) (Renaud, 1997; Thiel et al., 2009). Greater awareness is needed in both fisheries dependent and independent surveys to be able to collect data on lampreys during their marine phase, to improve our understanding, and implement better protection measures.

Acknowledgements

We are extremely grateful to all those who were involved in collecting and compiling the fisheries dependent and independent surveys. We are also grateful to the French Research Institute for Exploitation of the Sea (IFREMER) and the French marine fisheries and aquaculture administration (DPMA) to have given us access to their data.

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Table 1. Lamprey at sea records between 1966 and 2018 using fisheries dependent and independent data. SE = Standard Error, LLS = Set longlines, OTB = Otter beam Trawl, GTR = Trammel nets, PTM = mid- water pair trawl, GNS = set gillnets. Survey full names, dates and haul numbers within Table S1.

| Species | Data type | Total number of hauls | Total number | Percent presence (%) | Year | Mean length \pm SE (cm) | Length range (cm) | Seabed depth range (m) | Gear survey type / | Total number | Percent presence relative to catch (%) | Target species |
|-----------------------------|---------------------------|-----------------------|--------------|----------------------|------------------|---------------------------|-------------------|------------------------|--------------------|--------------|--|--------------------|
| <i>Petromyzon marinus</i> | ObsMer | 82,471 | 11 | 0.012 | 2009-2017 | 26.78 \pm 8.17 | 21-34 | 5-170 | LLS | 5 | 0.160 | Bass 0.10 |
| | | | | | | | | | GTR | 2 | 0.012 | Prawns 0.59 |
| | | | | | | | | | OTB | 2 | 0.007 | Sea bream |
| | | | | | | | | | PTM | 1 | 0.028 | 0.09 |
| | | | | | | | | | GNS | 1 | 0.013 | Meagre 0.14 |
| | ICES Datras | 54,865 | 199 | 0.153 | 1980-2017 | 26.55 \pm 0.8 | 13-80 | 5-162 | NS-IBTS | 175 | 0.231 | European Hake 0.15 |
| | | | | | | | | | DYFS | 11 | 0.229 | Sole 0.01 |
| | | | | | | | | | SWC-IBTS | 10 | 0.130 | NA |
| | | | | | | | | | FR-CGFS | 2 | 0.037 | |
| | | | | | | | | | EVHOE | 1 | 0.039 | |
| French scientific surveys | 13,422 | 28 | 0.201 | 1977-2018 | NA | NA | 5-157 | PECO/PECOS | 9 | 1.136 | NA | |
| | | | | | | | | Sold | 5 | 1.412 | | |
| | | | | | | | | PELGAS | 14 | 0.701 | | |
| | | | | | | | | | | | | |
| <i>Lampetra fluviatilis</i> | ObsMer | 6 | 0.002 | 2012 & 2015 | 24.5 \pm 2.35 | 14-29 | 13-50 | LLS | 5 | 0.040 | Meagre 0.14 | |
| | | | | | | | | PTM | 1 | 0.028 | Whiting 0.04 | |
| | ICES Datras | 198 | 0.208 | 1973-2018 | 30.05 \pm 0.34 | 19-42 | 0-104 | NS-IBTS | 135 | 0.195 | NA | |
| | | | | | | | | DYFS | 56 | 1.246 | | |
| | | | | | | | | BTS | 7 | 0.050 | | |
| | French scientific surveys | 4 | 0.030 | 1981-2018 | NA | NA | 1.8-45 | Bargip/Nourdem | 2 | 1.026 | NA | |
| | | | | | | | | Nurse | 1 | 0.041 | | |
| | | | | | | | Sold | 1 | 0.282 | | | |

Table 2. Summary table of lampreys observed from 1966 to 2018 within International Council for the Exploration of the Sea (ICES) divisions from fisheries dependent and independent data.

| Area | Hauls | <i>Petromyzon marinus</i> | | <i>Lampetra fluviatilis</i> | |
|---------------|-------|---------------------------|---------------------|-----------------------------|---------------------|
| | | Total number | Presence (%) | Total number | Presence (%) |
| 2.a | 302 | 0 | 0.000 | 0 | 0.000 |
| 3.a | 3513 | 53 | <u>1.621</u> | 36 | <u>0.832</u> |
| 3.b | 18 | 5 | 11.111 | 0 | 0.000 |
| 3.c | 60 | 0 | 0 | 0 | 0 |
| 4.a | 11900 | 9 | 0.034 | 0 | 0.000 |
| 4.b | 20544 | 76 | 0.131 | 93 | 0.248 |
| 4.c | 9219 | 40 | <u>0.206</u> | 69 | <u>0.532</u> |
| 5.b | 550 | 0 | 0.000 | 0 | 0.000 |
| 6.a | 6746 | 0 | 0.000 | 0 | 0.000 |
| 6.b | 84 | 0 | 0.000 | 0 | 0.000 |
| 7.a | 2033 | 4 | 0.098 | 0 | 0.000 |
| 7.b | 232 | 6 | 0.431 | 0 | 0.000 |
| 7.c | 416 | 0 | 0.000 | 0 | 0.000 |
| 7.d | 22251 | 7 | 0.022 | 2 | 0.009 |
| 7.e | 11144 | 1 | 0.009 | 0 | 0.000 |
| 7.f | 1344 | 0 | 0.000 | 0 | 0.000 |
| 7.g | 5721 | 1 | 0.017 | 0 | 0.000 |
| 7.h | 8577 | 0 | 0.000 | 0 | 0.000 |
| 7.j | 2296 | 0 | 0.000 | 0 | 0.000 |
| 7.k | 572 | 0 | 0.000 | 0 | 0.000 |
| 8.a | 25232 | 26 | 0.099 | 7 | 0.012 |
| 8.b | 13853 | 10 | 0.065 | 1 | 0.007 |
| 8.c | 410 | 0 | 0.000 | 0 | 0.000 |
| 8.d | 868 | 0 | 0.000 | 0 | 0.000 |
| 8.e | 47 | 0 | 0.000 | 0 | 0.000 |
| 9.a | 574 | 0 | 0.000 | 0 | 0.000 |
| Mediterranean | 2252 | 0 | 0.000 | 0 | 0.000 |

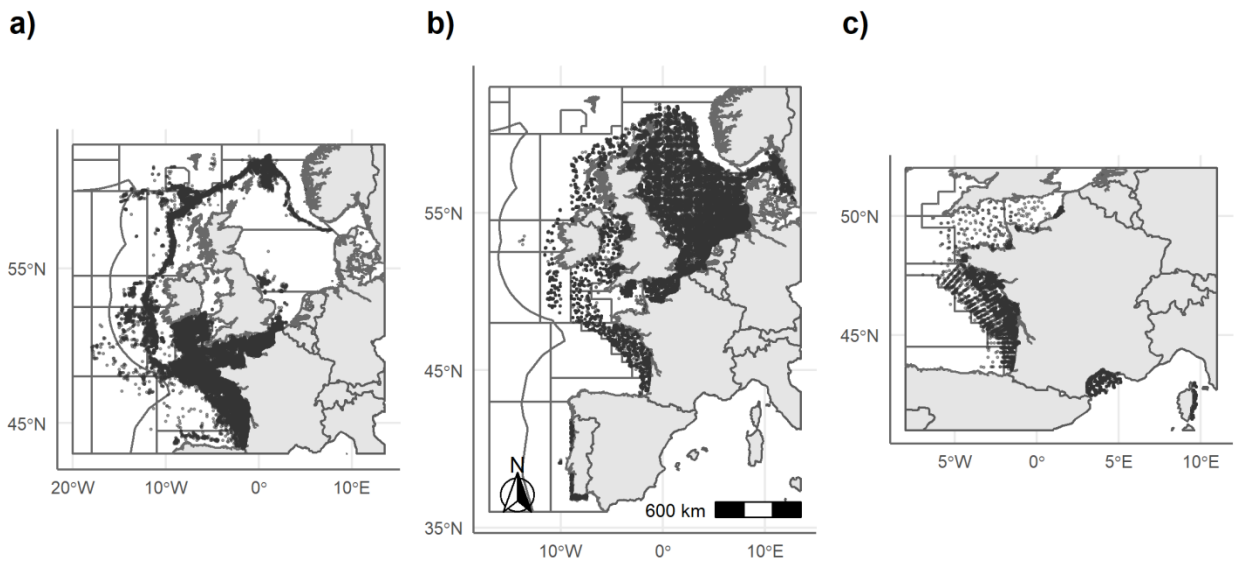


Fig. 1. Haul locations for a) fisheries dependent ObsMer surveys b) fisheries independent ICES Dattras and c) French national scientific surveys analysed for the presence of lamprey. Black solid lines delineate ICES statistical divisions.

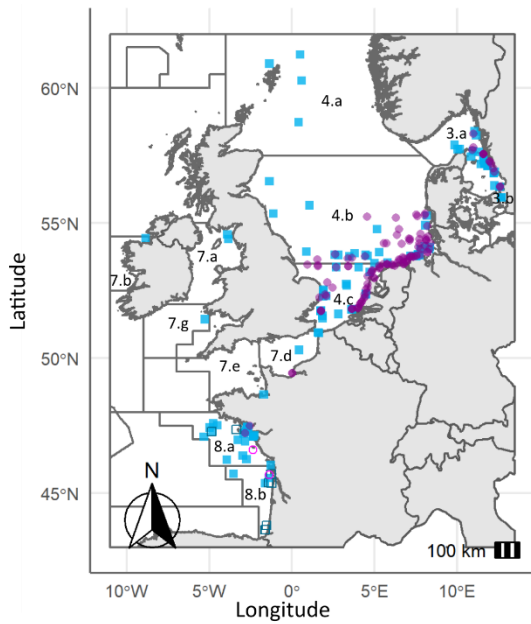


Fig. 2. Presence locations of *Petromyzon marinus* (blue squares) and *Lampetra fluviatilis* (purple circles) caught by fisheries dependent (hollow symbols) and independent (filled in symbols) data. Black solid lines delineate ICES statistical divisions and their coded names.

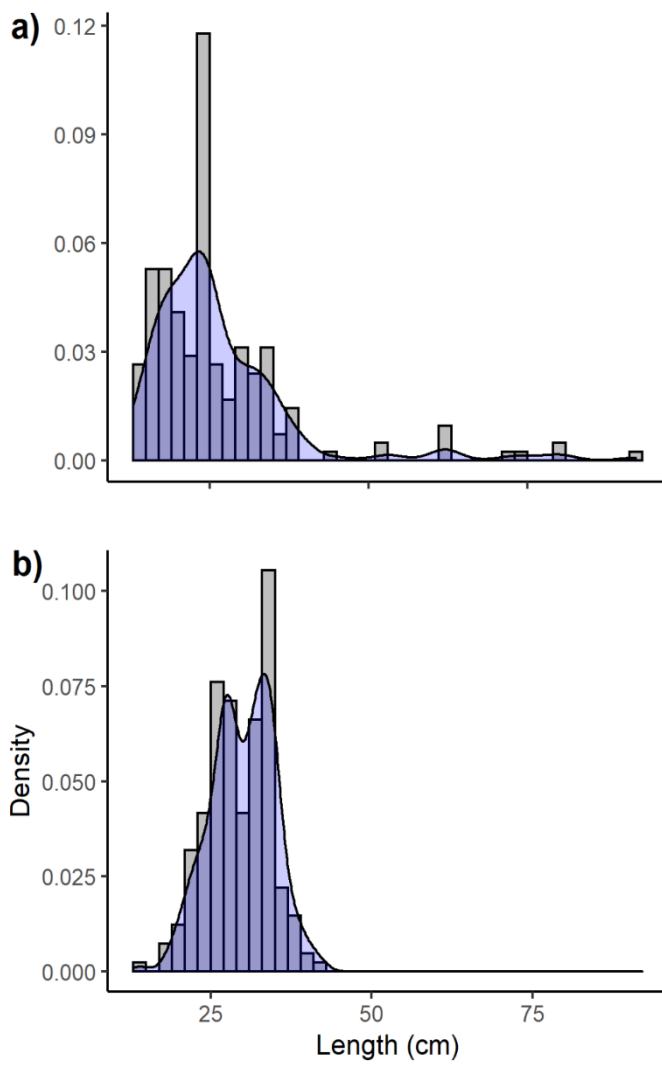


Fig. 3. Kernel smoothed density length histograms for a) *Petromyzon marinus* and b) *Lampetra fluviatilis*, combining both fisheries dependent and independent datasets.

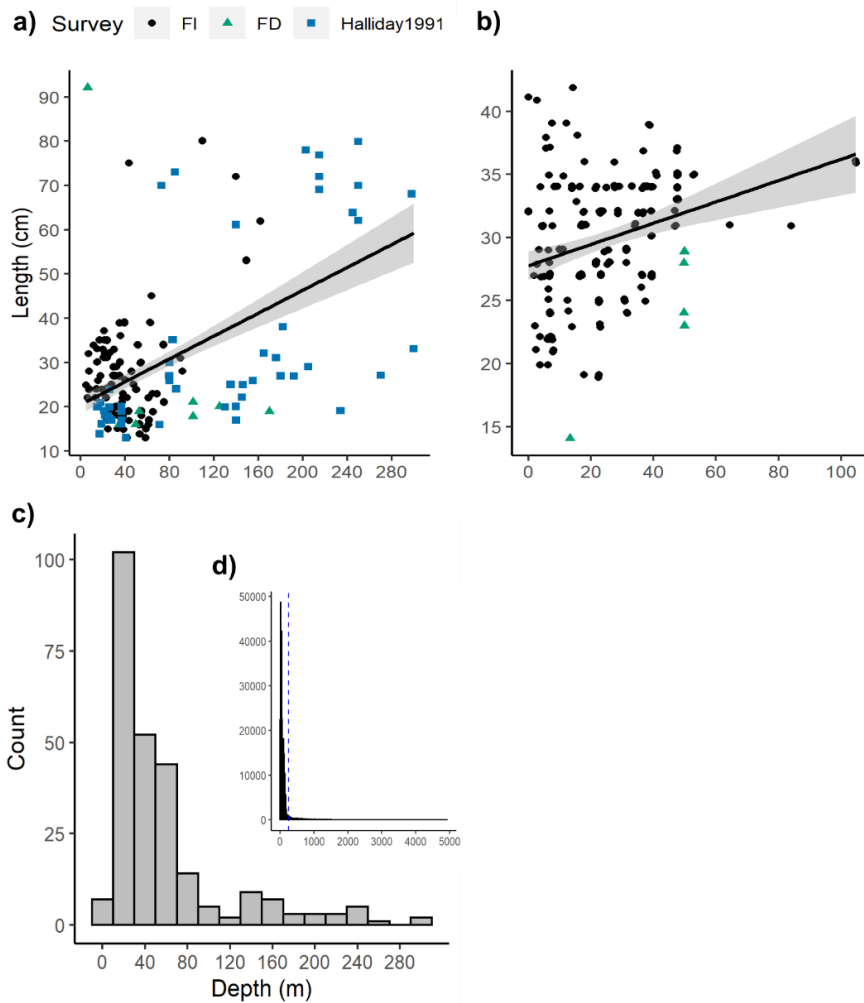


Fig.4. Lengths of a) *Petromyzon marinus* and b) *Lampetra fluviatilis* with depth, from fisheries independent (FI) and fisheries dependent (FD) data within north eastern Atlantic waters and data from Halliday (1991; north western Atlantic waters), with the model fitted lines and the shaded area indicating $\pm 95\%$ confidence intervals. Note, three points were removed from Halliday (1991) data that were > 1000 m. Depth histograms for c) hauls lamprey were observed within and d) all hauls. Dashed vertical line indicates the maximum depth lamprey observed (c).

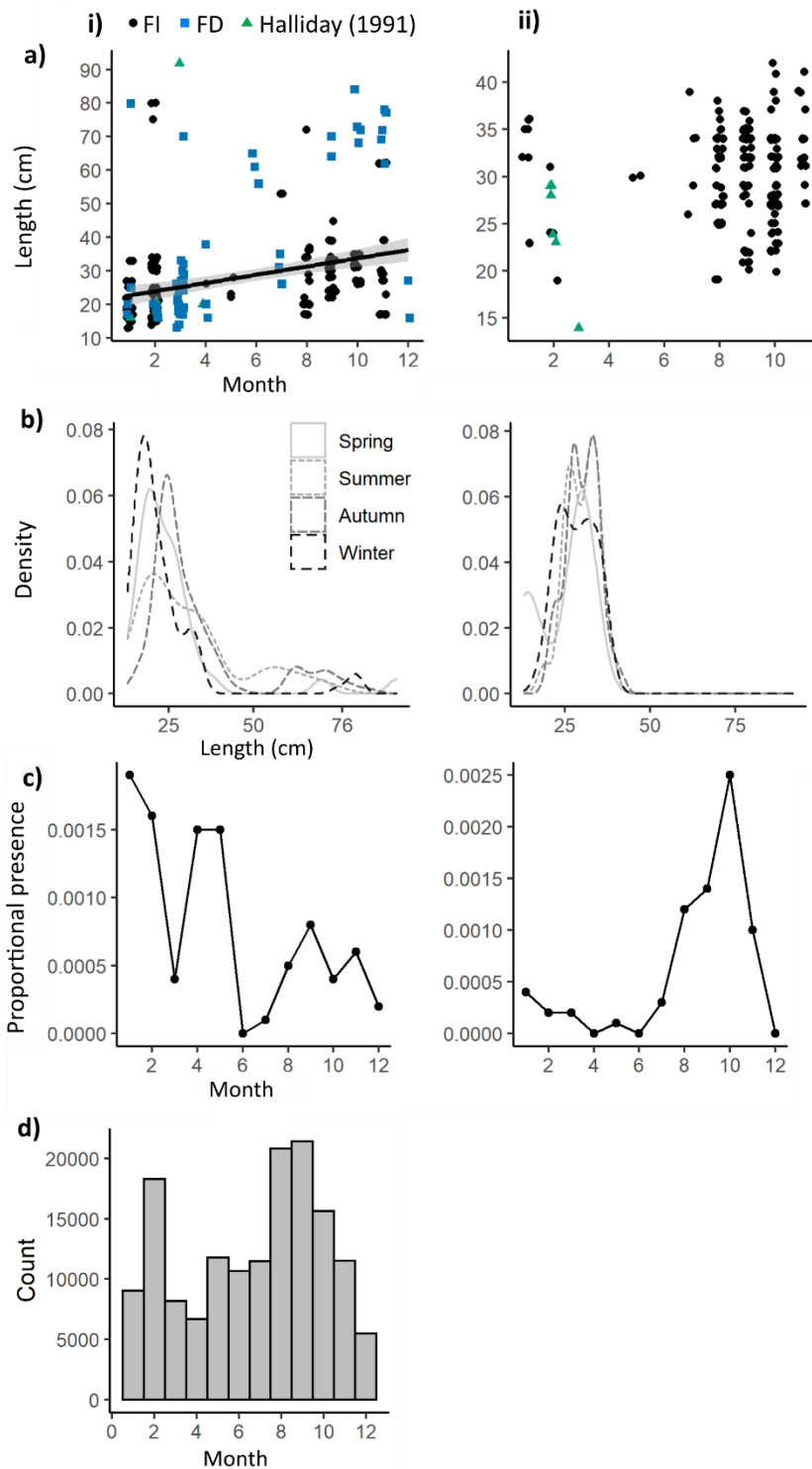


Fig. 5. Lengths of i) *Petromyzon marinus* and ii) *Lampetra fluviatilis* from marine waters by a) month using records from fisheries independent data (FI), Fisheries dependent data (FD) and data from Halliday (1991). b) Lamprey Kernel density plots by season. c) Proportion of lamprey presence per month. d) Histogram of the number of total hauls per month.

Appendix A1. Supplementary data

Table S1. Surveys extracted to be able to assess Lamprey presence. Note to all surveys took place every year.

| | Survey category | Full name (where available) | Acronym | Geographical region | Years | Number of hauls | Source |
|----|---------------------------|--|-----------------|---|-------------|-----------------|---|
| 1 | ICES Datras | Bottom Trawl Survey | BTS | Greater North Sea and Celtic Sea | 1987 - 2018 | 12,054 | 10.7489/1967-1 |
| 2 | | Bottom Trawl Survey | BTS-VIII | Bay of Biscay | 2011-2017 | 455 | http://datras.ices.dk |
| 3 | | Demersal Young Fish Survey | DYFS | Greater North Sea | 2002-2017 | 3932 | http://datras.ices.dk |
| 4 | | Evaluation Halieutique Ouest de l'Europe | EVHOE | Celtic sea and Bay of Biscay | 1997-2017 | 2575 | 10.7489/1958-1 Not |
| 5 | | French Channel Ground Fish Survey | FR-CGFS | Eastern English Channel | 1988-2018 | 2678 | DOI: 10.18142/11 |
| 6 | | North Sea International Bottom Trawl Survey | NS-IBTS | Greater North Sea | 1965-2018 | 30,290 | DOI: 10.7489/1922-1 |
| 7 | | Portuguese International Bottom Trawl Survey | PT-IBTS | Bay of Biscay and the Iberian coast | 2002-2017 | 574 | 10.7489/1963-1 |
| 8 | | Scottish West Coast Bottom Trawl Survey | SWC-IBTS | Celtic sea | 1985-2010 | 2307 | 10.7489/1957-1 10.7489/1924-1 |
| 9 | | | Arca | Bay of Biscay | 1995-1996 | 38 | Ifremer |
| 10 | French scientific surveys | Nourreries démersaux | Nourdem Bargip/ | Channel and Bay of Biscay (Loire and Seine) | 2015-2018 | 195 | Le Goff et al, 2017 |

| | | | | | | |
|----|---|------------|-------------------------|-----------|-----|------------------------|
| 11 | Etude de l'impact des marées noires de l'Erika | Black | Bay of Biscay | 2000 | 130 | Ifremer |
| 12 | Nurse (nourriceries) sur la Baie du mont Saint-Michel | BMSM2003 | Bay of Biscay | 2003 | 12 | Ifremer |
| 13 | Nurse (nourriceries) sur la baie de Bourgneuf | Bour | Bay of Biscay | 1980-1984 | 136 | Ifremer |
| 14 | CAMpagne MANche OCcidentale pluridisciplinaire | CAMANOC | English Channel | 2014 | 86 | DOI: 10.17600/14001900 |
| 15 | Campagne de comparaison de racasseurs lourds et légers sur la sélectivité des soles | Captusol01 | Bay of Biscay | 1984 | 76 | Ifremer |
| 16 | | CLA08_ | Bay of Biscay | 2008 | 25 | DOI: 10.17600/8040050 |
| 17 | Analyse des peuplements de crépidules en baie de bourgneuf | CREBOUR | Bay of Biscay | 2006 | 41 | Ifremer |
| 18 | EPIfaune BENthique du GOLfe du Lion | EPIBENGOL | Mediterranean | 2018 | 10 | DOI: 10.17600/18000589 |
| 19 | | Giro | Western English Channel | 1997 | 1 | Ifremer |
| 20 | Campagne sur les gradients de production côte-large incluant la baie de Vilaine et la rade de Brest | Isobaie09 | Bay of Biscay | 2009 | 23 | Ifremer |

| | | | | | | |
|----|--|---------------|-----------------------------------|-----------|------|---|
| 21 | Nurse (nourriceries) en estuaire externe de la Loire | Loir | Bay of Biscay | 1980-1986 | 136 | Ifremer |
| 22 | | Marika | Bay of Biscay | 2005 | 31 | Ifremer |
| 23 | Mediterranean trawl survey - Corse | MEDITS-CORSE | Mediterranean | 1994-2017 | 504 | http://www.ifremer.fr/SIH-indices-campagnes/ |
| 24 | Mediterranean trawl survey – Golfe du Lion | MEDITS-LION | Mediterranean | 1994-2018 | 1628 | http://www.ifremer.fr/SIH-indices-campagnes/ |
| 25 | Nurse (nourriceries) en 2003 | MISOLRE | Bay of Biscay | 2003 | 133 | Ifremer |
| 26 | Nurse (nourriceries) dans le golfe du Morbihan | Morb | Bay of Biscay | 1995-1996 | 78 | Ifremer |
| 27 | Nurse (nourriceries) dans le pertuis breton | Nonamebreton | Bay of Biscay | 1987 | 40 | Ifremer |
| 28 | Nurse (nourriceries) dans la Vilaine | Nonamvillaine | Bay of Biscay | 1996 | 36 | Ifremer |
| 29 | Nourriceries en Méditerranée | NOURMED | Mediterranean | 2018 | 91 | DOI: 10.17600/18000588 |
| 30 | Nourriceries Baie de Somme | NOURSOM | Channel | 1987-2018 | 1609 | https://sextant.ifremer.fr/record/98ac17c5-8d70-455e-9496-aafb0dd4ae17/ |
| 31 | Nourriceries golfe de Gascogne | Nurse | Bay of Biscay | 1981-2016 | 2428 | Ifremer |
| 32 | Nurse (nourriceries) dans la Vilaine | Nurvil | Bay of Biscay | 2004-2005 | 128 | Ifremer |
| 33 | | Peco/PECOS | Bay of Biscay and Western English | 1976-2006 | 792 | Ifremer |

| | | Channel | | | | | |
|----|--|--------------------------------|---------------|--|-----------|------------------------|----------------|
| 34 | Pélagiques Gascogne | PELGAS | Bay of Biscay | 2000-2018 | 1854 | DOI: 10.17882/59809 | |
| 35 | Nurse (nourriceries) dans les pertuis (breton et antioche) | Pertuis | Bay of Biscay | 1986-1987 | 168 | Ifremer | |
| 36 | Campagnes pour la compréhension des communautés sur les habitats à Haploops | Ploops | Bay of Biscay | 2009-2010 | 48 | Ifremer | |
| 37 | | RESSGASC | Bay of Biscay | 1984-2002 | 2344 | Ifremer | |
| 38 | Nurse (nourriceries) en baie de Vilaine mais en hiver (winter) | RetroB | Bay of Biscay | 2008 | 48 | Ifremer | |
| 39 | Suivi des Effets bioLogiques de la contamination chimique en Méditerranée | SELIMED-1 | Mediterranean | 2016 | 19 | DOI: 10.17600/16011900 | |
| 40 | Répartition de la distribution des soles sur la radiale cote-large de la baie de Vilaine | Sold | Bay of Biscay | 1988-1989 | 354 | Ifremer | |
| 41 | | Typo | Bay of Biscay | 1996-1997 | 180 | Ifremer | |
| 42 | Fisheries dependent data | French fisheries observer data | Obsmer | Greater North Sea, Celtic Sea, Bay of Biscay | 2003-2017 | 82,471 | Ifremer / DPMA |

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