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The establishment of European flounder (*Platichthys flesus*) in Icelandic waters

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FACULTY OF LIFE AND ENVIRONMENTAL SCIENCES

The establishment of European flounder (*Platichthys flesus*) in Icelandic waters

Theresa Henke

Dissertation submitted in partial fulfillment of a
Philosophiae Doctor degree in Biology

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Abstract

Biological invasions are a global phenomenon representing one of the biggest threats to biodiversity. Addressing species introductions, often marked by context dependency, requires the incorporation of multiple perspectives and disciplines to develop adequate management approaches. As humans are involved on multiple levels along the invasion process, this should furthermore encompass the consideration of human dimensions. European flounder (*Platichthys flesus*), a flatfish species native to western Europe, has been documented in Iceland since 1999. In the following years, European flounder rapidly spread and now mainly occurs in estuaries but is often encountered in freshwater habitats. Here it spatially overlaps with native salmonids which represent valuable recreational species, making the recreational angling community in Iceland an important stakeholder group. The overall goal of this thesis was to integrate interdisciplinary approaches to address specific aspects of the establishment of alien European flounder in Iceland, including its geographic origin, distribution, and public perception. Additionally, the thesis aimed at using alien European flounder in Iceland as a case study to address larger-scale questions in the field of invasion science. In this thesis, the most likely origin of European flounder was identified as the Faroe Islands, utilizing microsatellite analysis. Following these results that revealed uncertainty concerning whether the species was introduced due to human activity or arrived naturally, the views of stakeholders and specialists concerning this uncertainty were assessed, indicating that the identification of a species' introduction pathway is considered important but not prioritized over impact assessment and the development of management strategies. Involving the recreational angling community as a representative stakeholder group in the research has shown that European flounder is perceived highly negative but has furthermore highlighted spatial and temporal fluctuations in stakeholder perceptions. Exploring the knowledge of the recreational angling community further showed that utilizing stakeholder knowledge can represent a low-cost additional source in the monitoring of alien species. This thesis furthermore highlighted the dissensus of invasion science specialists regarding the terminology used to address and classify alien species.

Útdráttur

Ágengar tegundir eru ein stærsta ógnin við líffræðilega fjölbreytni á heimsvísu. Ágengar tegundir eru í eðli sínu þverfaglegt viðfangsefni, enda byggir landnám og fótfesta í nýjum heimkynnum á fjölda þátta bæði náttúrulegum og tengdum mannlegri hegðun og samfélagi. Fólk tekur þannig þátt í mögulegri fótfestu ágengra tegunda og mætir einnig afleiðingunum af þeim. Flundra (*Platichthys flesus*), flatfiskategund upprunnin í Vestur-Evrópu, fannst í fyrsta skipti á Íslandi við Ölfusárósa árið 1999. Næstu árin dreifðist flundran hratt út og finnst nú víða við strendur landsins, oft í árósum en líka í ferskvatnsbúsvæðum. Hún nýtir því að hluta til sömu búsvæði og íslenskir laxfiskar, lax, urriði og bleikja, en þessar tegundir gegna mikilvægu vistkerfishlutverki og eru mikilvægar til stangveiði víða um land. Þannig er stangveiðisamfélagið á Íslandi mikilvægur haghópur þegar kemur að flundru. Heildarmarkmið þessarar ritgerðar var að samþætta þverfaglegar nálganir til að fjalla um fjölda þátta sem tengjast landnámi flundrunnar á Íslandi, þar á meðal landfræðilegan uppruna hennar, útbreiðslu og viðhorf almennings. Að auki var ritgerðinni ætlað að nota flundru á Íslandi sem dæmi um hvernig má takast á við stærri spurningar á sviði vistfræði ágengra tegunda. Í þessari ritgerð er sýnt með stuttraðagreiningu á erfðaefni að líklegasti uppruni flundrunnar á Íslandi er Færeyjar. Það er því enn óljóst hvort flundran barst til Ísland náttúrulega eða með kjölfestuvatni. Þessi óvissa skiptir máli fyrir fræðilegar skilgreiningar á flundru sem ágengri tegund og voru sjónarmið bæði hagsmunaaðila og sérfræðinga til þessarar óvissu metin með spurningakönnun. Niðurstöðurnar sýndu að greining á því hvernig flundran nam land er talin mikilvæg af báðum hópum en ekki forgangsraðað fram yfir rannsóknir á áhrifum og þróun stjórnunaráætlana. Frekari greining á stangveiðisamfélaginu sem lykilhóp hagaðila sýndi mjög neikvætt viðhorf til flundru en ennfremur staðbundnar og tímabundnar sveiflur í viðhorfum. Greining á gögnum um staðsetningu flundrunnar úr hefðbundum leiðöngrum, rannsóknum og gögnum sem berast beint frá hagaðilum að þekking hagsmunaaðila getur verið ódýr en áhrifarík leið til að bæta við vöktun framandi tegunda. Þessi ritgerð varpaði enn fremur ljósi á misræmi á milli sérfræðinga í vistfræði ágengra tegunda þegar kemur að hugtakanotkun til að fjalla um og flokka framandi tegundir.

"You teach me, I forget,

You show me, I remember,

You involve me, I understand"

- E. O. Wilson (1929-2021)

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List of Publications

This thesis is based on the following four papers that are currently available either as publication or manuscript:

Paper I: Henke T., Pálsson S., Hemmer-Hanson J., Thorlacius M., Ólafsdóttir G. Á. (2024) The tale of the founder flounder - Assessing the origin of an alien fish in Icelandic waters. Hydrobiologia (In review)

Paper II: Henke T., Novoa A., Bárðarson H., Ólafsdóttir G. Á. (2024) Let‘s talk aliens – Stakeholder perceptions of an alien species differ in time and space. Neobiota 93: 117 – 141

Paper III: Henke T., Bárðarson H., Thorlacius M., Ólafsdóttir G. Á. (2024) Have you seen this fish? Important contribution of stakeholder observations in documenting the distribution and spread of an alien fish species in Iceland. Neobiota (accepted)

Paper IV: Henke T., and Ólafsdóttir G. Á. (2024) Floundering in-between definitions – Expert and stakeholder views on addressing alien species with uncertain introduction pathway. Manuscript

During the course of this PhD, the following papers were published to which I contributed:

1. Ólafsdóttir G. Á., Henke T., Chambers C. P., Ólafsdóttir S. H. (2024) Gaps in legislation and communication identified as stakeholders reflect on 30x30 policy in Icelandic waters. Marine Policy 170: 106422

2. Ólafsdóttir G.Á., Turnbull S., Jónsdóttir I., Nickel A., Karlsson H., Henke T., Nielsen E.E., Pálsson S. (2023) Genetic assignment predicts depth of benthic settlement for 0-group Atlantic cod. PLoS ONE 18(10): e0292495

3. Chambers C., Henke T., Barr B., Cook D., Costa Pierce B., Einarsson N., Kaiser B., Knutsson Ö., Kokorsch M., Nazarova N., Sutton T. (2021) Fisheries and aquaculture in the Arctic. In D. Natcher and T. Koivurova (Eds.), Renewable Economies in the Arctic: A State of Knowledge. Sustainable Development Working Group: Arctic Council.

Abbreviations

DAPC – Discriminant Analysis of Principal Components

eDNA – environmental DNA

GAM – Generalized additive model

IBD – Isolation by distance

IPBES – The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services

LEK – Local ecological knowledge

MDS – Multidimensional scaling

MFRI – Marine and Freshwater Research Institute, Iceland

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1 Introduction

1.1 Biological invasions – past, present, future

It is widely accepted that biological invasions are considered one of the main threats to global biodiversity (Caffrey et al. 2014; Bellard et al. 2022; IPBES 2023). But in comparison to other, long-established scientific disciplines, invasion science is a rather young field. Its establishment essentially dates back to 1958 and the publishing of the book ‘The ecology of invasions by animals and plants’ by Charles Elton, which influences the study of biological invasions to this day, over 50 years later (Richardson and Pysek 2008). At its essence, invasion science addresses the mechanisms of species introductions and how these influence the species’ new environment (Richardson and Ricciardi 2013). In the early years, the research focus predominantly laid on investigating the ecological aspects but over time broadened to a more diversified field built upon an interdisciplinary foundation (Richardson et al. 2011; Richardson and Ricciardi 2013; Vaz et al. 2017).

Despite the rather short time span in which biological invasions have been of academic interest, the earliest known records of species introductions date back to around 1500 (Seebens et al. 2017). Alien species have long been linked to global human movement, where especially in the earliest cases the motivation to introduce species into new environments was likely driven by the need for resources (Montgomery et al. 2014). Seebens et al. (2017) compiled a database documenting 45,813 first records based on 16,926 established alien species, 37% of which occurred between 1970 and 2014. In line with the documented increase in the numbers of introduced species post 1970 (Seebens et al. 2017), the number of publications addressing research on biological invasions has shown a strong incline since the 1990s (MacIsaac et al. 2011). It is not expected that the rate of species introductions will slow down, it has rather been projected that until 2050, the number of first introductions will increase by 36% (Seebens et al. 2020).

The continuous increase in the number of species introductions has been attributed to factors such as the growth of global trade, the expansion of global tourism activities as well as a changing climate (Pyšek et al. 2010; Bellard et al. 2016; Hulme 2021). Species are intentionally and/or unintentionally introduced via a multitude of different pathways. Based on the framework proposed by Hulme et al. (2008), introduction pathways can be classified as ‘Release’ (i.e. intentional introduction), ‘Escape’ (i.e. intentional introduction as a commodity but escapes unintentionally), ‘Containment’ (i.e. unintentional introduction with a specific commodity), ‘Stowaway’ (i.e. unintentional introduction attached to or within a transport vector), ‘Corridor’ (i.e. unintentional introduction via human infrastructures linking previously unconnected regions), and ‘Unaided’ (i.e. unintentional introduction through natural dispersal of alien species across political borders).

The ability to make predictions on how the number of introduced species will develop over time, what species are likely to become invasive and how extensive their impacts will be, would greatly benefit the development of management strategies and policies. There have been attempts to make predictions and some generalized concepts have been put forward.

One of the proposed concepts is the Tens rule, which proposes that of all the species that are daily transported between environments, 10% will be introduced into the recipient environment, of which 10% will be able to establish a population and finally 10% of the established species will become invasive (Williamson and Brown 1986). However, the empirical support for this concept has declined over the years (Jeschke et al. 2012; Pyšek et al. 2017). In most cases, predictions are hindered by the inherent complexity of biological invasions marked by context dependency (Catford et al. 2022) and uncertainty (Liu et al. 2011; Latombe et al. 2019).

This complexity is also evident in the terminology that has been developed in the field of invasion science over the past decades. There is a large variety in the terminology as well as the underlying definitions and understanding of the established terms (Russell and Blackburn 2017; Kapitza et al. 2019; Latombe et al. 2019; Shackleton et al. 2022). In the recently published IPBES report, the most holistic assessment to date, the four terms ‘native species’, ‘alien species’, ‘established alien species’, and ‘Invasive alien species’ are listed as the key terminology (Table 1-1). However, over the past decades, multiple terms have emerged that address and/or incorporate specific aspects beyond these key terms, such as the terms ‘neonative’, addressing species introductions that are attributed to human induced environmental changes (Essl et al. 2019), as well as the term ‘cryptogenic’ referring to species where native status and origin remain unclear (Carlton 1996). Previous studies have identified up to 59 different terms currently in use in the invasion science literature (Colautti and MacIsaac 2004; Falk-Petersen et al. 2006; Lockwood et al. 2013; Soto et al. 2024). It has been indicated that differences in the use of terminology depend on factors such as the addressed taxon (e.g. plants vs. mammals), where scientists and/or the study are located (e.g. North America vs. Europe), and the work background (e.g. academics vs. practitioners) (Humair et al. 2014; Shackleton et al. 2022). It has also been recognized that such dissensus in the terminology can be problematic for the reporting of alien species (Castro et al. 2023), as well as for the development of management strategies (Richardson et al. 2011; Essl et al. 2019). However, while several studies have attempted to unify the terminology (e.g. (Colautti and MacIsaac 2004; Blackburn et al. 2011; Soto et al. 2024), no widely implemented solution has been found.

Table 1-1 Key terminology and according definitions provided by IPBES (2023)

Term	*Definition*
Native species	A species (animal, plant or other organism) within its natural range, including shifting its range, without human involvement
Alien species	A species whose presence in a region is attributable to human activities that have enabled it to overcome the barriers that define its natural range
Established alien species	A subset of alien species that have produced a viable, self-sustaining population and may have spread
Invasive alien species	A subset of established alien species that spread and have a negative impact on biodiversity, local ecosystems and species. Many invasive alien species also have impacts on nature’s contributions to people (embodying different concepts, such as ecosystem goods and services and nature’s gifts) and good quality of life

1.2 The multitude of impacts

Species introductions can cause a wide array of severe impacts to recipient ecosystems, ranging from environmental to socioeconomic levels (Simberloff et al. 2013; Hawkins et al. 2015; Bacher et al. 2017; Diagne et al. 2021; IPBES 2023). Ecological impacts are often dependent on the trophic level of the introduced species (Thomsen et al. 2014), but often manifest as interspecific interactions such as resource competition and/or predation (Gallardo et al. 2015). A relevant example of this is the Nile perch (*Lates niloticus*, Linnaeus 1758), a fish species that has contributed to the collapse of large numbers of fish species via competition and predation upon its introduction to Lake Victoria (Taabu-Munyaho et al. 2016). Additionally, native fauna and flora can be impacted on a genetic level as the presence of an alien species can for instance induce interspecific hybridization and subsequent introgression or introduce maladaptive genes (Kelly et al. 2010; Kovach et al. 2015). Many species can also induce socioeconomic impacts, for example causing the collapse of entire fisheries such as documented for the invasion of the comb jelly (*Mnemiopsis leydii*, Agassiz 1865) in the Black Sea that resulted in the temporary collapse of the commercial anchovy fisheries (Kideys 1994; Knowler 2005). Generally, the costs associated with biological invasions are estimated to be substantial (Diagne et al. 2021). Negative impacts induced by biological invasions also extend to humans as they can cause for example the loss of income or reduce the availability of natural resources (Shackleton et al. 2019a) and even affect human health (Mazza et al. 2013). While research over the past decades has gathered an extensive amount of information on the negative impacts of biological invasions, it has also revealed that these are heavily context dependent, making it difficult to predict the outcome and severity of a species introduction (Ricciardi et al. 2013; Kumschick et al. 2014). While most scientific attention is paid to the negative impacts related to biological invasions, it also needs to be noted that there are cases in which benefits have been documented, for example as the introduced species provide the prospect of commercial utilization or aesthetic values (Shackleton et al. 2019a).

1.3 Managing biological invasions

Considering the severe impacts that biological invasions can cause, developing suitable management approaches is crucial. Preventing the arrival of alien species is the most desirable management achievement (Browne et al. 2009; Pyšek and Richardson 2010; Schwindt et al. 2023). However, preventative measures require the identification of already existing and potential future pathways as well as thorough management of these pathways and related vectors (Carlton and Ruiz 2005; Pyšek and Richardson 2010). Currently, such proactive management remains largely underdeveloped (Cuthbert et al. 2022). Where prevention fails and alien species are introduced to the environment, national strategies should be in place that entail early detection measures that are essential for rapid responses (Pyšek and Richardson 2010; Simberloff et al. 2013; Genovesi et al. 2014; Schwindt et al. 2023). Due to the often low abundances in which species arrive, early detection remains challenging but is increasingly improved by integrating various approaches such as citizen science or continuously advancing tools like eDNA (Martinez et al. 2019; Larson et al. 2020). Given a timely response, it is possible for an introduced species to be eradicated before it establishes and spreads within the new environment (Pyšek and Richardson 2010). The case of *Caulerpa taxifolia* ((M.Vahl) C.Agardh, 1817), a seaweed species listed among the 100 worst invasive species (Lowe et al. 2000), is a prime example of the importance of early detection. In 1984, *Caulerpa taxifolia* was accidentally introduced to the Mediterranean Sea which led to a far-reaching invasion along the coastlines of multiple countries outcompeting native seaweed species (Boudouresque et al. 1995; Meinesz et al. 2001). In the summer of 2000, a patch of the same species was detected near San Diego, California but due to early detection, this species introduction was addressed within less than three weeks and resulted in successful eradication before the species could spread (Anderson 2005). However, once a species has managed to establish a population and further spread has occurred, the chances of successful eradication quickly diminish (Simberloff 2014; IPBES 2023). When eradication is not possible, management becomes a question of containment and mitigation (IPBES 2023) but there is not one blueprint of management approaches that suits all species, but management strategies should rather be developed on a case-by-case basis (Simberloff 2014).

One of the crucial components to develop suitable management approaches is the availability of timely occurrence data of alien species (Groom et al. 2015; Cardoso et al. 2017; Latombe et al. 2017). It has been recommended that countries provide up-to date, publicly available occurrence records of alien species at least every five years (Latombe et al. 2017). Currently, comprehensive alien species monitoring, and management remains at an underdeveloped state in many countries (Latombe et al. 2017; Schwindt et al. 2023). In many cases, limited addressing of alien species is linked to the unavailability of adequate resources and funding for the relevant agencies and institutions (Piria et al. 2017; Robinson et al. 2020). Given the limited funds available, decisions need to be made on where to dedicate these funds to and what steps and/or species to prioritize (Kumschick et al. 2012; Robertson et al. 2021). Several studies have proposed guidelines to guide the decision making on prioritizing (Kumschick et al. 2012; McGeoch et al. 2015; Giakoumi et al. 2019)

1.4 Human dimensions

Humans represent a fundamental component linked to biological invasions. From causing the intentional and unintentional introduction of species and experiencing the induced impacts, humans withhold the ability and responsibility to manage current invasions and prevent future ones (Wilson et al. 2016; Pysek et al. 2020). Though the early focus of invasion science predominantly laid on studying the ecological aspects, the importance of incorporating the human dimensions in the study of biological invasions is increasingly recognized (Vaz et al. 2017; Shackleton et al. 2019a, Garcia-Diaz et al. 2022). In order to understand the extent of impacts experienced by humans, it is crucial to explore the general perceptions of representative stakeholder groups towards an introduced species while also considering how these views might vary between parties (Garcia-Llorente et al. 2008; Jefferson et al. 2015; Shackleton et al. 2019b). Understanding stakeholder perceptions can help in the process of determining where resources are best spent addressing emerging an alien species (Shackleton et al. 2019b). It can furthermore help identify opposing views regarding the implementation of management measures and mitigate arising issues in time (Novoa et al. 2018). Tension across different parties have been documented for various alien species such as Asian carp in Minnesota, US (Kokotovich and Andow 2017) or invasive cacti in South Africa (Novoa et al. 2016).

Research has shown that perceptions towards alien species are shaped by various factors such as the species' characteristics, potential benefits or economic threats due to the species' presence as well as personal experiences and emotional connection with the invaded ecosystem (Fisher and van der Wal 2007; Kueffer 2013; Verbrugge et al. 2013; Shackleton et al. 2019b). It has also been pointed out that stakeholder's awareness about biological invasions can influence their perceptions and in turn their support for management (Garcia-Llorente et al. 2008; Verbrugge et al. 2013; Courchamp et al. 2017; Novoa et al. 2017). Perceptions are not static and are known to change over time (Shackleton et al. 2019b) and this change can be actively shaped, especially via increasing public awareness. To increase the awareness among the public, the scientific community needs to conduct active outreach and effectively communicate the issue to various stakeholder groups in ways that go beyond the traditional approach of top-down provision of information but rather establishes genuine dialogue between parties (Nisbet and Scheufele 2009; Courchamp et al. 2017).

1.5 Novel tools

In accordance with the field's development towards interdisciplinarity (Vaz et al. 2017), various novel tools and data sources have been integrated in invasion science over the last decades often to counteract limited resource availability and/or the inherent biases of traditional approaches in the detection and monitoring of alien species (Hargrove et al. 2015; Jarić et al. 2020b; Robinson et al. 2020). Over the recent years, citizens have been increasingly involved in the collection of geospatial data in many disciplines (See et al. 2016). In invasion science stakeholders have contributed to monitoring activities of alien species across various taxa such as aquatic species (Ferreira-Rodríguez et al. 2020; Herrero et al. 2023) and plants (Marchante et al. 2016; César de Sá et al. 2019; Gervazoni et al. 2023).

Since the early 2000s, citizen science has established as a popular concept, where members of the public are involved in research processes and contribute for instance to data collection and processing (Bonney et al. 2009; Bonney et al. 2016). It has been shown that citizen science projects often result in increased public awareness as well as a better understanding among the public about scientific processes and knowledge (Bonney et al. 2016). Citizen science has also become popular in invasion science. Thomas et al. (2017) for example has shown that following training on the aspects of early detection of alien species, voluntary reporting by employees working on Barrow Island, Western Australia, has been linked to nearly all newly detected alien species. An additional source of data can be found in the experiential knowledge of stakeholders and can benefit the reconstructing of alien's species invasion history and spread (Latombe et al. 2017). Ferreira-Rodríguez et al. (2020), for example, have combined stakeholder knowledge and expert opinions with available distribution data to further assess the spread of the alien Asian clam *Corbicula* sp. in the Lower Danube region. In addition to citizen science approaches, the experiential knowledge of stakeholders, i.e. local ecological knowledge (LEK) that has developed over time due to interaction with local ecosystems and the utilization of local natural resources (Olsson and Folke 2001; Löki et al. 2023). Recreational anglers are often more likely to encounter rare or new species as they spend considerable time in their local environment and have successfully been involved in research activities (Silvano and Begossi 2012; Giovos et al. 2019; Löki et al. 2023).

Traditional tools that have been utilized to document stakeholder perceptions as well as their knowledge on defined topics include surveys and interviews. In invasion science, these approaches have been common in exploring the views of specific stakeholder groups (Garcia-Llorente et al. 2008; Trenouth and Campbell 2013) as well as the public's views towards specific alien species (Verbrugge et al. 2013; Novoa et al. 2017; Luna et al. 2019). While many studies have benefited from traditional approaches, they still entail certain disadvantages such as requiring significant resources, an often limited geographic reach and potential biases, which inspired the development of novel tools to counteracts some of these limitations (Newing 2011; Scharkow and Vogelgesang 2011; Di Minin et al. 2015). The recently established fields of iEcology (Jarić et al. 2020a) and conservation culturomics (Ladle et al. 2016) utilize novel tools to access digital data sources from platforms such as news media, social media, and digital encyclopedias (Correia et al. 2021). Approaches under the umbrella of invasion culturomics (Jarić et al. 2021) have been used for example to improve the monitoring of plant pest species (Tateosian et al. 2023) and to explore recreational anglers' and spear fishermen's perceptions following a changing distribution of a marine invasive species (Sbragaglia et al. 2022). As promising as these novel tools are to advance research in invasion science and other disciplines, they are not without limitations as certain challenges and biases remain. Among the things that need to be considered when applying these approaches are the potential for misinterpretation (Ficetola 2013); the ethical use of potentially sensitive information (Correia et al. 2021), spatiotemporal biases (Jarić et al. 2020b; Jarić et al. 2021) and limitations of using non-English, non-major languages (Funk and Rusowsky 2014; Ladle et al. 2016). Studies are needed to address these limitations as well as to validate the data accuracy (Jarić et al. 2020b; Jarić et al. 2021).

1.6 Aquatic biological invasions in Iceland

Ragnarsdóttir and Metúsalemsson (2020) listed 36 alien species associated with streams, lakes and coastal areas of Iceland, including five fish species. While the report highlights that for many alien species documented in Iceland data on occurrence and impacts is limited, several species have been addressed over the last decade. Among these species are the Atlantic rock crab (*Cancer irroratus*, Say, 1817), introduced via ballast water from the east coast of North America and first observed in Iceland in 2006 (Gíslason et al. 2014; Gíslason et al. 2017; Gíslason et al. 2021), pink salmon (*Oncorhynchus gorbuscha*, Walbaum, 1792) which has been increasingly abundant in Iceland among other countries since 2017 stemming from a subsequent spread from Norway where this species is invasive (Lennox et al. 2023), and alien tunicate species such as *Ciona intestinalis* (Linnaeus, 1767) that are increasingly documented in Icelandic waters (Micael et al. 2020; Ramos-Esplá et al. 2020; Micael et al. 2022). Recently, two additional marine alien species have been documented in Icelandic waters, namely the razor clam *Ensis terranovensis* (Vierna and Martínez-Lage, 2012) (Gunnarsson et al. 2023) and the mollusc *Melanochlamys diomedea* (Bergh, 1894) (de Montety et al. 2024).

1.7 European flounder

European flounder (*Platichthys flesus*, Linneaus 1758) is a flatfish species of the Pleuronectidae family and is native to the coastal regions of western Europe (Summers 1979;

Wilson and Veneranta 2019), though declines in the species population have been reported from the northern Baltic Sea (Jokinen et al. 2015) and from central coastal areas of Portugal southwards (Cabral et al. 2007). The species is highly abundant in estuarine waters, especially utilizing these habitats as feeding and nursery grounds (Summers 1979; Freitas et al. 2009; Souza et al. 2013). During the winter months, European flounder migrates into fully marine habitats for spawning (Summers 1979), though Morais et al. (2011) have suggested that spawning might also take place in estuarine habitats. European flounder is considered to be the only catadromous flatfish species in Europe (Summers 1979), but the species' plasticity in utilizing marine, estuarine and freshwater habitats has been highlighted (Daverat et al. 2012; Le Pichon et al. 2014; Dias et al. 2020). European flounder has repeatedly been reported in the Great Lakes in North America where it was introduced via ballast water (Cudmore-Vokey and Crossman 2000; Ricciardi and MacIsaac 2000). However, no established population and subsequent spread have been documented (Cudmore-Vokey and Crossman 2000; Ricciardi and MacIsaac 2000).

In 1999, European flounder was first officially documented in Icelandic waters after a specimen was caught at the mouth of the river Ölfusá in southwest Iceland and submitted to the Marine and Freshwater Research Institute (MFRI) where it was identified (Jónsson et al. 2001). In 2000, further specimens were reported near the town Höfn, located in the southeast corner of Iceland (Astthorsson and Palsson 2006). From these early locations on, a rapid spread of European flounder was documented along the southern and western coasts, eventually reaching the North (Astthorsson and Palsson 2006; Gunnarsson et al. 2015) as well as a counter clockwise spread at slower speed along the eastern coast (NA 2017). The population has spread to most parts of the country (Kristinsson 2011; Ragnarsdóttir and Metúsalemsson 2020). Two opposing hypotheses have been raised regarding European flounder's introduction pathway, suggesting that it was either introduced via ballast water from western European coasts (Thorarinsdóttir et al. 2014; Gunnarsson et al. 2015) or arrived from the Faroe Islands (Jónsson et al. 2001; Thorarinsdóttir et al. 2014), where the species is native (Joensen and Tåning 1970). Currently, European flounder in Iceland is classified as potential invasive (Gunnarsson et al. 2015) but no official monitoring activities are conducted.

So far, limited scientific attention has been paid to identifying potential impacts of European flounder in Iceland. A spatial overlap with native European plaice (*Pleuronectes platessa*, Linneaus 1758), a closely related flatfish species, has been documented particularly for nursery grounds (Henke et al. 2020). Hybridization between these two species throughout their mutual native range is well documented, occurring both naturally as well as artificially induced, and can frequently be observed especially in areas of the Baltic Sea such as along its western boundary (He et al. 2020) and the Bornholm basin (Kijewska et al. 2009). European flounder X European plaice hybrids are often difficult to morphologically identify and are hypothesized to potentially lead to misidentification and errors in stock assessments (Kijewska et al. 2009; He et al. 2020). In Iceland, hybridisation between European flounder and European plaice and the impacts thereof has not previously been addressed. Ecological impacts of European flounder have been addressed in some small-scale studies suggesting likely competition with, as well as direct predation on native European plaice (Henke et al. 2020) and native salmonids (O´Farrell 2012; Hlinason 2013).

Due to the high spatial overlap with the three native salmonid species Atlantic salmon (*Salmo salar*, Linnaeus 1758), brown trout (*Salmo trutta*, Linnaeus, 1758) and Arctic char (*Salvelinus alpinus*, Linnaeus, 1758) (O´Farrell 2012; Hlinason 2013), the recreational angling community represents an important stakeholder group as all three species are highly sought-after recreational species. With 31.5% of the population practicing recreational angling, it is a very popular activity in Iceland (Toivonen et al. 2000). In 2018, an estimated 4.9 billion krona (37 million USD) was spent on Atlantic salmon and brown trout angling permits in Iceland (Institute of Economic Studies 2018). Several regulations on recreational angling of the three salmonid species have been implemented, including the requirement of logging catches of Atlantic salmon, brown trout, and Arctic char in logbooks (Act 61/2006).

Figure 1-1 Juvenile European flounder and European plaice. The picture of juveniles of European flounder (bottom) and European plaice (top) shows the morphological similarity between species. The species can be morphologically differentiated based on the spiny scales present at the base of the dorsal and anal fins for European flounder and the bony structures located behind the eyes for European plaice.

1.8 Aims of the thesis

The objectives of this thesis can be divided into aims specifically addressing European flounder in Icelandic waters and aims addressing larger-scale questions in invasion science. Concerning European flounder ecology and management in Icelandic waters, this thesis addresses four main aims. Firstly, to identify the most likely source population of European flounder found in Iceland (**Paper I**). Secondly, to explore the perceptions of an important stakeholder group, the recreational angling community in Iceland, towards European flounder as well as the public interest in this species (**Paper II**). Thirdly, to combine and compare different sources of European flounder location data to study estimates of the species' spread in Iceland (**Paper III**). As well as to investigate the views of specialists and stakeholders in regard to the uncertainty surrounding the European flounder's introduction pathway (**Paper IV**).

Using European flounder in Iceland as a case study for a broader aim of invasion science, we addressed four overarching goals. Firstly, to explore how stakeholder perceptions towards alien species change in time and space (i.e. invaded vs native regions) (**Paper II**). Secondly, to evaluate how data collected using novel tools of the fields conservation culturomics and iEcology compare to data collected by directly interacting with stakeholders (**Paper II, III**). Thirdly, to investigate the value of incorporating stakeholder-knowledge-based distribution data in the monitoring of alien species (**Paper III**). And finally, to explore specialist's views on addressing and classifying species with uncertain introduction pathways (**Paper IV**).

2 Methods

2.1 Microsatellite analysis

Between 2020 and 2021 we collected European flounder samples from 15 sites around Iceland using a beach seine (1.5 x 10 m, mesh size = 6 mm) (Figure 2-1). Samples collected in the summer of 2017 were used to complement the catches at two sites, Önundarfjörður and Borgarfjörður. An additional site, Hofsá in northeast Iceland was sampled in 2020 but no European flounder was caught. The sampling design covered the entire country with a minimum of three sites per quarter of Iceland. Additionally, we collected samples of European plaice from 15 sites around Iceland during the annual flatfish survey conducted by the MFRI in August 2021, during which we also collected 6 additional European flounder samples from the southwest of Iceland (Figure 2-1).

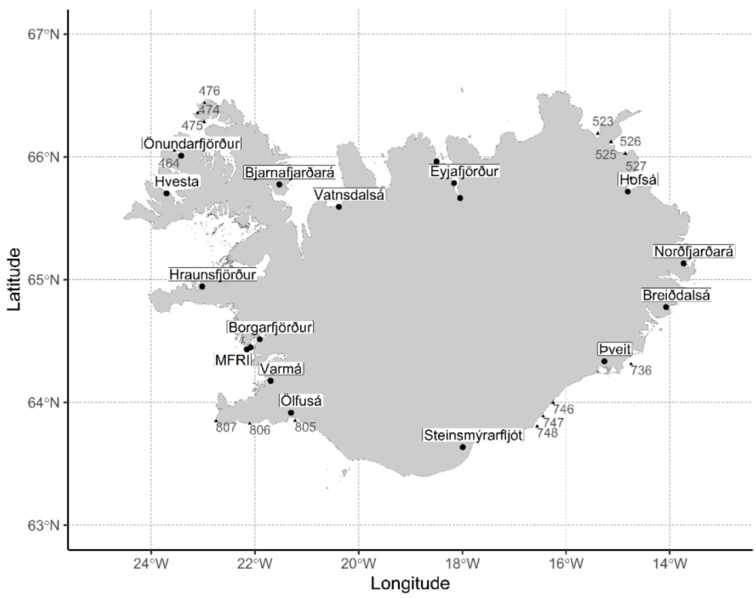

Figure 2-1 Sampling locations in Iceland. The map consists of sampling sites for European flounder marked in black site names as well as sampling sites for European plaice marked in grey numbers representing trawling stations of the MFRI flatfish survey.

Reference data stemming from European flounder populations throughout the species' native range (Hemmer-Hansen et al. 2007) as well as previously unpublished data from samples collected in Iceland in 2007 were contrasted against the recent samples collected in Iceland to identify the likely geographic origin of European flounder found in Iceland.

2.2 Survey administration

In total, four online surveys were developed and administered. In October 2019, a survey including 17 questions was opened, targeting the recreational angling community in Iceland to determine their perceptions towards European flounder (**Paper II**) and to collect information on their experience with and knowledge of European flounder (i.e. locations of occurrence) (**Paper III**). A similar survey was administered to recreational angling communities throughout the European flounder's native range in May 2021, including 15 questions, to contrast views between invaded and native regions (**Paper II**). In March 2023, a follow-up survey was administered to the recreational angling community in Iceland that included 9 questions and aimed to document temporal changes in their perception towards European flounder (**Paper II**) as well as their views and priorities in addressing European flounder and biological invasions in Iceland generally (**Paper IV)**. The fourth survey targeted specialists working in the field of invasion science and a broader group of scientists working in Iceland. This survey included 8 questioned and was opened for participation when it was advertised at 12th International Conference on Biological Invasions (Neobiota) held in Tartu, Estonia in September 2022 (https://www.elus.ee/index.php/en/neobiota-tartu-2022/). The goal of this survey was to elucidate specialist's views on terminology and management approaches in the case of an alien species with uncertain introduction pathway (**Paper IV**). Each survey informed participants about the background and intent of the survey and research project. All surveys were widely advertised via diverse (social) media platforms, especially Facebook and Twitter (i.e. 'X'). This was complemented by opportunistic advertising in newspapers and a podcast (**Paper II, III, IV**).

2.3 Additional data sources

In a systematic review of an Icelandic digital library (www.timarit.is) using the keywords 'flounder', 'flundra', and 'ósalura', we extracted all newspaper articles published between 1999 and 2022 that either focused on or mentioned European flounder in the context of Iceland. In a similar approach we manually identified and extracted all conversations posted in a Facebook group popular among the Icelandic recreational angling community between 2013 and 2022 that focused on or mentioned European flounder. We collected quantitative data on articles and conversations to explore temporal changes in the interest in this species as well as the textual data to identify in which context European flounder is mentioned (**Paper II**). From the Facebook conversations we furthermore extracted locations that were mentioned in the context of European flounder (**Paper III**). To approximate the public interest in European flounder in Iceland, we extracted data on Google searches for the keywords 'flounder' and 'flundra' between 2004 and 2023 based on Google Trends using the gtrendsR package (Massicotte and Eddelbuettel 2022) as well as information on the monthly page visits of the species' Icelandic Wikipedia page between July 2015 and February 2023 using the pageviews package (Keyes and Lewis 2020). We investigated the public's interest and its temporal fluctuations as well as the context in which European flounder was mentioned using conservation culturomics tools (Ladle et al. 2016) (**Paper II**), while extracting geographic locations of European flounder mentioned on social media (i.e. Facebook group) falls under the umbrella of iEcology (Jarić et al. 2020a) (**Paper III**).

In order to compare European flounder locations named by recreational anglers in the first Icelandic survey and extracted from Facebook conversations to previously collected distribution data we gathered all data available in the databases of the MFRI (**Paper III**). This data provided by MFRI stemmed from four different databases. The marine databases provided locations documented during the major annual marine surveys conducted by the institute for stock measurement purposes as well as occasional research projects while the freshwater database provided locations of European flounder caught during routine sampling across recreational rivers assessing salmonid stocks. Freshwater locations were further complemented by catch information submitted by recreational anglers alongside the salmonid catches they are by law required to document in logbooks. The fourth database comprised of catch locations voluntarily submitted by stakeholders, mainly fishermen.

2.4 Statistical analysis

Data preparation and statistical analysis was carried out using the software R (version 4.3.2, (R Development Core Team 2023) (**Paper I – IV**). We additionally used the software GenAleX (version 6.503; (Peakall and Smouse 2006; Peakall and Smouse 2012) to explore and transform the raw microsatellite data and the software STRUCTURE (version 2.3.4, (Pritchard et al. 2000) to identify patterns in admixture proportions between samples of European flounder and European plaice (**Paper I**). In paper I, we calculated descriptive statistics and genetic distance using the R packages hierfstat (Goudet and Jombart 2022) and pegas (Paradis 2010). Genetic distances between samples and potential clusters were explored using a multidimensional scale (MDS) plot as well as a discriminant analysis of Principal Components (DAPC).To explore potential population structure in European flounder within Iceland, we conducted an isolation by distance analysis, plotting the genetic distance between samples (F_{ST} /(1- F_{ST}) according to Rousset (1997)) against the approximate geographic distance (in km; manually approximated with online measuring tool and measured within the known distribution of European flounder along the Icelandic coasts) and tested its significance using the Mantel test embedded in the Vegan package (Oksanen et al. 2022). Furthermore, linear regressions were calculated to explore potential correlation between the average allelic richness in Icelandic samples and the geographic distance to the source population in the Faroe Islands, as well as the expected heterozygosity and the geographic distance.

Likert questions embedded in the online surveys (**Paper II & IV**) were analyzed using the likert package (Bryer and Speerschneider 2016) and polarization scores for each likert item were calculated using the agrmt package (Ruedin 2021). To assess significant differences in the answers between groups, we applied the Mann-Whitney U test where we compared between two different groups (**Paper II & IV**), and the Wilcoxon signed rank test when temporal differences in the answers of the same group were tested (**Paper II**). To explore potential correlation between the likert items and selected survey variables, we employed the Kendall Tau Rank correlation (**Paper II**).

In **paper II**, we analyzed textual data extracted from newspaper articles and Facebook conversations applying topic and word frequency analysis. Prior to the analysis we manually preprocessed the data in several steps that included the removal of stop words, numbers and punctuation, the stemming of words (Sumathy and Chidambaram 2013) as well as the manual translation of Icelandic terms into English. Topic analysis, which is based on Latent dirichlet allocation and the two principles that documents consist of a mix of topics and that topics consist of a mix of words, was conducted using topicmodels package (Grün and Hornik 2011, 2023). The analysis returns a pre-defined number of topics, the most frequent words assigned per topic as well as the composition of topics for each analyzed document.

For the European flounder distribution data (**Paper III**), we first estimated significant differences in the geographical representation between the six different data sources (i.e.

marine surveys, freshwater surveys, logbooks, online surveys and iEcology) applying a pairwise Dunn test with Bonferroni correction utilizing the dunn.test package (Dinno 2024). We then fitted generalized additive models (GAM) using the mgcv package to the number of unique sites for each source with available time stamps in order to compare the annual detection of unique sites, as well as to the latitude of documented European flounder locations to examine how well the sources documented the temporal spread. Both GAMs included the smooth term year with source as an interaction term to account for differences between the four sources.

We classified the answers provided by participants in the specialist survey, when asked what terminology they seem most suitable to apply to the case of European flounder under the remaining uncertainty, were classified into six categories based on a developed classification scheme (Figure 2-2) to indicate the level of confidence in which the answer was provided. The classifications were visualized in a Sankey diagram using the plotly package (Sievert 2020) (**Paper IV**). The provided terminology was subsequently analyzed for the frequency per term.

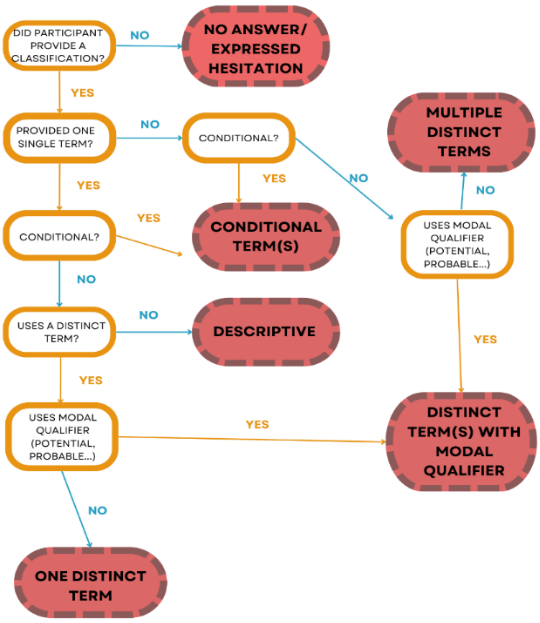

Figure 2-2 Classification scheme for survey answers. This scheme was used for categorizing the confidence in which participants provided a response when asked what terminology they deem most appropriate to the case of European flounder in Iceland.

3 Main results and discussion

3.1 The origin of Icelandic European flounder (Paper I)

Since the first documentation of alien European flounder in Icelandic waters, two opposing hypotheses on the species' origin and introduction pathway have been raised, one stating that it arrived from the Faroe Islands potentially via natural dispersal (Jónsson et al. 2001; Thorarinsdóttir et al. 2014) and one suggesting the ballast water driven introduction from the coasts of central Europe (Thorarinsdóttir et al. 2014; Gunnarsson et al. 2015). Comparing samples collected around Iceland to reference data (Hemmer-Hansen et al. 2007) using microsatellite analysis, has revealed a closer genetic distance between Icelandic and Faroese populations than between Icelandic and other European populations (i.e. Irish Sea, Trondheim, Thyborøn) (Figure 3-1). This suggest that the most likely source population of European flounder found in Iceland is located in the Faroe Islands, supporting the hypothesis raised by Jónsson et al. (2001) and Thorarinsdóttir et al. (2014). However, the current results don´t allow drawing firm conclusions on the introduction pathway, specifically on whether European flounder arrived naturally in Iceland or was introduced due to anthropogenic activities. Investigations on population structure within Iceland only revealed weak indications of isolation by distance and only allow for limited conclusions to be drawn on the invasion dynamics of European flounder in Iceland. Therefore, further studies should be conducted using more extensive genomic analysis that could help identify the point of introduction and how European flounder spread further in subsequent years.

Furthermore, we identified nine European flounder x European plaice hybrids among the samples, comprised of seven individuals morphologically classified as European flounder and two individuals morphologically classified as European plaice, and signs of introgression between the species. Hybridization between European flounder and European plaice is frequently observed throughout their mutual native range and has been suggested to potentially lead to errors in stock assessments due to misidentifications of pure specimens (Kijewska et al. 2009; He et al. 2020). Implications of the observed hybridization and introgression can currently not be estimated and would require additional investigations.

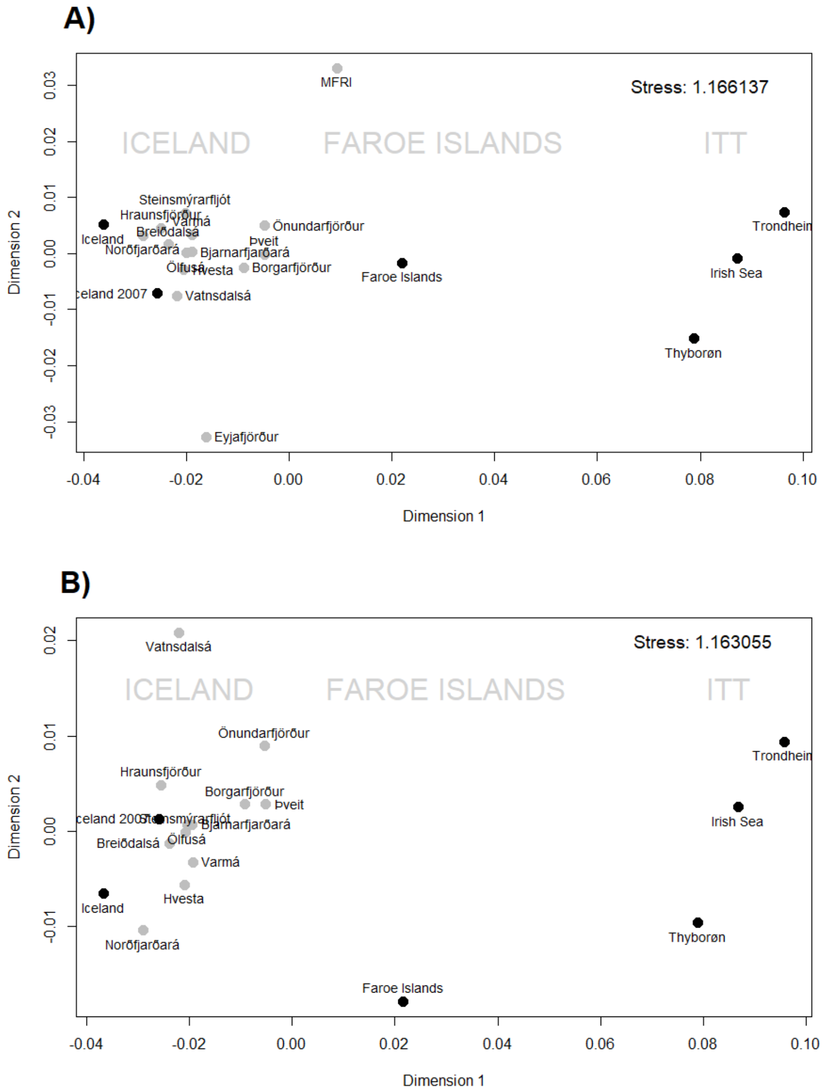

Figure 3-1 MDS plots. A) MDS plot presenting the genetic distance between Icelandic, Faroese and ITT populations. B) In order to display the genetic distances between Icelandic populations in more detail, we excluded the two clear outliers (MFRI and Eyjafjörður) from A. For both plots the stress value is displayed within the graphs. Plotting dimension 3 did not provide additional insights and was therefore not included.

3.2 Stakeholder perceptions of alien species in time and space (Paper II)

The results of the surveys among the recreational angling community in Iceland showed that European flounder is perceived highly negative and considered to be a pest (Figure 3-2 A). By contrasting the views in Iceland to the positive views of recreational angling communities throughout the European flounder's native range (Figure 3-2 C), we have shown that these negative perceptions are likely not driven by the species' characteristics itself. In regions where European flounder is native, it is considered a popular target in recreational angling, especially for anglers with limited experience as it is readily available in accessible areas (Skerritt 2010). It is more likely that recreational anglers in Iceland perceive a negative impact in the presence of European flounder in Icelandic waters, as it co-occurs with native salmonid species that are highly sought after species in recreational angling activities and of high monetary value (Institute of Economic Studies 2018). By repeating the initial survey ~3.5 years later, we have further shown that stakeholder perceptions can fluctuate over time. While European flounder is still perceived negatively ~3.5 years later, the follow-up survey in 2023 showed a significant change towards less negative views (Figure 3-2 B). Previous research has shown that among the drivers shaping stakeholder's perceptions towards an alien species are prolonged exposure, awareness and knowledge (Garcia-Llorente et al. 2008; Sharp et al. 2016; Courchamp et al. 2017). The documented change in the perceptions among recreational anglers in Iceland could have potentially been driven by increased exposure to the topic as it was increasingly covered in on social media as well as multiple other media sources such as newspaper articles (Jónsson 2019; Bjarnason 2020), national TV (Ólafsdóttir 2021), and a podcast interview (Ólafsson and Harðarson 2023).

Furthermore, we used European flounder in Iceland as a case study to assess whether the documented negative perceptions among the recreational angling community in the surveys would be detectable in the communication to the public (i.e. newspaper articles) as well as within the stakeholder group (i.e. Facebook conversations) applying novel, conservation culturomics tools. The results of the topic and word frequency analyses revealed a rather neutral tone in the communication that could not be linked to the negative perceptions previously recorded. The detected mismatch could be linked to working with Icelandic, a non-English, non-major language, which required translation work and limited the availability of text analysis tools, a major challenge that remains when applying these novel approaches (Funk and Rusowsky 2014; Ladle et al. 2016). The scale of the case study in Iceland and the limited amount of data (i.e. newspaper articles, Facebook conversations) produced since the first documentation of European flounder in Iceland, could have further contributed to the mismatch. We therefore suggest, that while valuable knowledge can be gained, novel conservation culturomics tools should be applied complementary to traditional tools in the case of small-scale study systems.

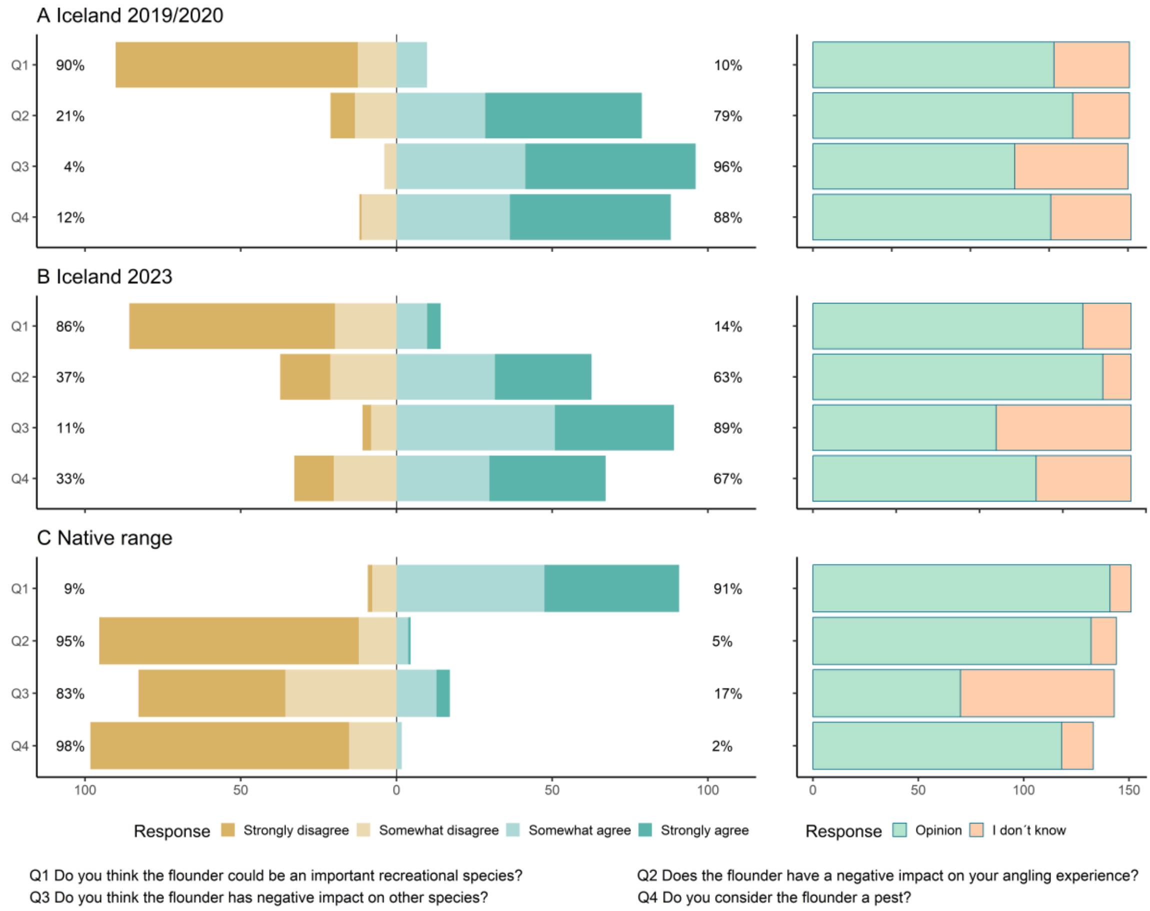

Figure 3-2 Perceptions of recreational angling communities towards European flounder. Survey participants' perception based on their responses to the surveys. The likert graphs show the responses of participants to rating their agreement (Strongly disagree – Strongly agree) to the questions. Barplots on the right plot indicate the number of participants that expressed an opinion on the question and the number of participants that answered, 'I don't know'. The results are given for the surveys conducted in Iceland in 2019/2020 (A), in Iceland 2023 (B), and in European flounder's native range (C).

3.3 Incorporating stakeholder knowledge in the monitoring of alien species (Paper III)

Our results show that stakeholder-based occurrence data, both using tools directly interacting with the target group (i.e. online surveys) and indirectly harnessing available online data (i.e. iEcology tools), represents a valuable tool in the monitoring of alien species when combined with existing aquatic surveys. In the case of European flounder in Iceland, the number of locations provided by the recreational angling community in an online survey by far exceeded the number of locations previously documented (Figure 3-3). The knowledge of recreational anglers has successfully been utilized in addressing conservation issues in aquatic environments in previous studies (e.g. Giovos et al. 2019; Löki et al. 2023). The confirmation of the species' presence in 11 out 12 representative locations around Iceland indicates the reliability of the data collected in the survey. All included sources of European flounder locations in Iceland overall indicated a similar geographic pattern in distribution and spread of the species within Iceland. However, each source inherently comes with (dis)advantages in the quantitative, geographical and temporal aspects of the documentation of distribution data. For example, while the data collected in the surveys among the recreational angling community showed a clear quantitative advantage over other sources, it lacks temporal information that can be obtained from the sources embedded in the MFRI databases. Based on the results, we recommend combining multiple, interdisciplinary sources in the monitoring of alien species to counteract the inherent biases of each individual source. Involving stakeholder groups in the monitoring of alien species additionally offers the opportunity to increase public awareness, a crucial element when addressing biological invasions (Dehnen-Schmutz et al. 2018).

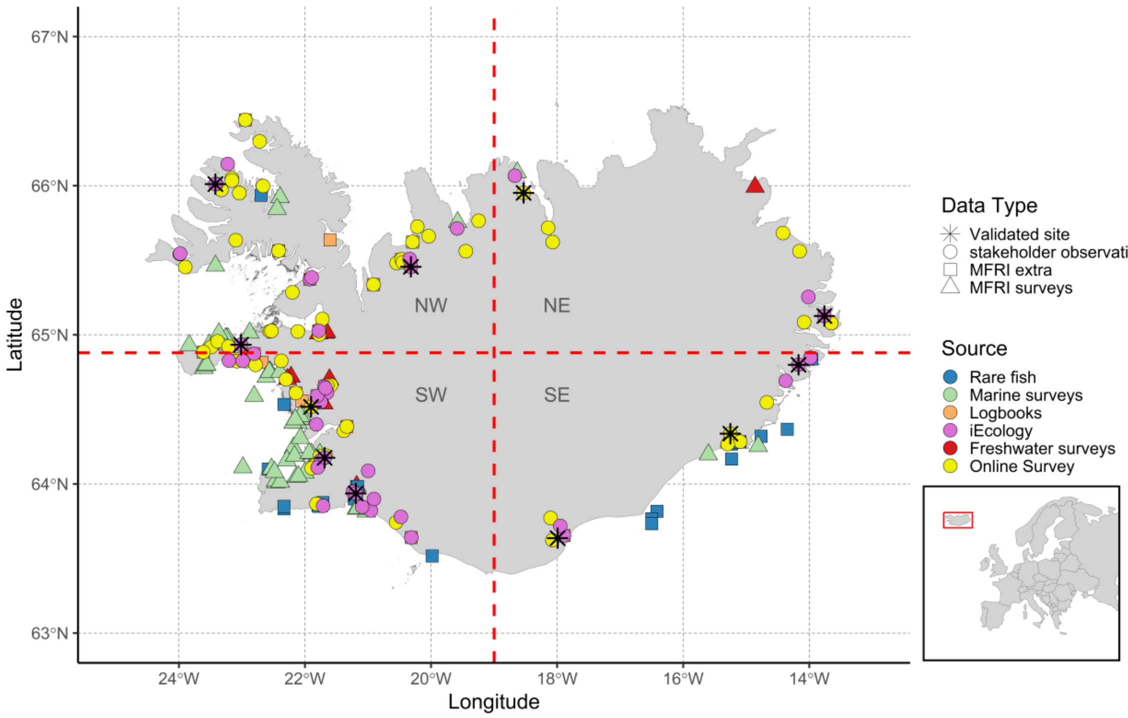

Figure 3-3 Unique sites of European flounder occurrence identified across different sources. A map of Iceland showing all identified unique sites. For each site the color indicates from the six sources of European flounder locations while the shape highlights the three different data types that we divided the sources into, namely stakeholder observations (Online survey & iEcology), MFRI extra (Logbooks and Rare fish), and MFRI surveys (including both marine and freshwater surveys). Locations validated by sampling are indicated with a black asterisk.

3.4 Classifying alien species under remaining uncertainty (Paper IV)

Despite several attempts, there is currently no far-reaching consensus throughout the field of invasion science on the application as well as definition of terminology (Colautti and MacIsaac 2004; Falk-Petersen et al. 2006; Lockwood et al. 2013; Soto et al. 2024). Determining the most applicable terminology is often further complicated by context-dependent and uncertain aspects entailed in the invasion history of the species in question as we have shown for the case of European flounder in Iceland. When asked what terminology they deem most suitable to classify European flounder, where uncertainty regarding its introduction pathway remains, specialists showed high confidence in providing an answer. However, the 83 participating scientists listed 26 different terms. The most common terminology listed by the international group of invasion scientists were the terms ‘invasive species’, ‘non-native species’ as well as ‘cryptogenic species’, while scientists based in Iceland (invasion and/or aquatic scientist) predominantly listed ‘non-native species’ followed by ‘invasive species’ and ‘alien species’ (Figure 3-4). Differences in the preferred terminology can be driven by various factors such as the taxa and discipline of interest, the position (academic or practitioners), or the geographic location (Humair et al. 2014; Shackleton et al. 2022). While the specialist’s views differed in regard to the terminology, they generally agreed on the importance of pathway identification but did not prioritize it over addressing potential impacts of a species and develop management strategies. Knowledge on the introduction is considered very beneficial as it can for instance inform on potential introduction pathways that require attention in form of management approaches (Carlton and Ruiz 2005; Pyšek et al. 2013; Genovesi et al. 2014; Chapman et al. 2015). The recreational angling community in Iceland, representing an important stakeholder group assigned the highest priority to assessing the impacts of European flounder on native species and the prevention of future alien species arriving. It is likely that this stakeholder group is primarily concerned about potential impacts on the native salmonid species given the high monetary value of recreational angling activities targeting these species (Institute of Economic Studies 2018). While the identification of the European flounder’s introduction pathway played a minor role in their priorities, many recreational anglers still stated that it matters to them whether the species arrived due to natural dispersion or human influence.

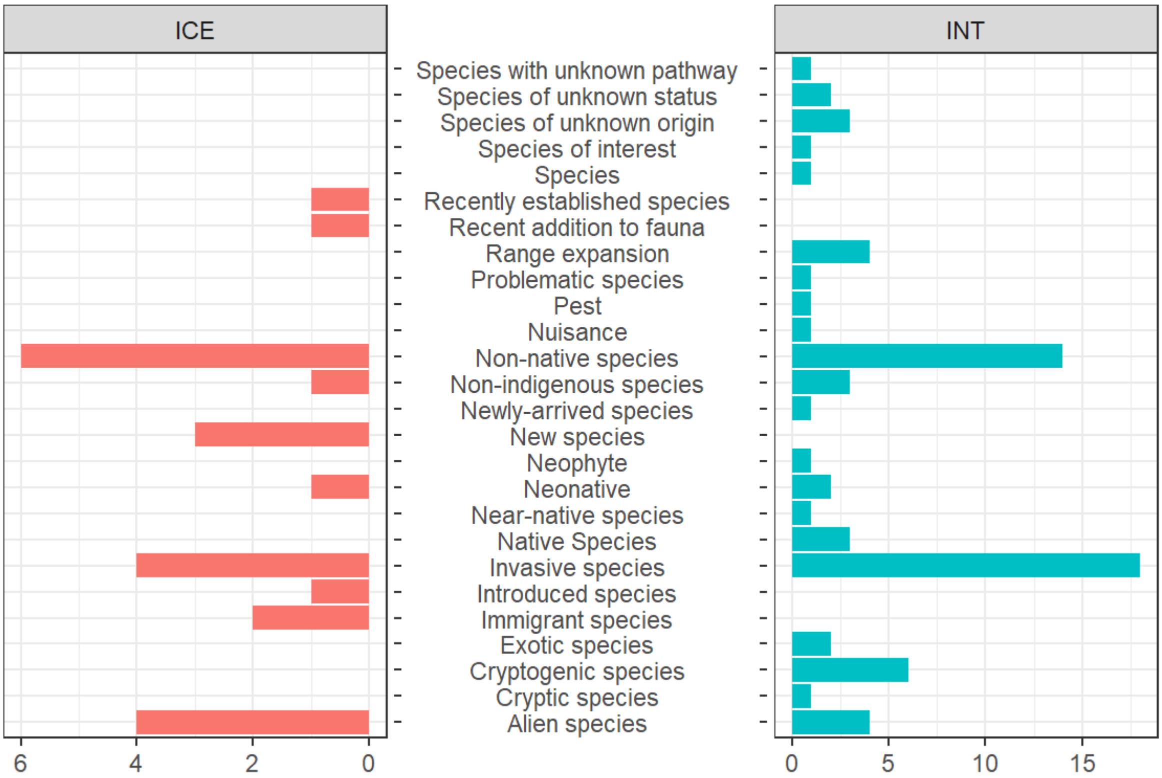

Figure 3-4 Frequency of terms named by specialists to classify European flounder in Iceland. Barplots indicate the frequency in which terms were used by international invasion scientists (blue) and aquatic scientists based in Iceland (red) to describe European flounder in Iceland.

4 Conclusions

Biological invasions are inherently marked by context dependencies and uncertainties on multiple levels. Addressing, managing, and in the best-case scenario preventing invasions therefore requires not only interdisciplinary approaches but also the incorporation of different perspectives (such as of scientists, managers, policy makers and impacted stakeholder groups). Utilizing multiple scientific methods as well as involving the views and knowledge of the recreational angling community in Iceland has not only allowed us to greatly expand the knowledge on alien European flounder in Icelandic waters, but it has further allowed us to address larger scale questions in invasion science using European flounder as a case study. Throughout this thesis, we have shown that involving stakeholders when addressing biological invasions can provide great insights into the species' invasion history and impacts as well as prevailing uncertainties.

While we have identified the most likely geographic origin of European flounder found in Iceland (**Paper I**), the resulting questions concerning the species' introduction pathway presented a great example to highlight the dissensus among the invasion science community regarding the use of terminology as well as the difficulties that arise related to the inherently present uncertainties in invasion science (**Paper IV**). The case of European flounder in Iceland further delivered a great example showing that stakeholder's perceptions towards an alien species can vary in time and space (**Paper II**) and that their experiential knowledge can greatly contribute to the recreation of a species' distribution and spread within the invaded ecosystem (**Paper III**).

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6 Paper I

The tale of the founder flounder - Assessing the origin of an alien fish in Icelandic waters

Henke T., Pálsson S., Hemmer-Hansen J., Thorlacius M., Ólafsdóttir, G. Á. (Submitted to Hydrobiologia)

Author contributions: T.H. and G.Á.Ó. Conceptualized the study and collected European flounder samples throughout Iceland in 2020-2021. T.H. processed the samples and prepared them prior to the microsatellite analysis conducted by J.H.H. M.T. provided European plaice samples and J.H.H provided reference data on different European flounder populations throughout Europe. T.H. conducted the data analysis under the guidance of G.Á.Ó., S.P., and J.H.H. T.H. wrote the initial manuscript which was revised by G.Á.Ó., S.P., J.H.H., and M.T.

Title: The tale of the founder flounder – Assessing the origin of an alien fish in Icelandic waters

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Abstract:

The geographic origin of an alien species is an important aspect of a species' invasion history used for classification and management plans but can additionally deliver information on introduction pathways that require the attention of managers and scientists. The invasion history of European flounder (Platichthys flesus), an alien flatfish species first documented in Icelandic waters in 1999, has not been fully elucidated. There have been different hypotheses on the European flounder's origin and introduction pathway, suggesting either a potentially natural arrival from the Faroe Islands or an introduction via ballast water from the coasts of northwestern Europe. To clarify the geographic origin of European flounder found in Iceland, we used microsatellite analysis of purposefully collected samples from 14 sites around Iceland and reference data stemming from previously published research of flounder population structure in the Faroese and other European populations. Our results indicate that the Faroese population is the most likely source of the European flounder found in Iceland. There was weak IBD between Icelandic samples and the Faroese population. Additionally, we identified 9 hybrids between alien European flounder and native European plaice (Pleuronectes platessa) and further documented signatures of introgression between the species. European flounder x European plaice hybrids are commonly found throughout the overlapping native range of both species but has previously not been documented in Iceland.

Keywords: biological invasions, origin, European flounder, microsatellite analysis, hybridization

Introduction:

As biological invasions continuously increase (IPBES 2023; Seebens et al. 2017), developing effective management approaches to prevent species' introductions becomes of paramount importance. Once a species arrives in a new environment and establishes a population that supplies further spread, the chances of eradication from the ecosystem become negligible for most taxa (IPBES 2023). The geographic origin of an alien species is a crucial part of a species' invasion history as alien species are, per definition, species that are introduced to new regions beyond the barriers of their native ranges under anthropogenic influence (IPBES 2023). While the geographic origin might not be the sole deciding factor for management, integrating knowledge on a species´ invasion history in management decisions will strengthen the outcome (Buckley et al. 2016). Critically, an understanding of the geographical origin of alien species can draw attention to potential pathways that require management to prevent future introductions (Carlton and Ruiz 2005; Chapman et al. 2015; Pyšek et al. 2013) and deliver potential insights into the level of invasiveness and impact of an alien species on native ecosystems (Paolucci et al. 2013; Pyšek et al. 2013). Population genetics has provided valuable information about biological invasions, including the identification of geographic origin of an alien species and the invasion dynamics within the invaded range (Lawson Handley et al. 2011; Sakai et al. 2001). For instance, using cytochrome (COI) sequencing to define the origin and the invasion route of the coffee berry borer (Hypothenemus hampei, Ferrari 1867) that is invading Hawaii (Chapman et al. 2015), or applying microsatellite analysis to investigate the invasion history of Carpobrotus, a wide-spread invasive genus of succulent plants (Novoa et al. 2023).

It is well established that biological invasions can have profound impacts on the recipient environment, most often affecting native species by inducing changes in the ecosystem as well as through competition and predation (IPBES 2023). Molecular tools have been used to study various genetic impacts of alien species (Lawson Handley et al. 2011). Alien species can impact native species via interspecific hybridization and subsequent introgression, introducing maladaptive genes or breaking down adaptive genotype combinations, especially in the case of rare species (Kelly et al. 2010; Kovach et al. 2015). Rapid spread and introgression of aliens can also contribute to undesired global homogenization (Olden et al. 2004). For example, Cutthroat trout (Oncorhynchus clarkia, Richardson 1836), a species that throughout its native range is threatened by the widespread invasive species rainbow trout (Oncorhynchus mykiss, Walbaum 1792) as hybridization and introgression is frequently observed (Kovach et al. 2015). Introgression between these two species is marked by changes in two traits, size at spawning and age of emigration as juveniles, producing larger cutthroat trout individuals that leave rivers at a younger age (Kovach et al. 2015). Despite documented selection against this rainbow trout introgression, fertile hybrids are produced which may eventually lead to an introgressed population and loss of adaptive cutthroat trout genetic variation (Allendorf and Leary 1988; Kovach et al. 2015).

European flounder (Platichthys flesus, Linnaeus 1758), a flatfish species native to the coastal regions of western Europe (Wilson and Veneranta 2019), was first documented in Iceland in 1999 (Jónsson et al. 2001) and is currently classified as potentially invasive (Thorarinsdóttir et al. 2014). The first documented sighting stemmed from the southwest of Iceland (Jónsson et al. 2001), and in 2000 catches were reported near the town of Höfn in southeast Iceland (Astthorsson and Palsson 2006). In the following years, a rapid spread of the species was documented clockwise along the southern and western coast to northern Iceland (Astthorsson and Palsson 2006; Gunnarsson et al. 2015; NA 2017), as well as counterclockwise from the southeast corner along the eastern coast, albeit at a slower speed (Henke et al. 2024; NA 2017). The arrival of the European flounder in Icelandic waters has sparked two opposing hypotheses on its source population. The initial hypothesis stated that the European flounder arrived from the Faroe Islands potentially via natural dispersal with currents (Jónsson et al. 2001; Thorarinsdóttir et al. 2014). European flounder in the Faroe Islands are considered native (Joensen and Tåning 1970) and represent the geographically closest population to Iceland. A later hypothesis suggested arrival of European flounder via ballast water from central Europe (Gunnarsson et al. 2015; Thorarinsdóttir et al. 2014). European flounder is previously known to have been introduced to the Great Lakes in North America via ballast water but failed to establish a population (Cudmore-Vokey and Crossman 2000; Ricciardi and MacIsaac 2000).

Despite a scarcity of studies evaluating the impact of European flounder on the Icelandic ecosystem, an overlapping niche use and potential competition with native fish species have been highlighted (Henke et al. 2020; Hlinason 2013; O´Farrell 2012). On nursery grounds in Icelandic waters, European flounder largely overlaps with juveniles of the native flatfish European plaice (Pleuronectes platessa, Linnaeus 1758) (Henke et al. 2020). Hybridization between European flounder and European plaice are known to occur both naturally and artificially and hybrids have been observed for instance at the western boundary of the Baltic Sea (He et al. 2020) and the Bornholm basin (Kijewska et al. 2009). European flounder x European plaice hybrids are considered to have an interspecies status as they show intermediate coloration (He et al. 2020). Based on morphological characteristics, hybrids are more similar to European plaice, although they can be differentiated by vertebrae counts and scale thorn patterns (He et al. 2020). It has been suggested that morphological classification could result in misidentification and in turn lead to errors in stock assessments and management (He et al. 2020; Kijewska et al. 2009).

Based on the premise of previously documented genetic difference between the Faroese populations and other European flounder populations, as well as low genetic divergence of other populations throughout Europe (Hemmer-Hansen et al. 2007), we aimed to 1) identify which of the two hypotheses was more likely: whether Icelandic European flounder is originating from the Faroe Islands, or from elsewhere in Europe possibly via ballast water by utilizing microsatellite analysis, 2) to analyze the species' spread dynamics within Iceland by exploring potential genetic structure of European flounder within Iceland, and 3) to assess whether there were any indications that introgression between European flounder and native European plaice had occurred in Iceland.

Methods

Sampling

Catches and reports of European flounder in Iceland indicated that it is most frequent and catchable in estuaries (Henke et al. 2024). The sampling plan for the current study was therefore based on reported sightings by recreational anglers (Henke et al. 2024), choosing 3 sites in each quarter of Iceland for the initial sampling conducted in 2020 (Table 1, Figure 1). For two sites, Önundarfjörður (n=29) and Borgarfjörður (n=19), samples were complemented by previously available individuals caught in the summer of 2017 (Table 1). In 2021, 4 sites Hvesta and Bjarnarfjarðará in northwest as well as Hörgá and Eyjafjarðará in north Iceland were sampled (Figure 1). In total, 16 sites around Iceland were sampled, and European flounder were caught in all of them apart from Hofsá in northeast Iceland

(Figure 1). All sampling was done using a beach seine (1.5 x 10 m, mesh size = 6mm) aiming for a sample size of 20-30 individuals per locality.

Due to low sample sizes, the sites “Svarfaðardalsá”, “Hörgá” and “Eyjafjarðará” in Eyjafjörður (NE Iceland), were merged to the group “Eyjafjörður” (n = 9) (Table 1, Figure 1). The remaining samples ranged in size from 14 (Vatnsdalsá) to 35 individuals (Breiðdalsá and Varmá) (Table 1). For the European reference samples, we used microsatellite data for 224 European flounder individuals from four European sites, namely the Faroe Islands, the Irish Sea, Trondheim (Norway) and Thyborøn (Denmark), previously published in Hemmer-Hansen et al., (2007). We also used previously unpublished microsatellite data from 42 Icelandic European flounder collected in southwest Iceland in 2007 (Table 1).

As hybridisation of European flounder and European plaice is common (He et al. 2020; Kijewska et al. 2009), we also collected 114 European plaice from northwest, northeast, southeast and southwest Iceland with 27 – 30 individuals collected across 3-4 stations per region (Figure 1; Table 1). This sampling was conducted during the annual flatfish survey conducted by the MFRI in August 2021 and intended to identify potential hybrids in our samples of European flounder and to assess potential introgression between the species. During the same survey six European flounder were caught at three sampling stations in the southwest of Iceland (Figure 1; Table 1), these were pooled to one group and included in the analysis.

We created maps displaying the sampling locations for the Icelandic European flounder and European plaice using the sf package (Pebesma 2018; Pebesma and Bivand 2023) in R (R Development Core Team 2023). The underlying geospatial data for these maps was retrieved from the National Land Survey of Iceland (Iceland 2020).

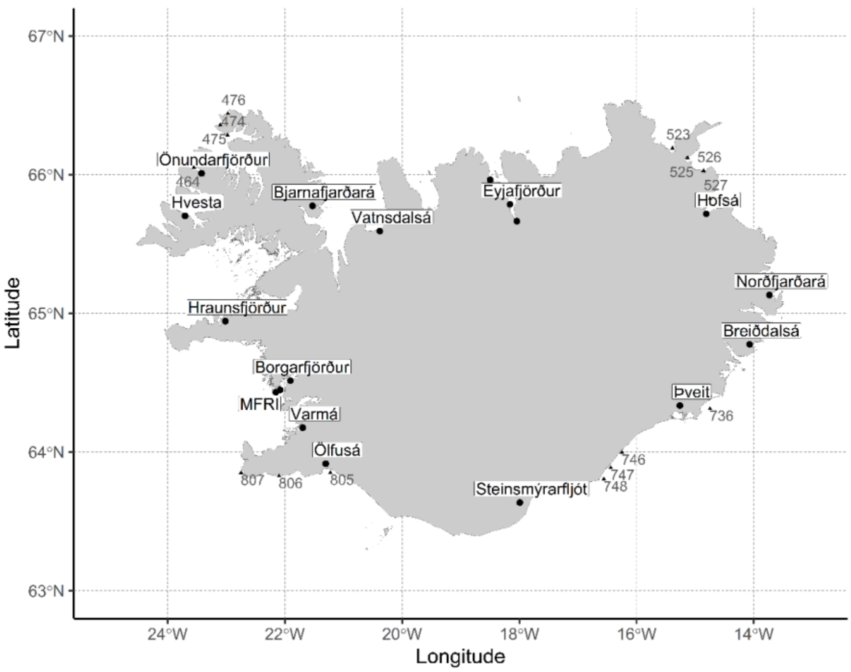

Figure 1 Sampling locations in Iceland, consisting of sampling sites for European flounder marked in black site names as well as sampling sites for European plaice marked in grey numbers representing trawling stations of the MFRI flatfish survey.

Table 1: Sampling information for each site including date, coordinates, sample size (n) and, where available, salinity, as well as size range and mean size of individuals per sample. Information on the numbers of putative hybrids of European flounder samples identified as European plaice is presented in supplementary Table 2.

Sampling site	*Region*	*Date*	*Coordinates (Lat/Lon).*	*n*	*Salinity*	*Size (cm) Range (Mean)*
Icelandic *P. flesus*						
Ölfusá	SW Iceland	05.07.2020	63.9172, -21.3041	**34**	0	2 – 21.9 (6.7)
Varmá	SW Iceland	06.09.2020	64.1766, -21.6955	**34**	4.8	2 – 21.3 (4.2)
Borgarfjörður	SW Iceland	05.07.2020	64.5154, -21.9063	**11(19)**	23	6.6 – 24.4 (10.7)
MRFI samples	SW Iceland	2021		**6**		25 – 46 (35.25)
Station 845		25.08.2021	64.4487, -22.0817	2		25 – 32 (28.5)
Station 846		26.08.2021	64.4323, -22.1555	3		30 – 46 (40.5)
Station 849		26.08.2021	64.7972, -23.5590	1		41
Hraunsfjörður	NW Iceland	06.07.2020	64.9446, -23.0154	**26**	1.8	5.4 – 25.9 (10.8)
Hvesta	NW Iceland	17.08.2021	65.7029, -23.7036	**30**	0	2.9 – 5.5 (4.3)
Önundarfjörður	NW Iceland	2017	66.0102, -23.4218	**(29)**		2.6 – 11.4 (6.3)
Bjarnarfjörður	NW Iceland	20.08.2021	65.7755, -21.5281	**28**	0	3.5 – 11.2 (5.9)
Vatnsdalsá	NW Iceland	09.07.2020	65.5932, -20.3819	**14**	0.6	5.4 – 31.6 (24.4)
Eyjafjörður (pool)	NE Iceland			**9**	0	3.5 – 35.5 (13.1)
Svarfaðardalsá		17.08.2020	65.9624, -18.4967	1	0.06/0.6	
Hörgá		12./13.08.2020	65.7863, -18.1604	3	9	
Eyjafjarðará		12.08.2021	65.6641, -18.0425	5	9	
Nordfjarðará	NE Iceland	19.08.2020	65.1328, -13.7351	**25**	17	2.8 – 29.1 (21.9)
Breiðdalsá	SE Iceland	20.08.2020	64.7771, -14.0715	**35**	10.6	6 – 29.4 (21.6)
Þveit	SE Iceland	20.08.2020	64.3362, -15.2617	**19**	0	5 – 26.2 (13.6)
Steinsmýrarfljót	SE Iceland	21.08.2020	63.6368, -17.9919	**29**	0	6.6 – 11.8 (9.3)
Icelandic *P. platessa*						
SW *P. platessa*	SW Iceland	2021		**30**		
Station 805			63.8522, -21.2233	10		
Station 806			63.828, -22.1003	10		
Station 807			63.8512, -22.747	10		
NW *P. platessa*	NW Iceland	2021		**29**		
Station 464			66.0505, -23.5523	9		
Station 474			66.2852, -22.9787	4		
Station 475			66.3582, -23.1023	10		
Station 476			66.44, -22.9722	6		
NE *P. platessa*	NE Iceland	2021		**27**		
Station 523			66.1907, -15.3877	3		
Station 524			66.1213, -15.1323	4		
Station 526			66.0278, -14.8578	10		
Station 527			65.826, -14.7488	10		
SE *P. platessa*	SE Iceland	2021		**28**		
Station 736			64.3135, -14.7493	10		
Station 746			63.9983, -16.2503	2		
Station 747			63.8873, -16.4415	8		
Station 748			63.8062, -16.5598	8		
Reference *P. flesus*						
Iceland 2007	Iceland		-	**42**		
Faroe Islands	Faroe Island		62, -6.45	**78**		
Thyborøn	Denmark		57, 8	**48**		
Irish Sea	Ireland		54, -4	**49**		
Trondheim	Norway		64.6, 11	**49**		

Genotyping/microsatellite analysis

DNA was extracted using DNeasy extraction kits (QIAGEN) as well as Chelex (Estoup et al. 1996). Following the methodology of Hemmer-Hansen et al. (2007), all samples were scored for the nine microsatellites LIST 1001 (Watts et al. 1999) GenBank Accession no. AF149831), PL142 and PL167 (Hoarau et al. 2002) Accession nos. AF406750 and AF406751) and StPf1001, StPf1002, StPf1004, StPf1005, StPf1015 and StPf1022 (T.J. Dixon, J.B. Taggart, S. G. George, unpublished data, accession nos: AJ315970, AJ315975, AJ315973, AJ315974, AJ538212, AJ538320) on a SeqStudio Genetic Analyzer. All microsatellites were developed specifically for European flounder or successfully adapted from applications for European plaice (Hemmer-Hansen et al. 2007). We included individuals originally genotyped in Hemmer-Hansen et al. (2007) in each run to ensure consistent and calibrated genotyping across studies.

Data preparation and statistics

We conducted initial data exploration and transformation for further analysis using the software GenAleX (version 6.503; (Peakall and Smouse 2006; Peakall and Smouse 2012). As high numbers of null alleles in the data can bias the analysis (Carlsson 2008), we determined the amount of null alleles using the poppr package (Kamvar et al. 2015; Kamvar et al. 2014) and excluded the locus PL142 due to a high amount of null alleles (19.76%, supplementary Table 1). As European plaice samples were not scored for StPf1015, this locus was omitted from analyses that concerned both species (i.e. analyses for hybridisation) but included in the analyses solely concerning the population structure of European flounder.

Due to the potential of hybridisation between European flounder and European plaice we analysed our samples for indications of hybridisation and introgression applying the Bayesian clustering approach implemented in the software STRUCTURE (version 2.3.4, Pritchard et al. (2000)). We grouped the Icelandic samples consisting of European flounder (excluding the reference samples collected in 2007, Table 1) and European plaice in three groups: 1) Icelandic European plaice (all adults); 2) pooled adult European flounder samples with an arbitrary size minimum set at 20 cm under the assumption that defining morphological characteristics will be clearly visible at this size; and 3) all remaining European flounder samples. We performed a STRUCTURE analysis using K = 2 and running 10 iterations with MIGPRIOR set to 0.05. We ran the analysis with prior population information (Popflag) for groups 1 and 2 and under the assumption of admixture for individuals without population information. The burn-in consisted of 100.000 runs followed by 200.000 Markov Chain Monte Carlo (MCMC) iterations. We additionally ran the analysis without MIGPRIOR and prior population information, but as this returned similar results, we based the identification of hybrids on the results of the initial analysis. We classified all samples with a q-value of less than 0.9 as hybrids. All hybrids as well as all cases of European flounder samples classified as “true” European plaice (q-value < 0.1 for European flounder cluster) (Supplementary Table 2) were excluded from all further analysis concerning the population structure of European flounder.

To explore the genetic diversity of the Icelandic samples, both European flounder and European plaice, as well as the reference populations, we calculated the number of alleles per group (A), allelic richness, expected heterozygosity (HE), observed heterozygosity (HO), and the inbreeding coefficient (FIS) using the R-packages hierfstat (Goudet and Jombart 2022) and pegas (Paradis 2010) as well as stats and base (R Development Core

Team 2023). We further analysed the genetic population structure of the European flounder by estimating genetic distance between sampling groups and reference populations as pairwise FST values and estimated the corresponding p-values using the hierfstat package (Goudet and Jombart 2022). As sequential Bonferroni correction using hierfstat package (Goudet and Jombart 2022) indicated no significant pairwise FST values between Icelandic sampling locations, we pooled all Icelandic samples together to examine the genetic distance between Iceland and the Faroe Islands as well as a pooled group consisting of the remaining three reference populations, i.e. Irish Sea, Thyborøn, and Trondheim (ITT group). To visualise the patterns in genetic distances between all sample groups, we generated a multidimensional scale (MDS) plot.

To identify potential clusters of individual European flounder, we ran a discriminant analysis of Principal Components (DAPC) with the number of retained principal components identified applying crossvalidation using the adegenet package (Jombart 2008; Jombart and Ahmed 2011). To further investigate the population structure of European flounder and infer the most likely number of populations (K) present in the data, we performed further Bayesian clustering analyses with STRUCTURE (version 2.3.4, Pritchard et al. (2000)). Under the assumption of admixture and correlated allele frequency, we ran these analyses for K = 1-6 with 10 iterations per K, and a burn-in of 100.000 runs followed by 200.000 MCMC iterations. Using the software STRUCTURE harvester (Earl and vonHoldt 2011), we identified the most likely K using the method of Evanno et al. (2005).

To explore the population structure within Iceland and to identify potential points of introductions we conducted an isolation by distance analysis by plotting the genetic distance between sampling groups against the geographic distance. We calculated the genetic distance as FST /(1- FST) according to Rousset (1997) and approximated the geographic distance between populations using a measuring tool available at www.map.is. We conducted these measurements within the known distribution range of European flounder along the southern and western coasts of Iceland as well as large parts of the northern and eastern coasts (Henke et al. 2024). As the spread of the European flounder to the northeast corner of Iceland has only recently been confirmed in 2023 (Henke et al. 2024), we conducted the distance measurements excluding this area under the assumption that spread between samples has not occurred through here, i.e. the furthest distance was between Eyjafjörður in the north along the western and southern coasts to Norðfjarðará in the east, following the Icelandic coastline to mirror the habitat utilization of European flounder of staying within coastal waters. We tested for significance by applying the Mantel test using the Vegan package (Oksanen et al. 2022). To examine whether the genetic distance between Icelandic populations and the source population (i.e. Faroese population) increases with geographic distance to the source population in the Faroe Islands, we calculated linear regression between pairwise genetic and geographic distances between sampling locations using the stats package (R Development Core Team 2023). We furthermore calculated linear regression between the average allelic richness across all eight loci in each sample and the according geographic distance to the Faroese population, as well as the expected heterozygosity and the geographic distance, to examine for potential population bottlenecks within Iceland.

Results

In total, 328 European flounder samples and 114 European plaice samples were collected in Iceland for this study (Table 1) and scored for the nine loci. These samples were complemented by the data of 266 European flounder samples, scored for the same nine loci, representing populations from the Faroe Islands, Thyborøn (Denmark), the Irish Sea, Trondheim (Norway) (Hemmer-Hansen et al. 2007), and Iceland (collected in 2007). Locus PL142 showed a high number of null alleles (19.76 %) with more than 45% of data missing for the sites Borgarfjörður, Breiðdalsá, Ölfusá, and Önundarfjörður (Supplementary Table 1).

European plaice and European flounder hybridisation

The Bayesian clustering analysis run on the three groups of Icelandic European plaice (group 1) and European flounder (group 2 – adults) and European flounder (group 3 – juveniles) using prior population information revealed 23 individuals that had been morphologically classified as European flounder (Vatnsdalsá = 19; Norðfjarðará = 3, Eyjafjörður = 1) but scored a q-value of less than 0.1 and were consequentially classified as European plaice (Figure 2, supplementary Table 2). Furthermore, 7 individuals previously classified as European flounder (MFRI = 1; Norðfjarðará = 1; Varmá = 1, Breiðdalsá = 1; Vatnsdalsá = 2; Eyjafjörður = 1) as well as 2 individuals previously classified as European plaice were identified as likely European flounder x European plaice hybrids ($0.1 < q < 0.9$) (Figure 2; supplementary Table 2). That represents 1.8 and 2.0 percent for European plaice and European flounder, respectively, or a similar frequency of hybrids identified for both species. We subsequently omitted all 32 individuals that were identified as European plaice or hybrids from analysis specific to European flounder population structure (Figure 1).

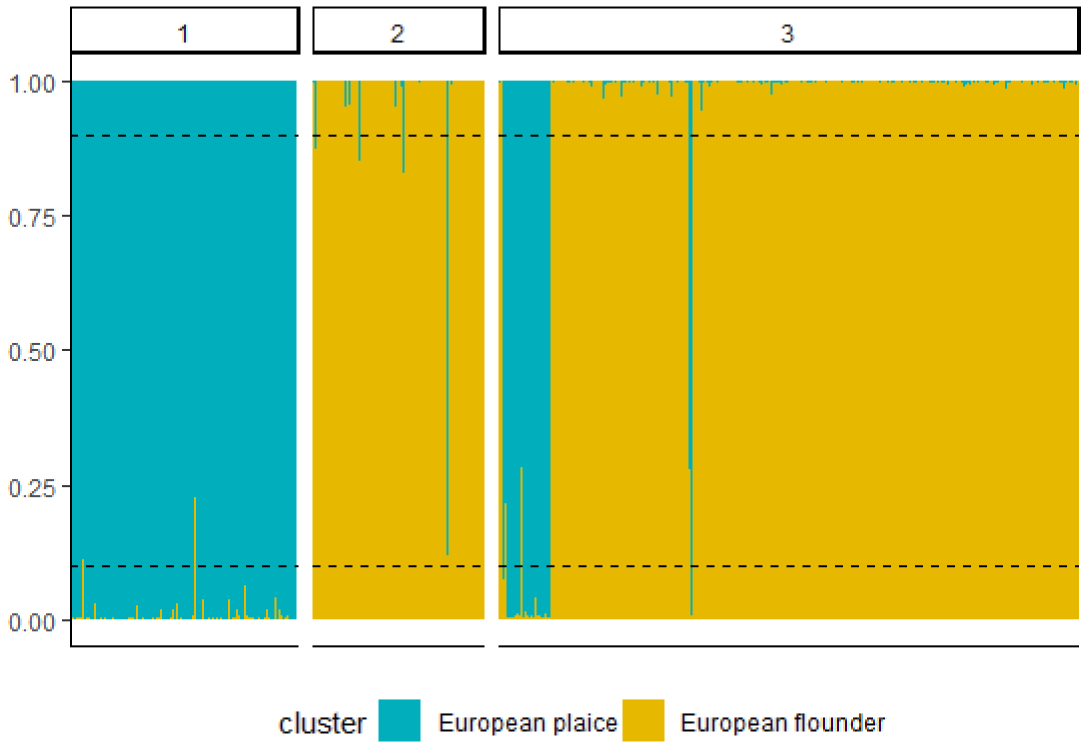

Figure 2. Barplots of genetic assignments of Icelandic European flounders and European plaice individuals to two clusters (K) based on microsatellite variation, using a Bayesian assignment test with prior population information. Pooled groups are indicated by numbers with 1 = adult European plaice; 2 = adult European flounder (> 20 cm); and 3 = remaining

European flounder. Dashed lines set at 0.1 and 0.9 indicate the threshold q-value of 0.9 below which an individual is considered a hybrid.

For European flounder in Iceland, the average number of alleles per sampling group ranged from 3.0 to 5.1 and HE ranged from 0.454 to 0.546. The FIS coefficient only significantly deviated from 0 for the Ölfusá samples, where we recorded a heterozygote deficiency (Supplementary Table 1). The average number of alleles across loci was higher in the reference populations than in Iceland, ranging from 6.3 for the Faroese population to >10 for the remaining three populations with Thyborøn showing the highest number of alleles with 10.9 (Supplementary Table 3). Expected heterozygosity (HE) ranged from 0.583 to 0.71 and there were two instances of heterozygote deficiency detected for the Faroese and Irish Sea population but no significant FIS values within the reference samples (Supplementary Table 1).

Genetic structure

The pairwise FST values ranged from 0 to 0.126 (Figure 3), but no values were significant after sequential Bonferroni correction. When pooling the samples into three groups "Iceland", "Faroe Islands", and "ITT" the pairwise FST values between groups were Iceland – Faroe Islands = 0.039 ($p = 0.01$), Iceland – ITT = 0.114 ($p = 0.01$), and Faroe Islands – ITT = 0.056 ($p = 0.01$) (Supplementary Table 4) and was significant after sequential Bonferroni correction (all 0.03, supplementary table 4). The genetic distances reflected the geographic distances of the Faroese and Icelandic populations from the mainland of Europe, as summarized by the MDS plot, where the Faroe Islands were placed between the clusters of Icelandic samples and the ITT populations (Figure 4). The results of the DAPC revealed a similar pattern but with a closer connection between the Icelandic samples and the Faroese population than of the Faroese to the ITT samples (supplementary Figure 1). STRUCTURE harvester (Earl and von Holdt 2011) results suggested a most likely number of groups as 2. Examining $K = 2$, there was a clear distinction between Iceland and the ITT sites (Figure 5). While Icelandic individuals were predominantly assigned to group 1, the ITT individuals were overwhelmingly assigned to group 2. The Faroese population placed in-between as an admixed population with both clusters present (Figure 5). When increasing K to 3, Icelandic individuals show admixture of group 1 and 2, while the Faroese mainly assigned to group 1 and ITT to group 3 (Figure 5).

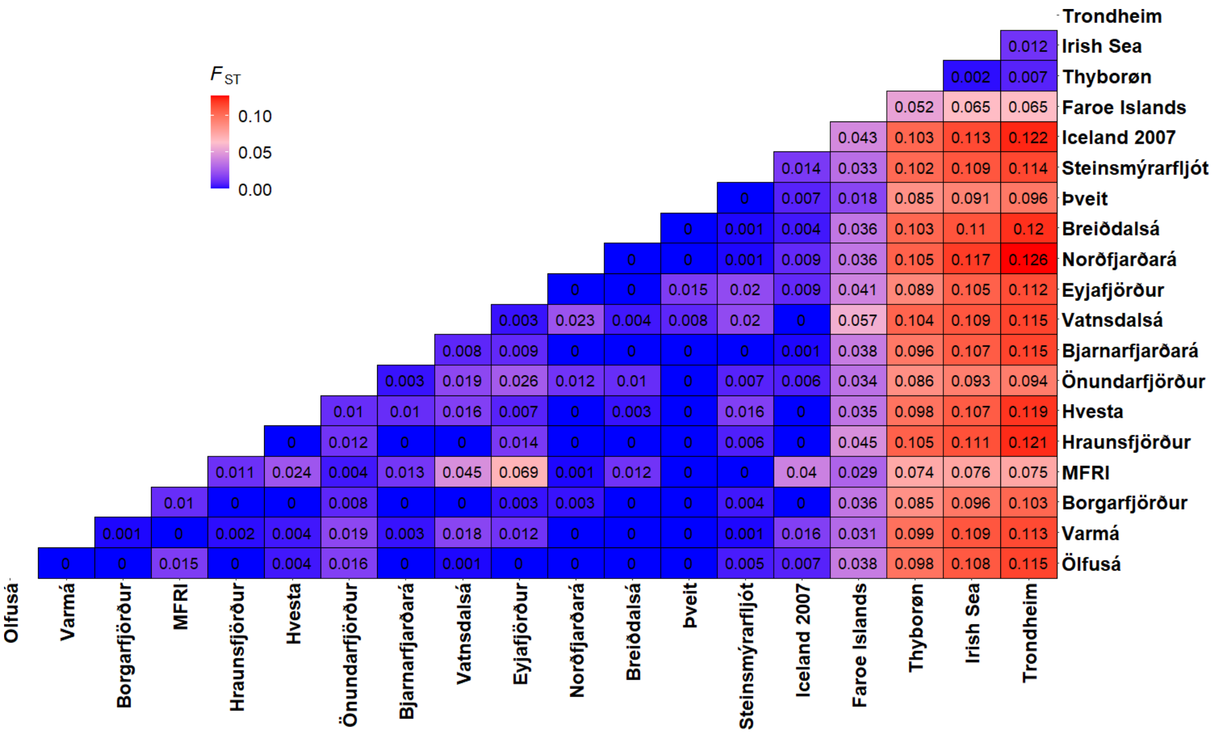

Figure 3 Heatmap indicating the pairwise F_{ST} -values between Icelandic and reference populations. Pairwise F_{ST} -values are shown in different colors ranging from blue representing low values to red representing high values. None of the associated p-values remained significant after applying sequential Bonferroni correction

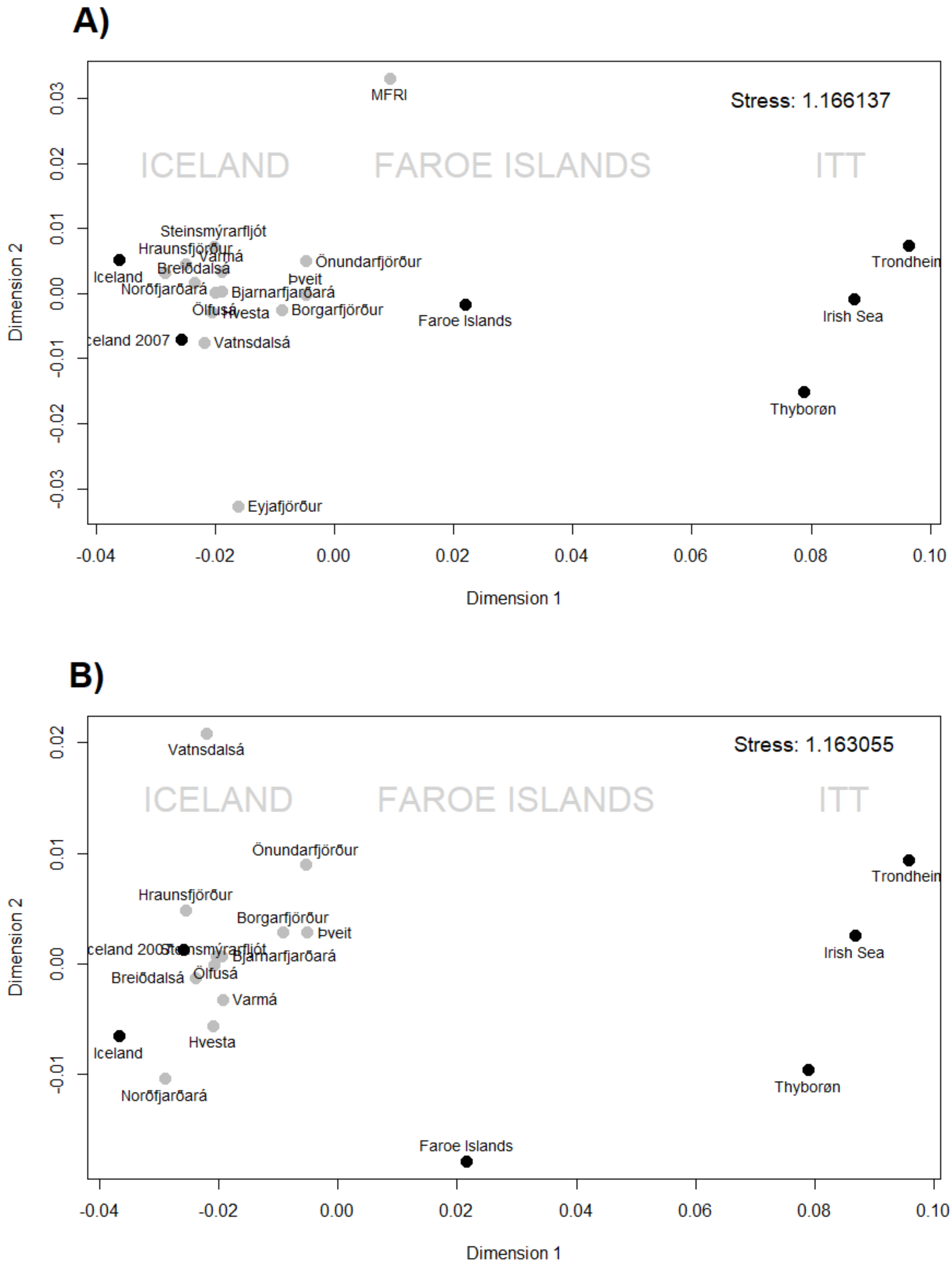

Figure 4. A) MDS plot presenting the genetic distance between Icelandic, Faroese and ITT populations. B) In order to display the genetic distances between Icelandic populations in more detail, we excluded the two clear outliers (MFRI and Eyjafjörður) from A. For both plots the stress value is displayed within the graphs. Plotting dimension 3 did not provide additional insights and was therefore not included.

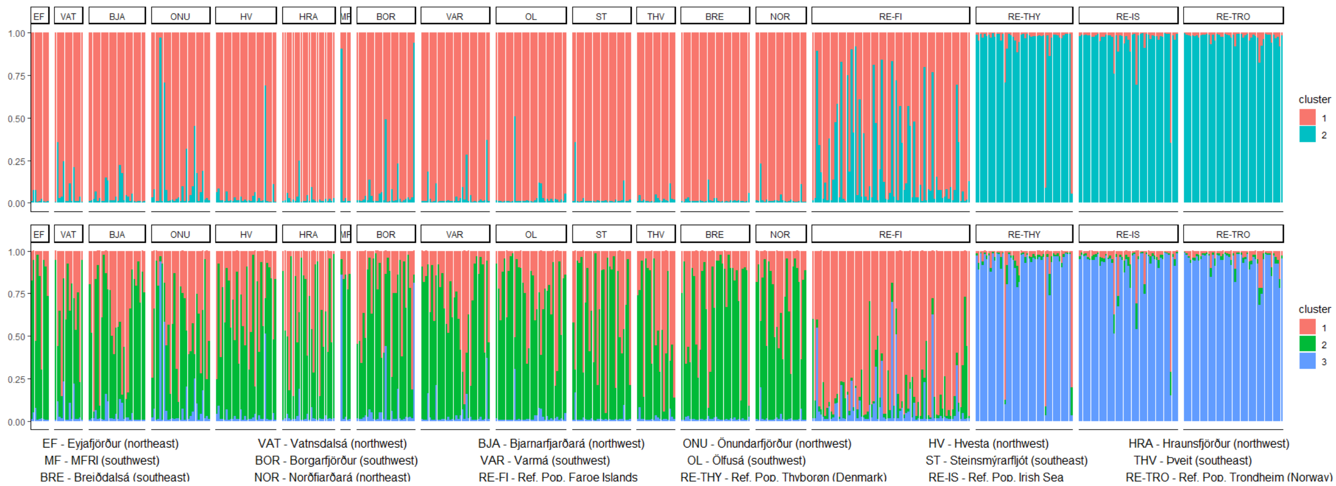

Figure 5. Barplots of the admixture proportions for each individual indicating the genetic structure of European flounder in the 14 samples from Iceland as well as the reference populations.

Genetic variation within Iceland

Considering all Icelandic European flounder groups, the isolation by distance analysis returned no significant result (Mantel test: $R^2 = 0.1414$, $p = 0.123$). When excluding the groups MFRI and Eyjafjörður from the analysis, due to being strong outliers in the MDS, the results remained non-significant (Mantel test: $R^2 = 0.209$, $r = 0.055$) (Figure 6 A). However, linear regression between geographic (i.e. measured distance in km between each Icelandic sample and the Faroese population) and genetic (i.e. pairwise FST values for each Icelandic sample with the Faroese population) distance between Icelandic samples and the Faroese population showed that genetic distance significantly increased with geographic distance ($R2 = 0.34$, $p = 0.0207$; Figure 6B). Conversely, allelic richness in Icelandic groups was not significantly correlated with the geographic distance to the Faroese population ($p = 0.7045$), neither was the expected heterozygosity ($p = 0.664$).

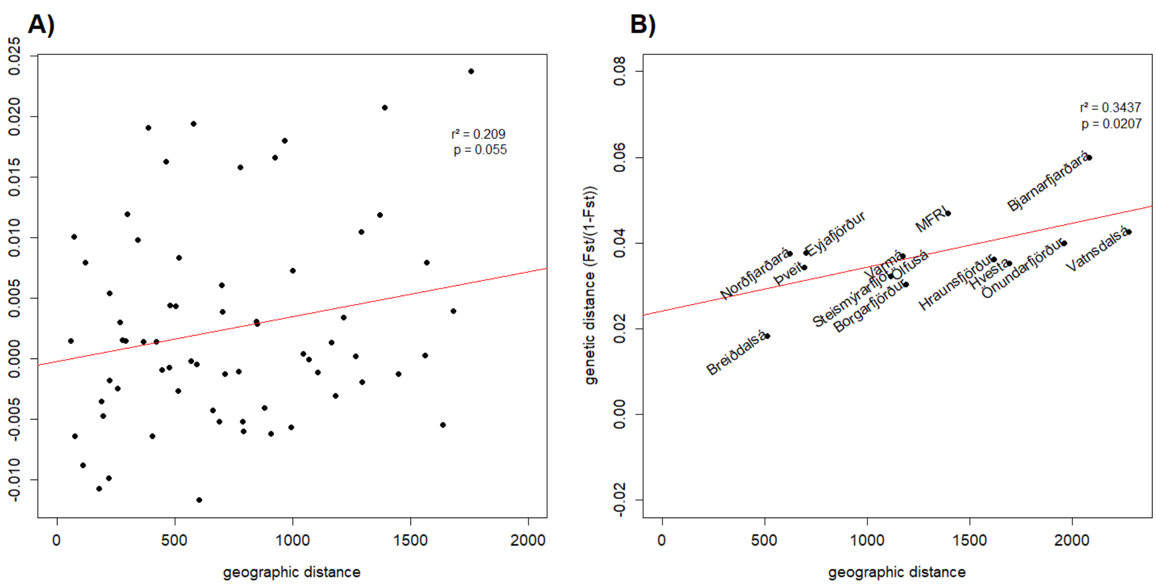

Figure 6: The plots illustrate the results of the Isolation by distance. (A) Genetic distances between Icelandic sample . s (F_{ST} /(1- F_{ST}) according to (Rousset 1997)) are plotted against the geographic distance (obtained as described in methods) for all Icelandic populations excluding the previous outliers Eyjafjörður and MFRI. (B) We specifically display the genetic distance between each Icelandic sample and the source population in the Faroe Islands in relation to the according geographic distance.

Discussion

In this study we explored the geographic origin of European flounder found in Icelandic waters based on the two hypotheses of natural colonisation or introduction with ballast water (Jónsson et al. 2001; Gunnarsson et al. 2015). We have shown that the native Faroese population of European flounder represents the most likely source population. There was limited population structure within Iceland indicative of a broad and rapid spread whereas significant IBD between Icelandic samples and the Faroese population suggests stepwise colonization. Moreover, there were clear signs of hybridisation between alien European flounder and native European plaice as well as indications of introgression between the species.

Geographic origin of Icelandic European flounder

Contrasting Icelandic samples against reference data stemming from four European populations within the species' native range (Hemmer-Hansen et al. 2007) highlighted that European flounder found in Icelandic waters most likely originated from the Faroe Islands. Since the first official documentation of the species in 1999 (Jónsson et al. 2001) two different hypotheses had been raised addressing where it arrived from. While it had been suggested that European flounder arrived from the Faroe Islands (Jónsson et al. 2001; Thorarinsdóttir et al. 2014), potential arrival via ballast water from western Europe has also been discussed (Gunnarsson et al. 2015; Thorarinsdóttir et al. 2014). The study of Hemmer-Hansen et al. (2007) indicating a genetic difference between the Faroese and other European populations offered a valuable opportunity to address the origin of this alien species using established methodology. The current analyses show that Icelandic populations are genetically more closely related to the Faroese population than to any other population in Europe.

In the Faroe Islands, European flounder is a native species (Joensen and Tåning 1970). The Faroese population shows lower allelic richness in comparison to other European populations and Hemmer-Hansen et al. (2007) argued that this reduced allelic richness was the result of a founding event after the last glaciation and is upheld by restricted geneflow due to oceanographic and bathymetric barriers. The comparatively lower allelic richness found in Icelandic European flounder suggests that another founding event took place upon the species' arrival in Iceland. Reduced genetic diversity can be a limiting factor for the successful establishment of an alien species (Lawson Handley et al. 2011). However this has not been the case for , European flounder in Iceland that has successfully established, a population that has rapidly spread to most regions of the country (Henke et al. 2024). Throughout its native range, European flounder is known to show high plasticity in the utilization of different aquatic habitats along salinity gradients, including full saline, estuary and freshwater habitats (Daverat et al. 2012; Le Pichon et al. 2014). This plasticity could have facilitated the establishment of European flounder in Iceland.

Invasion dynamics of European flounder in Iceland

Our results show isolation by distance based on samples from Iceland and the likely origin of the Faroe Islands, but no population structure within Iceland. Investigating the population structure of an alien species within the invaded range can provide insights into the invasion dynamics, that is, inferences on the invasion routes of alien species have traditionally been made by using two types of methods, direct methods based on current and historical species' observations and indirect methods using genetic patterns based on molecular analyses (Lawson Handley et al. 2011). For example, Rato et al. (2023) used microsatellites to explore the colonization routes of an alien gecko in the Mediterranean. Their study revealed that while the Iberian Peninsula has historically been the main source for individuals spreading, most introductions that occur currently stem from mainland Italy and are likely driven by the plant nursery industry (Rato et al. 2023).

The current analysis shows a significant relationship between genetic and geographic distances when comparing Icelandic to Faroese sampling locations and a weak (although non-significant) isolation by distance within Iceland. These results suggest that a stepwise process could have partially contributed to the spread of flounder within Iceland and/or effects from contemporary gene flow from the Faroese source population. Stepwise colonization processes have been documented for other introduced species such as the invasive yellow fever mosquito (Aedes aegypti) in North America (Pless et al. 2022). Understanding where in Iceland European flounder first arrived would provide additional information that could contribute to assessing the most likely introduction pathway. Although, the flounder source population most likely originated from the Faroe Islands they could have arrived in Iceland either by introduction via ballast water or by natural dispersion. However, any genetic analyses could further be complemented by combining them with direct methods in an interdisciplinary approach. Henke et al. (2024) has shown the benefits of combining local ecological knowledge with traditional scientific sampling when reconstructing the current spread of European flounder in Iceland. By building upon the methodology applied in Henke et al. (2024) with particular focus on the temporal factor of species' observations, the resulting distribution data could be incorporated with more detailed information on the invasion dynamics suggested by further genetic analyses for a better understanding how the European flounder spread throughout Iceland.

Future classification of European flounder in Iceland

The remaining uncertainty on how flounder arrived in Iceland, by natural dispersion or introduction via ballast water, has implications on the classification of European flounder in Iceland. Given the common definition of alien species as "a species whose presence in a region is attributable to human activities that have enabled it to overcome the barriers that define its natural range" (IPBES, 2023), European flounder would no longer be considered an alien species in the case of natural dispersal. When the dynamics of an alien species' introduction remain unclear, but one or more pathways of introduction are known to be possible for this species, it is considered polyvectic (Carlton and Ruiz 2005). We argue that neither potential introduction pathway can be confidently excluded, and therefore propose to preserve the current classification as "potentially invasive" (Thorarinsdóttir et al. 2014) with the addition of the term "polyvectic".

Interspecific hybridisation between European flounder and European plaice

We identified 9 hybrids among the Icelandic samples, of which two were initially morphologically identified as European plaice and 7 as European flounder as well as signatures of introgression beyond first generation hybrids in all 9 individuals. In Iceland, interspecific hybridisation between fish species has been observed between European eel (Anguilla Anguilla) and American eel (Anguilla rostrata) (Pujolar et al. 2014) and has frequently been discussed in the context of escaped farmed salmonids caught in streams alongside native salmonids (Guðmundsson et al. 2017; Guðmundsson et al. 2023). Identifying European flounder x European plaice hybrids among the samples is in line with the literature, as this is a well-known phenomenon throughout the species' mutual native range (He et al. 2020; Kijewska et al. 2009). The geographical distribution of the identified hybrids currently does not appear to be linked to a specific pattern. Adult hybrids, initially morphologically identified as either European flounder or European plaice, were found in samples along Iceland's east and west coast. Juvenile hybrids were identified in northern and eastern Iceland. No samples provided more than one hybrid, except for Eyjafjörður in northern Iceland where two juvenile hybrids were detected (despite a low total sample size of 9). However, the current sampling includes considerable variation in European flounder size as well as both freshwater and marine environments, complicating inferences on these dynamics. Future studies should include specifically designed sampling to assess patterns in the hybridization between European flounder and European plaice in more detail.

Interspecific hybridisation and introgression can cause severe negative impacts in the context of biological invasions (Huxel 1999). Concerning the hybridisation between European flounder and European plaice, it has been suggested that potential misidentifications of pure specimens when solely morphologically analysed, could lead to errors in stock assessments and the development of management strategies as hybrids are more likely to resemble European plaice (He et al. 2020; Kijewska et al. 2009). Potential consequences of the observed hybridization and introgression among the two species in Iceland will have to be assessed in future studies.

Conclusion

Population genetic studies addressing biological invasion can greatly expand our knowledge on different aspects of an alien species' invasion history. In this study we showed that the native Faroese population of European flounder was a likely source for alien European flounder found in Iceland. However, our results only allowed for limited inferences on the invasion dynamics of this species within Iceland and should be further investigated using higher resolution genetic methods, and sampling of different life-stages, in order to gain additional insights on where and potentially how European flounder first arrived in Iceland. Moreover, hybrids of European flounder x European plaice were identified as well as signs of introgression between the species.

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Supplementary files

Supplementary Table 1 Calculated amount of missing data for each sampling group and locus based on the raw data.

	PL 167	STPF1015	PL142	STPF1004	STPF1002	STPF1022	STPF1005	STPF1001	LIST1001	**Mean**
Bjarnarfjarðará	3.57	3.57	3.57	3.57	3.57	3.57	-	3.57	3.57	**3.17**
Borgarfjörður	6.9	-	48.28	-	3.45	-	3.45	10.34	3.45	**8.43**
Breiðdalsá	17.65	2.94	52.94	8.82	20.59	-	-	5.88	11.76	**13.4**
Eyjafjörður	22.22	-	11.11	-	22.22	-	-	-	11.11	**7.41**
Faroe Islands	-	-	1.28	-	1.28	-	-	5.13	-	**0.85**
Hraunsfjörður	-	-	30.77	-	3.85	-	-	-	-	**3.85**
Hvesta	-	-	-	-	-	-	-	-	-	**-**
Irish Sea	10.2	-	8.16	10.2	2.04	2.04	2.04	-	-	**3.85**
MFRI	20	-	20	20	20	-	-	-	-	**8.89**
Norðfjarðará	-	-	19.23	-	-	-	-	3.85	-	**2.56**
Ölfusá	2.86	2.86	57.14	-	2.86	5.71	5.71	11.43	-	**9.84**
Önundarfjörður	17.24	6.9	55.17	10.34	20.69	17.24	-	20.69	10.34	**17.62**
Steinsmýrarfljót	-	-	3.45	-	-	-	-	-	-	**0.38**
Þveit	-	-	36.84	10.53	-	-	-	5.26	-	**5.85**
Thyborøn	-	-	-	-	-	2.08	-	2.08	-	**0.46**
Trondheim	-	-	-	-	-	-	-	-	-	**-**
Varmá	5.71	2.86	34.29	5.71	11.43	-	-	5.71	5.71	**7.94**
Vatnsdalsá	-	-	28.57	-	-	-	-	-	-	**3.17**
Total	**4.37**	**1.05**	**19.76**	**2.97**	**4.55**	**1.75**	**0.7**	**4.37**	**2.1**	**4.62**

Supplementary Table 2 A list of individuals identified as hybrids as well as European flounder that were classified as true European plaice during Bayesian assignment test at k=2. For each individual the table lists it´s pooled group (1 – adult European plaice, 2 – adult European flounder, 3 – Juvenile European flounder), its original sampling group, its genetic assignment, Q-values for each cluster as well as the amount of missing data.

Pooled group	**Sampling group**	**Genetic assignment**	**Cluster 1 (Plaice)**	**Cluster 2 (Flounder)**	**Missing data**
1 – adult European plaice	Plaice SW	Hybrid	0.774	0.226	0.43
	Plaice NE	Hybrid	0.888	0.112	0.14
2 – adult European flounder	MFRI	Hybrid	0.127	0.873	0
	Norðfjarðará	Hybrid	0.15	0.85	0
	Varmá	Hybrid	0.172	0.828	0.71
	Breiðdalsá	Hybrid	0.881	0.119	0
3 – juvenile European flounder	Vatnsdalsá	Plaice	0.926	0.074	0
		Hybrid	0.786	0.214	0.29
		Plaice	0.996	0.004	0
		Plaice	0.998	0.002	0.14
		Plaice	0.997	0.003	0
		Plaice	0.998	0.002	0
		Plaice	0.995	0.005	0.14
		Plaice	0.989	0.011	0.14
		Plaice	0.993	0.007	0.71
		Hybrid	0.718	0.282	0.43
		Plaice	0.997	0.003	0.14
		Plaice	0.986	0.014	0.86
		Plaice	0.995	0.005	0
		Plaice	0.997	0.003	0.14
		Plaice	0.994	0.006	0.29
		Plaice	0.996	0.004	0.57
		Plaice	0.958	0.042	0.43
		Plaice	0.994	0.006	0.29
		Plaice	0.992	0.008	0.43
		Plaice	0.997	0.003	0.14
		Plaice	0.997	0.003	0.29
	Norðfjarðará	Plaice	0.988	0.012	0
		Plaice	0.998	0.002	0
		Plaice	0.998	0.002	0
	Eyjafjörður	Hybrid	0.722	0.278	0
		Plaice	0.993	0.007	0

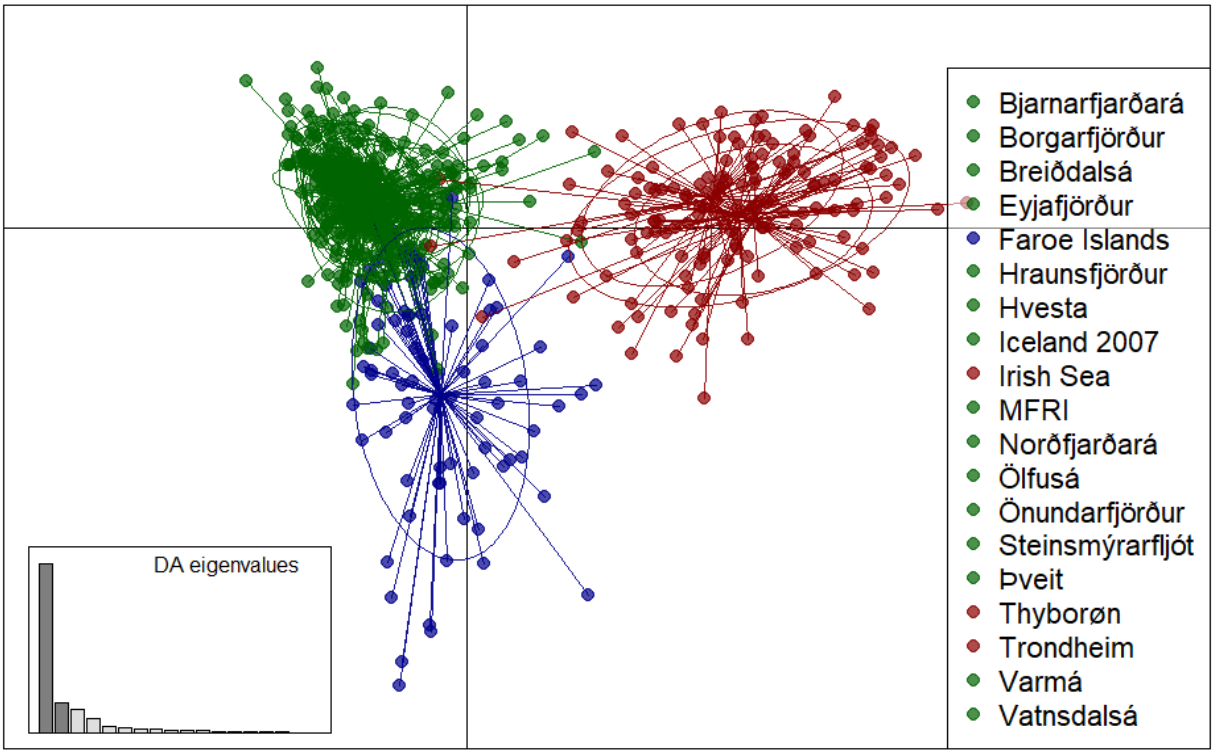
Supplementary Table 3 Descriptive statistics of each population including allele range, expected heterozygosity (H_E), observed heterozygosity (H_O), number of alleles both per locus and per population, allelic richness, and the F_{IS} values

Population		*PL167*	*StPf 1015*	*StPf 1004*	*StPf 1002*	*StPf 1022*	*StPf 1005*	*StPf 1001*	*List1001*	*A*	*H_E/ H_O*	*F_{IS}(combined Fishers value)*
Ölfusá	Range	194-230	129-141	140-196	177-183	170-214	105-107	237-293	083-085	4.40	0.519/	0.103
	H_E/H_O	0.62/0.71	0.6/0.62	0.48/0.51	0.54/0.56	0.79/0.79	017/0.00	0.79/0.74	0.11/0.11		0.505	(0.0000)
	N alleles	5	3	6	3	8	2	6	2			
	All. Rich.	2.922	2.733	2.797	2.385	4.550	1.555	4.207	1.392			
Varmá	Range	194-230	129-141	140-196	175-183	162-214	101-107	237-269	083-085	4.88	0.507/	0.058
	H_E/H_O	0.6/0.58	0.52/0.56	0.53/0.52	0.56/0.52	0.74/0.74	0.06/0.06	0.79/0.73	0.19/0.15		0.480	(0.9999)
	N alleles	5	3	7	4	10	2	6	2			
	All. Rich	2.780	2.568	3.189	2.465	4.203	1.223	4.260	1.614			
Borgarfjörður	Range	170-230	129-141	140-196	175-183	170-214	107-117	237-263	083-085	5.10	0.546/	0.096
	H_E/H_O	0.61/0.52	0.68/0.69	0.6/0.55	0.64/0.46	0.79/0.83	0.07/0.07	0.79/0.58	0.1/0.11		0.476	(0.9998)
	N alleles	6	4	8	4	10	2	5	2			
	All. Rich.	2.947	3.293	3.485	2.928	4.748	1.268	4.207	1.376			
MFRI	Range	194-230	129-137	140-150	177-183	170-214	107-117	237-263	085-085	3.00	0.454/	-0.056
	H_E/H_O	0.66/0.8	0.28/0.33	0.18/0.2	0.54/0.6	0.74/0.64	0.29/0.33	0.76/1	0/0		0.494	(1.0000)
	N alleles	4	2	2	3	5	2	5	1			
	All. Rich.	4.000	1.800	2.000	3.000	4.556	1.800	4.578	1.00			
Hraunsfjörður	Range	170-230	129-141	140-196	177-183	170-218	101-107	237-263	083-085	4.75	0.485/	-0.026
	H_E/H_O	0.61/0.69	0.6/0.77	0.42/0.46	0.61/0.52	0.73/0.73	0.04/0.04	0.77/0.73	0.04/0.04		0.498	(1.0000)
	N alleles	7	4	6	3	9	2	5	2			
	All. Rich.	2.996	2.782	2.710	2.752	4.308	1.154	4.056	1.154			
Hvesta	Range	194-230	129-141	140-196	175-183	170-214	107-117	237-271	085-087	4.90	0.496/	-0.002
	H_E/H_O	0.56/0.47	0.53/0.47	0.59/0.67	0.65/0.7	0.69/0.77	0.03/0.03	0.79/0.83	0.06/0.07		0.5	(1.0000)
	N alleles	4	4	9	4	8	2	6	2			
	All. Rich.	2.477	2.601	3.419	3.033	3.844	1.133	4.235	1.251			
Önundarfjörður	Range	194-230	129-141	150-196	177-183	170-214	101-117	237-293	083-089	4.60	0.522/	0.140
	H_E/H_O	0.55/0.46	0.58/0.56	0.45/0.46	0.66/0.39	0.83/0.88	0.19/0.14	0.7/0.57	0.11/0.12		0.445	(0.9936)
	N alleles	4	4	5	3	9	3	6	3			
	All. Rich.	2.463	2.748	2.570	2.896	5.055	1.716	3.739	1.440			
Bjarnarfjarðará	Range	194-230	121-141	150-196	177-183	170-214	101-107	237-263	083-085	4.25	0.51/	0.029
	H_E/H_O	0.57/0.59	0.61/0.52	0.47/0.44	0.63/0.59	0.81/0.78	0.04/0.04	0.77/0.85	0.1/0.11		0.49	(1.0000)
	N alleles	4	4	5	3	9	2	5	2			
	All. Rich.	2.544	2.936	2.734	2.837	4.730	1.143	4.033	1.388			
Vatnsdalsá	Range	194-208	129-141	150-196	175-183	170-214	101-117	237-271	083-085	4.40	0.507/	0.024
	H_E/H_O	0.58/0.36	0.66/0.64	0.41/0.5	0.56/0.71	0.74/0.64	0.14/0.14	0.74/0.79	0.07/0.07		0.482	(0.9994)
	N alleles	5	3	4	4	8	3	6	2			
	All. Rich.	2.843	2.913	2.590	2.759	4.340	1.571	4.049	1.286			
Eyjafjörður	Range	194-204	129-141	140-196	177-183	170-214	107-107	237-259	085-085	3.30	0.487/	-0.127
	H_E/H_O	0.61/0.86	0.57/0.67	0.64/0.89	0.46/0.43	0.78/0.78	0/0	0.64/0.78	0/0		0.55	(1.0000)
	N alleles	4	3	5	2	6	1	4	1			
	All. Rich.	3.140	2.695	3.709	1.997	4.515	1.000	3.146	1.000			
Norðfjarðará	Range	194-230	129-141	140-196	177-183	174-214	107-107	237-293	083-089	4.00	0.480/	0.133
	H_E/H_O	0.55/0.48	0.46/0.4	0.56/0.48	0.59/0.6	0.73/0.56	0/0	0.7/0.58	0.12/0.12		0.403	(0.9997)
	N alleles	3	3	5	3	7	1	6	4			
	All. Rich.	2.405	2.241	3.197	2.703	3.923	1.000	3.982	1.480			
Breiðdalsá	Range	194-230	129-141	140-196	177-183	170-214	107-107	237-263	083-085	3.90	0.496/	0.150
	H_E/H_O	0.61/0.54	0.56/0.42	0.57/0.52	0.52/0.37	0.74/0.71	0/0	0.77/0.59	0.12/0.13		0.41	(0.8914)
	N alleles	4	3	6	3	7	1	5	2			
	All. Rich.	2.806	2.576	3.224	2.507	4.141	1.000	4.042	1.445			
Þveit	Range	194-230	129-141	140-196	177-183	170-214	101-107	237-293	083-085	4.00	0.497/	-0.008
	H_E/H_O	0.54/0.42	0.53/0.68	0.47/0.47	0.55/0.68	0.78/0.68	0.05/0.05	0.8/0.78	0.15/0.16		0.492	(1.0000)
	N alleles	4	3	5	3	7	2	6	2			
	All. Rich.	2.414	2.628	2.840	2.376	4.580	1.211	4.449	1.519			
Steinsmýrarfljót	Range	194-230	129-141	140-196	177-183	170-214	101-107	237-263	083-085	4.00	0.487/	0.029
	H_E/H_O	0.51/0.48	0.55/0.52	0.53/0.59	0.62/0.52	0.78/0.79	0.03/0.03	0.77/0.79	0.03/0.03		0.47	(1.0000)
	N alleles	4	3	5	3	8	2	5	2			

	All. Rich	2.260	2.644	3.011	2.748	4.255	1.138	3.962	1.138			
Iceland 2007	Range	194-230	129-141	142-196	175-183	170-214	101-117	237-263	083-085	4.75	0.518/ 0.497	0.031 (1.0000)
	H_E/H_O	0.54/0.44	0.65/0.77	0.58/0.57	0.67/0.57	0.75/0.78	0.05/0.05	0.77/0.71	0.07/0.07			
	N alleles	4	3	8	4	9	3	5	2			
	All. Rich	2.315	2.851	3.340	3.204	4.245	1.205	4.025	1.268			
Plaice Iceland SW	Range	134-198	0-0	140-204	183-191	264-358	103-113	209-267	087-095	10.30	0.792/ 0.725	0.078 (0.5177)
	H_E/H_O	0.93/0.96	1/0	0.84/0.6	0.43/0.44	0.89/0.78	0.71/0.63	0.91/0.89	0.74/0.77			
	N alleles	19	0	10	3	17	6	19	5			
	All. Rich.	17.503	-	9.494	2.778	15.162	5.912	16.842	4.976			
Plaice Iceland NW	Range	130-206	0-0	140-190	183-191	264-374	103-113	209-265	087-095	9.90	0.775/ 0.736	0.034 (0.7677)
	H_E/H_O	0.94/0.92	1/0	0.8/0.48	0.45/0.52	0.9/0.89	0.69/0.79	0.88/0.86	0.66/0.69			
	N alleles	23	0	10	3	18	6	16	5			
	All. Rich.	21.274	-	9.354	2.998	16.248	5.959	14.086	4.855			
Plaice Iceland NE	Range	134-222	0-0	148-174	183-191	264-382	101-113	213-267	087-093	10.10	0.791/ 0.742	0.047 (0.6216)
	H_E/H_O	0.92/0.95	1/0	0.82/0.56	0.41/0.48	0.91/0.92	0.78/0.81	0.89/0.77	0.68/0.7			
	N alleles	21	0	9	3	20	7	15	4			
	All. Rich.	20.496	-	8.654	3.000	18.571	6.730	13.934	3.954			
Plaice Iceland SE	Range	136-230	0-0	148-190	183-191	230-334	103-113	207-275	085-095	9.90	0.802/ 0.705	0.124 (0.0000)
	H_E/H_O	0.89/0.85	1/0	0.79/0.48	0.54/0.48	0.9/0.88	0.72/0.71	0.9/0.86	0.76/0.68			
	N alleles	17	0	13	3	16	6	21	6			
	All. Rich.	15.075	-	12.461	3.000	15.102	5.974	17.794	4.976			
Faroe Islands	Range	172-230	129-141	142-196	177-191	170-218	101-117	235-295	083-087	6.30	0.583/ 0.583	0.001 (1.0000)
	H_E/H_O	0.66/0.65	0.42/0.41	0.75/0.78	0.59/0.57	0.81/0.9	0.22/0.23	0.81/0.74	0.38/0.37			
	N alleles	10	3	8	4	11	3	8	3			
	All. Rich	3.243	2.253	4.060	2.605	4.537	1.735	4.473	2.112			
Thybo røn	Range	166-228	121-141	142-194	141-191	168-218	101-117	247-351	083-087	10.90	0.688/ 0.695	-0.009 (0.9999)
	H_E/H_O	0.82/0.81	0.41/0.4	0.83/0.88	0.66/0.69	0.88/0.85	0.59/0.6	0.88/0.94	0.4/0.4			
	N alleles	15	5	17	7	15	3	22	3			
	All. Rich.	4.807	2.520	5.140	3.314	5.576	2.750	5.803	2.033			
Irish Sea	Range	172-228	121-145	144-192	143-191	166-230	101-117	237-293	083-087	10.40	0.675/ 0.648	0.032 (0.9926)
	H_E/H_O	0.8/0.84	0.37/0.37	0.79/0.77	0.7/0.69	0.88/0.77	0.65/0.6	0.81/0.8	0.33/0.35			
	N alleles	16	6	16	7	15	4	16	3			
	All. Rich.	4.851	2.458	4.883	3.795	5.629	2.927	4.935	1.973			
Trond heim	Range	172-212	121-145	136-196	175-191	168-218	99-117	237-341	083-087	10.50	0.71/ 0.73	-0.029 (1.0000)
	H_E/H_O	0.75/0.71	0.48/0.53	0.8/0.86	0.67/0.71	0.88/0.92	0.67/0.71	0.88/0.9	0.49/0.49			
	N alleles	14	6	15	6	17	5	18	3			
	All. Rich.	4.229	2.905	4.768	3.246	5.619	3.133	5.699	2.306			

Supplementary Table 4 Genetic distances and the according p-values between the three groups (i.e. Iceland, Faroe Islands, and ITT) that European flounder individuals were pooled into.

	Pairwise F_{ST} value	p-value	After Holm Bonferroni correction
Iceland – Faroe Islands	0.039	0.01	0.03
Faroe Islands – ITT	0.056	0.01	0.03
Iceland – ITT	0.114	0.01	0.03



Supplementary Figure 1 Results of the Discriminant Analysis of Principal Components (DAPC). Samples are marked in three different colors with green representing Icelandic samples, blue representing the Faroese Islands samples and red representing the samples pooled to the ITT group (i.e. Irish Sea, Thyborøn, Trondheim)

7 Paper II

Let’s talk aliens – Stakeholder perceptions of an alien species differ in time and space

Henke T., Novoa A., Bárðarson H., Ólafsdóttir G. Á. (2024)

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Research Article

Let's talk aliens - Stakeholder perceptions of an alien species differ in time and space

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Abstract

Humans play an integral role in biological invasions, from aiding introductions of alien species to experiencing their impacts and holding the ability to manage them. The importance of understanding the dynamics of stakeholders' perceptions on alien species is therefore increasingly recognized. In this study, we used anonymous online surveys to contrast recreational anglers' perceptions towards European flounder (*Platichthys flesus*, Linnaeus, 1758) in Iceland, where it is classified as a potentially invasive species, to the perceptions prevailing amongst recreational anglers in the species' native range. We furthermore explored potential temporal changes in the perception of Icelandic recreational anglers. Our results indicate that Icelandic recreational anglers have a highly negative perception towards the European flounder, while in its native range, recreational anglers have positive perceptions towards this species. In Iceland, we have furthermore detected a significant change towards less negative perceptions between the surveys administered in October 2019 and March 2023. Finally, we compared the results of the online surveys and novel, conservation culturomics tools to further explore stakeholder perceptions and public interest in Iceland. The comparison highlighted some limitations that should be considered when using culturomics in very small societies or for small languages. For example, the text mining approaches on newspaper articles and social media conservations detected neutral perceptions in the communication to the public and within the targeted stakeholder group via social media in contrary to the perceptions detected in the online surveys. Moreover, we detected short-term peaks in the public's interest in European flounder and potential drivers of those peaks using Wikipedia pageviews but Google Trends provided mixed and unreproducible results. Overall, our study highlights that stakeholders' perceptions towards an alien species as well as the public's interest in it vary over time and space, though the drivers of these changes are often difficult to identify.

Key words: Angling community, biological invasions, communication and outreach, conservation culturomics, culturomics, digital data, European flounder, *Platichthys flesus*, recreational angling community, stakeholder perceptions, surveys

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Introduction

Biological invasions are widely accepted as one of the main drivers of biodiversity loss globally (Caffrey et al. 2014; Bellard et al. 2022; IPBES 2023). Invasive alien species (IAS) are causing a wide array of severe environmental and socioeconomic impacts in the invaded areas (Hawkins et al. 2015; Bacher et al. 2017; Diagne et al. 2021). While early research on biological invasions focused mainly on ecological aspects, it is increasingly recognized that their human dimensions need to be considered (Shackleton et al. 2019a). Humans play a crucial role in every step of the invasion process, from driving both intentional and unintentional introductions, to experiencing the impacts of invasive species, and having the ability to prevent future invasions and manage current ones (Pyšek et al. 2020).

It is important to understand the perceptions of stakeholders towards IAS, while recognizing that these might drastically differ between groups (Garcia-Llorente et al. 2008; Jefferson et al. 2015; Shackleton et al. 2019b). Stakeholder perceptions are essential to assess social impacts caused by IAS and can aid the prioritization of resources dedicated to management (Shackleton et al. 2019b). Furthermore, they enable managers to understand and mitigate opposition to management actions prior to implementing them (Novoa et al. 2018). Thus, awareness of biological invasions is an important driver of stakeholders' perceptions and support for management (Verbrugge et al. 2013; Courchamp et al. 2017; Novoa et al. 2017). Increasing public awareness requires good communication and outreach efforts that go beyond the classical model of top-down provision of information (Nisbet and Scheufele 2009) by initiating genuine dialogue between experts, stakeholders, and the public (Courchamp et al. 2017).

Traditional tools to document perceptions include surveys and interviews. These tools have been used to assess the perceptions of the general public on specific alien species and their management (Verbrugge et al. 2013; Novoa et al. 2017; Luna et al. 2019), as well as the perceptions of specific stakeholder groups (Garcia-Llorente et al. 2008; Trenouth and Campbell 2013). However, traditional tools require significant resources, have a limited geographic reach and potential interviewer and respondent biases, which has encouraged the development of novel approaches (Scharkow and Vogelgesang 2011; Di Minin et al. 2015). The newly established field of conservation culturomics uses digital data (Ladle et al. 2016), sourced from various platforms such as web pages, video-sharing platforms, news media, social media, and digital encyclopedias (Correia et al. 2021). These novel approaches are considered promising for the field of invasion science (Jarić et al. 2021) as they have the potential to provide valuable data (Ladle et al. 2016), especially in combination with other sources (Toivonen et al. 2019). Conservation culturomics techniques have been applied, for instance, to explore additional sources to improve the monitoring of plant pest species (Tateosian et al. 2023) and to elucidate the effects of a changing distribution of a marine IAS on recreational anglers' and spear fishermen's perceptions (Sbragaglia et al. 2022). But as promising as these approaches are, they come with their own set of challenges and biases. For example, when working with digital data, it is important to consider the potential for misinterpretation (Ficetola 2013) as well as the ethical use and the safe keeping of potentially sensitive information (Correia et al. 2021).

European flounder is a flatfish species native to the coastal areas of Western Europe (Hemmer-Hansen et al. 2007). It is a catadromous species (Summers 1979) with plasticity in its utilization of marine, estuarine and freshwater habitats (Daverat et al. 2012; Le Pichon et al. 2014). European flounder was first officially reported in Icelandic waters in 1999 after a specimen was caught in the southwest of Iceland and reported to the Marine and Freshwater Research Institute of Iceland (Jónsson et al. 2001). European flounder has previously been introduced to the Great Lakes in North America via ballast water, but without established populations (Cudmore-Vokey and Crossman 2000; Ricciardi and MacIsaac 2000). In Iceland, reports of European flounder in the years following its first record, indicated a rapid spread and established populations in most parts of the country where it was predominantly encountered in estuarine and freshwater habitats (Kristinsson 2011; Ragnarsdóttir and Metúsalemsson 2020). Despite its current classification as potentially invasive (Gunnarsson et al. 2015), knowledge of its impacts remains scarce. Small-scale studies indicate competition with native salmonids in estuaries and rivers (O'Farrell 2012; Hlinason 2013) and European plaice (*Pleuronectes platessa*, Linnaeus, 1758) on estuarine nursery grounds (Henke et al. 2020). European flounder in Iceland most abundantly occupies similar habitats as native Atlantic salmon (*Salmo salar*, Linnaeus 1758), brown trout (*Salmo trutta*, Linnaeus, 1758) and Arctic char (*Salvelinus alpinus*, Linnaeus, 1758) which are all highly sought-after recreational species and potentially impacted by competition with this alien species (O'Farrell 2012; Hlinason 2013). Therefore, we identified the Icelandic recreational angling community as one of the main stakeholders affected by European flounder in Iceland. Angling is very popular amongst the public in Iceland with 31.5% of the population participating in angling activities according to a Gallup survey conducted in 2000 (Toivonen et al. 2000). However, it is also economically important. A recent study carried out by the Institute of Economic Studies at the University of Iceland (Institute of Economic Studies 2018) estimated that total expenditure on Atlantic salmon and brown trout angling permits in Iceland in 2018 was approximately 4.9 billion krona (37 million USD) and that the economic importance of angling had increased by 120% from an earlier study carried out in 2004 (Institute of Economic Studies 2004).

The aim of this paper is to use a combination of classical and novel techniques from the field of conservation culturomics to examine (1) stakeholder perceptions towards European flounder, a recently established alien fish in Iceland, and how these change over time, (2) differences in perceptions of recreational anglers operating in the species' native and introduced range, and (3) temporal changes in the public's interest in an IAS as well as how this topic has been communicated to the public. Overall, we hypothesize that (1) recreational anglers in Iceland will have a more negative perception of European flounder than recreational anglers in the native range, (2) perceptions in Iceland change over time, and (3) traditional and novel techniques provide similar insights into the perceptions of the specific stakeholder group towards an IAS, while these culturomics approaches will highlight a more neutral tone in the communication to the public. To achieve our aim and test these hypotheses, we administered online surveys to compare recreational anglers' perceptions on European flounder in Iceland and across its native range, as well as collected information on (1) how this species was communicated within the stakeholder group and to the public, as well as (2) the public's interest in this topic using internet search volume as a proxy.

Methods

Survey design and administration

To document and contrast the perception of Icelandic (introduced range) and western European (native range) recreational angling communities towards European flounder, we created three anonymous online surveys. All three surveys were centered around four likert-style questions: 1) „Do you think the flounder could be an important recreational angling species?“, 2) „Does the flounder have a negative impact on your angling experience?“, 3) „Do you think the flounder has a negative impact on other species?“, 4) „Do you consider the flounder a pest?“ (Suppl. material 1). Other questions varied between surveys, as described below, and detailed in Suppl. material 1.

Two surveys were administered in Iceland to capture any changes in the perception of European flounder between 2019 and 2023. The first survey was administered in 2019 at the start of the first large-scale and interdisciplinary research project on European flounder in Iceland, which is still ongoing. This project engaged the Icelandic recreational angling community in the study of European flounder invasions in Iceland by creating awareness about European flounder as an alien species, examining potential social impacts experienced by recreational anglers and encouraging them to report sightings of the European flounder. While the research project was not intended as a continuous engagement effort, the positive feedback from the recreational angling community following these interactions (mainly via social media) indicated their interest in the topic and inspired the follow-up survey in 2023. The first survey was open for participation between October 2019 and June 2020. It included 17 questions to collect information on the participants' angling behavior, such as how often they fish annually and which species they target, as well as their experience with European flounder (Suppl. material 1). With frequent reminders, we shared the survey on the social media platform Facebook, frequently accessed by approximately 65% of the Icelandic population (Kemp 2024). Posts were made both on public pages of Icelandic research institutions as well as a specific group popular among Icelandic recreational anglers (Suppl. material 2). Additionally, the survey received coverage in a national Icelandic newspaper (Statistics Iceland 2024) in November 2019, encouraging participation (Jónsson 2019); Suppl. material 2). We received a total of 209 submissions. The second survey was administered in February 2023 as part of another project and, after close monitoring of the number of participants, was closed in March 2023 once a comparable number as the previous survey was reached. This survey contained nine questions of which 6 questions were relevant for this project and represented a subset of the first survey (Suppl. material 1). Again, we mainly advertised the survey via social media (Suppl. material 2). Additionally, the survey was covered in an episode of a popular Icelandic flyfishing podcast in March 2023 (Ólafsson and Harðarson 2023); Suppl. material 2). 193 people took part in this survey.

A survey aimed at recreational anglers in the European flounder's native range was administered in May 2021, again monitoring the participation numbers until the goal of ~200–220 was reached. Like the first survey conducted in Iceland, it included questions about the participants' angling behavior and their experience with European flounder. However, as recreational angling in the target countries is often conducted in coastal habitats where anglers are likely to encounter several flatfish species, a verification question was included to ensure the participants recognized the target species. In this verification question we asked participants to identify European flounder out of three pictures showing similar-looking flatfish species, European plaice (*Pleuronectes platessa*) and Common Dab (*Limanda limanda*). A verification question was assumed unnecessary for the Icelandic survey as recreational angling in Iceland conducted by the target group is mostly in freshwater habitats where European flounder is the only flatfish species present. We contacted representative institutions for advice on how to best reach the respective recreational fishing communities. We then advertised the survey in Facebook groups popular among recreational anglers in Denmark, Faroe Islands, Finland, Germany, Norway, and Sweden (Suppl. material 2). Throughout the native range a total of 224 people responded to the survey. Informed consent was obtained from all individual participants included in the study. An introduction was included in all surveys, informing participants about the background and intent of the study as well as about the anonymous nature of the survey and the confidential treatment of the resulting data.

Extracting digital data on European flounder from different sources in Iceland

We conducted a systematic review of newspaper articles published between 1999 and 2022 available on timarit.is, a digital library aiming to provide access to newspapers and periodicals published in Iceland, the Faroe Islands and Greenland. We searched the database using the keywords 'flounder' as well as the two Icelandic terms for European flounder 'ósalúra' and 'flundra' and additionally allowed the search to include all grammatical declension of the Icelandic terms. Furthermore, we searched websites of popular newspapers in Iceland using the same keywords for any unaccounted articles (http://mbl.is, http://fiskifrettir.vb.is, http://skessuhorn.is, http://bbl.is/baendabladid). We manually checked all returned articles, excluding those that were not newspaper articles referring to European flounder in Iceland and manually extracted all text data. For the quantitative analysis we categorized all articles by whether they focused on European flounder or just mentioned it.

To explore mentions of European flounder in conversations on social media in Iceland, we opted for Facebook as target social media platform as this platform is used by over 60% of the Icelandic population (Suppl. material 2) and there was only a low number of tweets on Twitter mentioning European flounder in Iceland of which most were initiated by scientists. On Facebook we identified the group „Veiðidellan er frábær…" [The fishing passion is great...] as the most active group among the recreational angling community in Iceland based on the number of members (14.289 members as of 21.12.2022, Suppl. material 2) as well as personal recommendations of recreational anglers. We searched the group for any mention of European flounder in either original posts or comments to other posts from the establishment of the group in 2013 until the end of 2022 using the same search terms as for newspaper items. We manually extracted all returned conversations and categorized them as 'focused' conversations or 'mentions' when European flounder was part of the original post or was just mentioned in the comment section, respectively. We excluded all conversations that were initiated by the authors of this study from qualitative analysis. These posts were part of the ongoing research project on European flounder.

We used Google Trends to extract information on Google searches for the keywords 'flounder' and 'flundra' in Iceland (the keyword 'ósalúra' returned no results) between 2004–2023 using the gtrendsR package (Massicotte and Eddelbuettel 2022). Google Trends returns the Search Volume Index which represents normalized, non-real-time data going back as far as 2004 (Cebrián and Domenech 2024). Each data point is weighed against the total search queries for the given location and time frame and the overall results are then scaled to a range of 0 to 100 with 100 representing the maximum value (Google 2023). While Google

Trends returns relative data, Wikipedia pageview statistics provide raw counts for how often a Wikipedia page has been requested in a given time (Wikipedia 2023). We extracted the monthly page visits for the Icelandic Wikipedia page for European flounder between July 2015 and February 2023 using the pageviews package (Keyes and Lewis 2020).

Data preparation and analysis

Unless otherwise specified, all data processing and analysis were carried out in R (R version 4.2.2, R Development Core Team (2023).

Survey data

We reviewed all survey responses and excluded submissions where participants were either not from the target country or did not at least partly respond to the likert-style questions intended to capture their perception. Additionally, submissions to the native range survey were omitted when participants failed to recognize European flounder in the verification question (Suppl. material 1). In the likert-style survey question addressing the participants' perception, the response option 'I don't know' was graphically located to the side of response options indicating (dis) agreement. In our opinion, due to this graphical placement, we cannot say with certainty whether the respondent, by choosing the 'I don't know' option, intended to express a neutral perception (i.e. neither agree nor disagree) or a lack of knowledge. The responses to the likert-style perception question were graphed using the likert package (Bryer and Speerschneider 2016). For each likert item the polarization score was calculated using the agrmt package (Ruedin 2021), a metric ranging from 0 – 1, indicating to what degree the opinions expressed are separated along the range of ranked options, with 0 indicating all responses fall in the same category while 1 indicates that responses are evenly split between two opposing categories (van der Eijk 2001). We statistically compared responses to this question across all three surveys (Suppl. material 1 question 13 of survey A), question 4 of survey B), and question 10 of survey C). To test if perceptions had changed between the two Icelandic surveys, representing a pre and post evaluation of the same target group, we applied the Wilcoxon signed rank test, to test for a significant difference between data using the wilcox.test() function of the stats package (R Development Core Team 2023). To examine if perceptions differed between recreational anglers in Iceland and in European flounder's native range, we applied the Mann-Whitney U test, due to the independency of sampled groups, using the wilcox.test() function with the parameter 'exact' set to false. To explore potential relationships between the ordinal perception variables and selected variables we employed the Kendall Tau Rank correlation using the cor.test() function of the stats package. The explanatory variables included fishing activity, Atlantic salmon importance, brown trout and Arctic char importance and European flounder experience. The binary variable 'angling activity' represented the number of days participants spent fishing per season with the options of 'less than 10 days' (pooled options '6–10 days', '1–6 days', and 'I don´t fish') and '10 or more days'. The three native salmonids as target species were split into two variables with Atlantic salmon in one and brown trout and Arctic char combined in the other to reflect the differences in the monetary value of the angling licenses. While the underlying data for the previous three variables were collected across all three surveys, questions regarding the participants' previous experience with European flounder making up the fourth exploratory variable, were only included in the first Icelandic and the native range survey. This variable summarized the participants' responses to whether they are documenting and/or keeping European flounder catches, specifically targeting European flounder and having cooked and/or consumed European flounder.

Text mining

To qualitatively explore stakeholders' perceptions and media cover of European flounder in Iceland since its arrival, we analyzed the content of all extracted newspaper articles, Facebook conversations as well as participants comments in the Icelandic surveys. The timeline of the collected data was arbitrarily split into three periods. We defined the first threshold as '2013' when the targeted Facebook group was first established. The second threshold was set at 'October 2019' marking the beginning of the research project on European flounder in Iceland, and the adjacent outreach to the public and recreational angling community. This outreach included the active engagement of stakeholders in research activities and updating them about the outcomes as well as opportunistic coverage of the research on national television (Ólafsdóttir 2021), newspapers and a podcast. This approach allowed us to not only explore potential changes in how European flounder has been communicated to and by the public, but to furthermore compare between sources in each time period, where applicable. For each period and data source we combined all text data, resulting in the six individual text corpora 'Newspapers until 2013', 'Newspapers between 2013 and October 2019', 'Newspapers since October 2019', 'Facebook conversations between 2013 and October 2019', 'Facebook conversations since October 2019' and 'Survey comments since 2019'. To create uniform corpora, we translated all sentences extracted in English into Icelandic as this was the most prevalent language across all text data.

Prior to analysis, the text data was preprocessed, including lower casing, the removal of stop words, numbers, and punctuation as well as the stemming of words (Sumathy and Chidambaram 2013). While there is a wide range of tools available to conduct these steps for English texts using R functions, resources are scarce for the Icelandic language. We therefore developed a manual approach for the preprocessing of our data. In a first step, we manually removed punctuation, numbers, and capital letters from all corpora. Then, we excluded Icelandic stop words based on two published lists (Jasonarson 2019; Friðriksdóttir and Jasonarson 2021). For the remaining words we created a list of word frequencies across all corpora which returned ~12 k unique words. To facilitate manual processing, we excluded all words with a frequency of less than five across all text data, reducing the number of individual words to 1667. This step was conducted under the assumption that words with the lowest frequencies are unlikely to have a significant effect on the overall results. From the remaining list we identified and removed additional stop words including auxiliary verbs, adverbs, given names and numbers. This resulted in 1436 words which were then translated into English. In replacement of automatic stemming, we adjusted the words manually by 1) removing (un)specific articles in translations; 2) exchanging all mentioned species' names with their respective scientific names; 3) reducing nouns and verbs to their common stem where applicable; and 4) combining adjective degrees, different tenses, active and passive voice, as well as singular and plural nouns. After implementing the translations and adjustments, we transformed all corpora using the tm package (Feinerer et al. 2008; Feinerer and Hornik 2023). To be adequately translated, some Icelandic terms required 2–3 words in English. To preserve these multiple-words translations as unique units, we connected the words visually as follows:

Icelandic: Vesturland **->** ***English:*** west Iceland -> ***in corpora:*** west.Iceland

All translations and stop word identifications were conducted by a native Icelandic speaker. To further ensure the quality of the preprocessing, all cases of difficult adjustments were reviewed by multiple authors. While we are confident to have achieved high quality results in the manual preprocessing, we recognize that some sources of errors may remain due to the subjective nature of manual approaches.

Topic and word frequency analysis

To exclude rare words from further analysis, all words with a frequency of less than five within a corpus were omitted from that specific, preprocessed corpus. Topic analysis was conducted based on Latent dirichlet allocation (LDA) using the LDA() function of the topicmodels package (Grün and Hornik 2011, 2023). The LDA algorithm is mainly guided by the two principles that documents consist of a mix of topics and that topics are made up by a mix of words. This analysis requires a predefined number of topics (k). Defining the ideal k using the FindTopicsNumber() function of the ldatuning package (Nikita 2020) remained unsuccessful, returning nonsensible results. Therefore, we continued rerunning the analysis using decreasing numbers of k until clear and distinct topics were revealed. The analysis returned both per-topic-per-word probabilities (β) as well as per-document-per-topic probabilities (γ). For each topic we defined a title based on the 10 words with the highest β-values. Based on the γ-values, we then calculated the topic composition for each of the six corpora. We generated a list of the most frequent terms for each text corpus from the transformed text data. We determined the frequency threshold for each corpus arbitrarily with the requirements that a maximum of 10 terms is retained and that all terms with the same frequency were omitted when including all of them would have increased the total terms retained to more than 10.

Results

Stakeholder perceptions of European flounder based on online surveys

For the first Icelandic survey, 205 out of 209 submissions were included in the analysis. 72% of these participants stated that they fish over 10 days annually, mostly in western Iceland with 50% reporting the southwest of Iceland and 26% the northwest. While 39% of the participants (very) often targeted Atlantic salmon, brown trout and Arctic char were (very) often targeted by 69% and 66% of the participants, respectively, (Suppl. material 3). In the 2023 Icelandic survey, 191 out of 193 responses were retained for analysis, of which 27% took part in the first survey, 30% were not sure about their previous participation, and 43% took part for the first time. 71% of participants fished for more than 10 days annually, of which 38%, 57% and 64% targeted Atlantic salmon, brown trout and Arctic char (very) often, respectively. We originally received 224 responses in the native-range survey of which 20 responses were omitted due to either incomplete answers or the respondents not fishing in the European flounder´s native range. An additional 50 answers were excluded due to failing to recognize European flounder in the verification question, leaving 154 answers for analyses. 91% of the participants considered for analysis were fishing 10 or more days annually. Fishing was conducted in nine countries with most participants fishing in Germany (36%) and Denmark (34%), followed by Norway (13%) and Sweden (13%). Atlantic salmon was (very) often targeted by 15% of the participants, and brown trout and Arctic char by 31% and 6%, respectively. When asked about additional species targeted, participants listed 50 different species. Atlantic cod (*Gadus morhua*, Linnaeus, 1758) was most often named, followed by northern pike (*Esox lucius*, Linnaeus, 1758) and European perch (*Perca fluviatilis*, Linnaeus, 1758) (Suppl. material 3).

Participants of the first Icelandic survey generally disagreed that European flounder could have a value as recreational species (90% of expressed opinions). 79% agreed that European flounder had a negative impact on their own angling experience, 96% agreed that European flounder negatively affects other freshwater species, and 88% considered European flounder as a pest (Fig. 1A). Across all statements the polarization score ranged from 0.1068 on European flounder value as recreational target species to 0.2626 on European flounder's negative effect on the angling experience (Suppl. material 4). The only significant correlation was a positive one between the importance of Atlantic salmon for participants and a strong agreement on European flounder's negative impact on the participants' angling experience (0.1778, p=0.00695, Suppl. material 5).

While a similar pattern of perceptions was observed in the follow-up survey in 2023, there was a statistically significant change towards less negative perceptions in the responses to all statements (Fig. 1, Suppl. material 6). In 2023, 86% of the participants expressing an opinion did not see a potential value of European flounder in recreational angling (Fig. 1B). 63% agreed that European flounder had a negative impact on their angling experience, 89% agreed that European flounder negatively affects other freshwater species, and 67% consider European flounder as a pest. When only including the 27% of participants indicating their participation in the previous survey, the change remained significant for all questions apart from question 1 addressing the potential recreational importance of European flounder. The polarization scores were generally higher in the second Icelandic survey and ranged from 0.1749 regarding European flounder's recreational value, to 0.4061 regarding the species' impact on the angling experience (Suppl. material 4). Here, a significant negative correlation was detected between the importance of brown trout and Arctic char as a targeted species and the agreement that European flounder is a pest (-2.4702, p = 0.0135; Suppl. material 5).

Perceptions among participants of the native range survey differed significantly from perceptions in Iceland (Suppl. material 6), with 91% of those expressing an opinion, agreeing that European flounder could be an important recreational angling species (Fig. 1C). However, 95% disagreed that European flounder is negatively impacting their angling experience, 83% disagreed that there is a negative impact on other freshwater species, and 98% disagreed that European flounder is a pest (Fig. 1C). The lowest polarization score (0.0622) was on whether European flounder is considered a pest and the highest (0.2476) regarding European flounder's impact on other species (Suppl. material 4). Participants with more prior experience with European flounder were more likely to agree that European flounder

Figure 1. Survey participants' perception towards European flounder based on their responses to the surveys. The likert graphs show the responses of participants to rating their agreement (Strongly disagree – Strongly agree) to the questions. Barplots on the right plot indicate the number of participants that expressed an opinion on the question and the number of participants that answered, 'I don't know'. The results are given for the surveys conducted in Iceland in 2019/2020 (**A**), in Iceland in 2023 (**B**) and in European flounder's native range (**C**).

could be recreationally valuable (τ = 3.2528, p = 0.00114), but less likely to agree that European flounder negatively impacts their angling experience (τ = -3.5273, p = 0.0004), negatively impacts other species (τ = -2.0508, p = 0.0403) or that European flounder is a pest (τ = -2.469, p = 0.01355) (Suppl. material 5).

Quantitative representation of European flounder in Icelandic digital sources

The systematic review of newspaper articles returned 99 articles published in Iceland between 2000 and 2022 referring to the European flounder (Fig. 2A). 35 articles were focused on European flounder in Iceland while 64 mentioned the species in relation to other topics. For most years there was a mix of focused and mentioning reporting. Generally, the reporting increased over the first years following the initial documentation of European flounder in Icelandic waters, reaching a first peak in 2005 with seven articles. Following the highest peak in 2011 with 17 articles, the reporting decreased over the following years until 2017 when no article was published featuring the European flounder. Following the on-

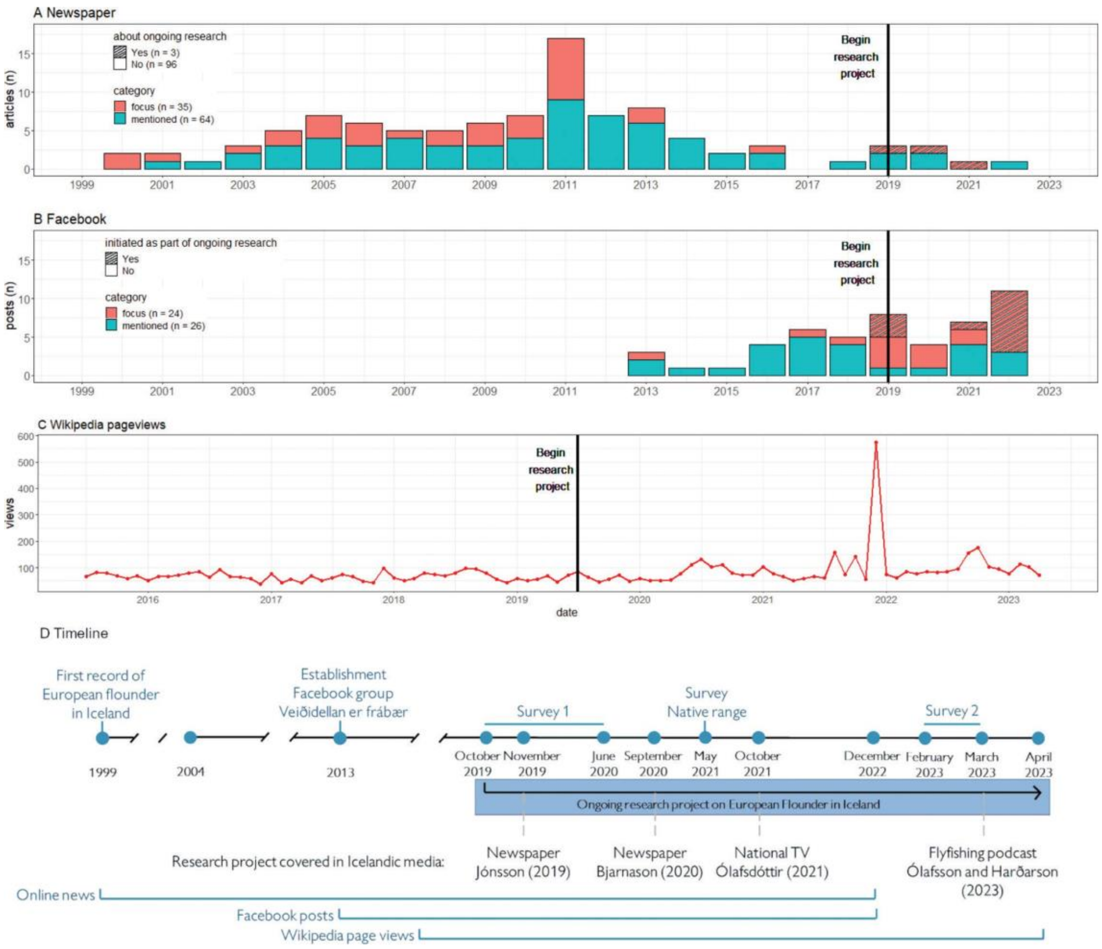

Figure 2. European flounder's presence in different media platforms as well as in search queries since 1999 **A** newspaper articles published in Iceland between 1999 and 2022 accessible on timarit.is **B** conversations in public Facebook group for recreational angling community in Iceland that either focus on or mention European flounder **C** monthly number of views of Icelandic Wikipedia article 'Flundra' between July 2015 and February 2023 **D** timeline indicating the timeline of this study, the timeline covered in the digital data as well as important dates such as the beginning of the ongoing research project on European flounder and the dates of the research covered in Icelandic media.

set of the current research the number of newspaper articles increased again with nine articles published between 2018 and 2022. Included in these numbers are two articles published in 2019 and 2020 that specifically reported on the current research (Jónsson 2019; Bjarnason 2020). We extracted 50 conversations from the target Facebook group that were posted between 2013 and 2022 (Fig. 2B). In 24 of these conversations, the original post referred to European flounder (focus), while 26 conversations mentioned European flounder only in the comments (mention). Prior to 2019, 17 conversations were classified as a mention. Since 2019, 30 conversations were recorded of which 9 were classified as a mention. Out of the conversations recorded since 2019, 12 (2019 = 3, 2020 = 0, 2022 = 8; Fig. 2B) were initiated by the authors of this study. These posts were created to inform the group about ongoing research activities on European flounder as well as to encourage survey participation. Their content was excluded from qualitative analysis to reduce potential biases.

Qualitative communication of European flounder in Icelandic (social) media content and survey comments

Across all text data, we detected three distinct topics reflecting the context in which European flounder was mentioned. Based on the ten words with the highest β values, we termed these topics 'Arrival and spread of European flounder in Iceland', 'General monitoring/surveying', and 'European flounder in recreational angling in Iceland' (Fig. 3). The main topic identified in newspaper articles published before 2013 was 'Arrival and spread of European flounder in Iceland'. Between 2013 and October 2019, the topic 'General monitoring/surveying' was most frequent among newspaper articles while it was 'European flounder in recreational angling in Iceland' in articles published since October 2019. In all analyzed Facebook conversations as well as the survey comments, the most common topic was 'European flounder in recreational angling in Iceland', while 'arrival and spread of European flounder' was least frequent. The survey comments were likely influenced by both the topic of the survey as well as its introduction to potential participants and can therefore not be considered objective. The results of the topic analysis remained similar when the survey comments were omitted, and we decided to include them in the results.

The frequency analysis returned the most frequent terms used in each source and time frame. A total of 23 unique terms were identified (Fig. 4). While 11 of these terms were corpus-specific, 12 recurred in two or more corpora. The most prominent terms, documented across all six corpora, were 'catch' and '*Platichthys flesus*'. The relative importance of the term '*Platichthys flesus*' fluctuated between corpora (Fig. 4). In the newspaper articles published before 2013, European flounder was the third most frequent term following 'catch' and 'year'. While it dropped down to rank 8 in the newspaper articles published between 2013 and October 2019, it was the most frequently used term in newspapers since October 2019. Across both Facebook and survey comments corpora, European flounder remained the most frequent word used, with percentages ranging from 21% for Facebook 2013 – October 2019 to 35% in the survey comments.

Public interest in *P. flesus* based on Google Trends and Wikipedia

The Google Trends analysis initially returned results indicating peaks of public interest in both the English (flounder) and the Icelandic (flundra) them throughout the chosen time frames. However, repeated runs of the analysis did not reproduce those results and showed remarkable differences both in the number of peaks and their timing. Because of these inconsistencies the Google Trends results are not included in any conclusions of this study. Wikipedia pageviews on the other hand produced reliable and reproducible results. Before October 2019 (i.e., the beginning of the research project on European flounder), the monthly views of the Icelandic Wikipedia page for European flounder stayed below 100 with slight fluctuations (Fig. 2C). Since the start of the research project, three time periods were recorded where the number of monthly page views appear elevated (>110). These include the periods June to September 2020, August to December 2021, as well as September to October 2022. Within the period of August to December 2021, there were three distinct spikes recorded with the strongest one exceeding 550 views in December 2021, while for the other two periods pageviews appeared generally elevated.

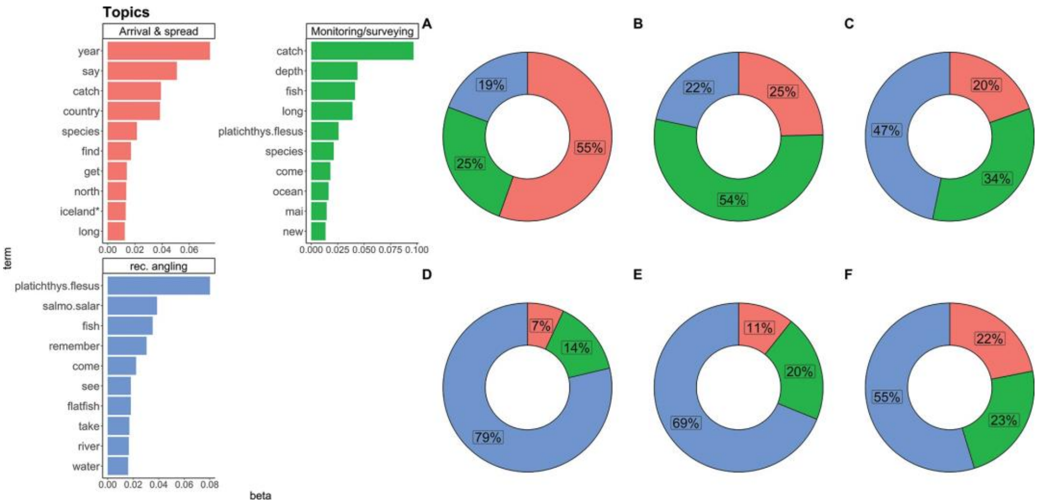

Figure 3. Identified topics newspaper articles, Facebook conversations and survey comments about European flounder. The three identified topics ‘Arrival and spread of European flounder’ (pink), ‘General Monitoring/surveying’ (green) and ‘European flounder in recreational angling’ (blue) and their respective 10 most frequent words are displayed in barplots on the left-hand side. The calculated topic composition for each of the six corpora are pictured in donut plots on the right-hand side **A** newspaper before 2013 (n = 72 articles) **B** newspaper 2013 – Oct. 2019 (n = 20 articles) **C** newspaper since Oct. 2019 (n = 6 articles) **D** facebook 2013 – Oct. 2019 (n = 25 posts) **E** facebook since Oct. 2019 (n = 13 articles) **F** survey comments (n = 22 comments)

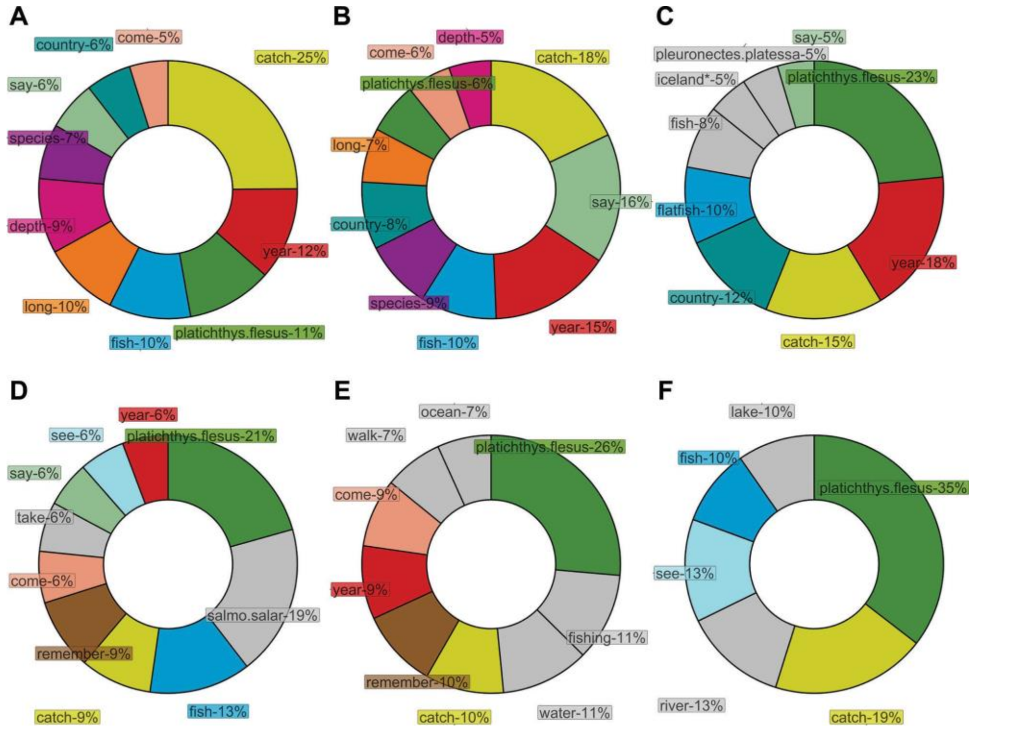

Figure 4. The most frequent terms identified for each corpus. The donut graphs display up to ten terms where corpus-specific terms are in grey and recurring terms are highlighted with individual colors **A** newspaper before 2013 (n = 72 articles) **B** newspaper 2013 – Oct. 2019 (n = 20 articles) **C** newspaper since Oct. 2019 (n = 6 articles) **D** facebook 2013 – Oct. 2019 (n = 25 posts) **E** facebook since Oct. 2019 (n = 13 articles) **F** survey comments (n = 22 comments)

Discussion

In this study we examined stakeholders' perceptions towards alien European flounder in Iceland using both traditional surveys and novel culturomics approaches. Our results from traditional surveys show that Icelandic recreational anglers have negative perceptions towards the European flounder, which stands in strong contrast to the positive perceptions documented among recreational anglers in the species' native range. However, the results we obtained by using novel culturomic approaches (Ladle et al. 2016) did not indicate similar negative perceptions in how the flounder has been communicated to the public in Iceland, or how it was discussed within the targeted stakeholder group of recreational anglers.

Stakeholder perceptions towards European flounder in Iceland and its native range

The survey results showed that recreational anglers in Iceland had strong opinions about European flounders' negative impact on their angling experience, on native species and, overall, considered it a pest. On the other hand, the results of the survey we distributed in the European flounder's native range showed that recreational anglers consider the species to have a recreational value and no negative effects. In its native range, European flounder is considered a popular sportfish especially for beginners as it is valued for its availability in shallow waters and its readiness to bite (Skerritt 2010). Perceptions towards alien species can be influenced by a variety of factors (Shackleton et al. 2019b). One possible explanation for this great difference in perceptions between invaded and native range could be that the strongly negative perceptions of recreational anglers in Iceland are likely to be less driven by the general characteristics of the species but rather its status as an alien species and its perceived threat to native species. Although research on the impacts of European flounder on native salmonids (O'Farrell 2012; Hlinason 2013) is limited, the overlap with this alien species could be perceived as a threat, especially considering that the Arctic char population in Iceland has been continuously decreasing since 2000 (Guðbergsson 2014), which coincides with the arrival of European flounder (Jónsson et al. 2001). Personal experience with an introduced species as well as emotional connectedness to impacted native species or ecosystems can drive perceptions (Fischer and van der Wal 2007; Kueffer 2013). The survey results indicate that Icelandic recreational anglers perceive a negative impact by the presence of European flounder while targeting more sought-after species, such as Atlantic salmon or brown trout. Considering the popularity of recreational angling in Iceland (Toivonen et al. 2000), anglers are likely to be emotionally attached to the fishing environment and its native species, therefore the European flounder is perceived as a threat even in the absence of scientific research on its ecological impacts. Additionally, perceived economic threats can influence attitutes towards alien species (Verbrugge et al. 2013). Especially those stakeholders with financial interest, such as river owners, could fear that the presence of European flounder could influence license purchases and therefore cause financial damage.

The follow-up survey conducted in 2023 documented a significant change in perception. Most notably that 1) less people consider the European flounder as a pest and 2) less people perceive it to have a negative impact on their angling experience. However, the available data does not enable us to pinpoint the specific driver of these change in perceptions. One potential explanation is that the continuous engagement with the recreational fishermen, mostly via social media, led to an increased media coverage. The research was covered across multiple media sources, spanning newspaper articles (Jónsson 2019; Bjarnason 2020), national TV (Ólafsdóttir 2021), and a podcast interview (Ólafsson and Harðarson 2023). Through this increased exposure, stakeholders might have gotten more familiar with the presence of European flounder in the Icelandic ecosystem. While this has not increased the species' recreational value in their eyes, it decreased their perception of the European flounder as a threat to their angling activities. This is in line with previous research suggesting that in addition to prolonged exposure, awareness and knowledge among the public and stakeholders can shape perceptions (e.g. (Garcia-Llorente et al. 2008; Sharp et al. 2016; Courchamp et al. 2017) which in turn is influenced by how an issue is communicated by the scientific community (Nisbet and Scheufele 2009). Overall, little attention has been paid to the socio-economic impacts of alien species in Iceland (Kourantidou et al. 2022). This study therefore provides an important addition to our knowledge of human aspects and, especially, the social impacts of an alien species in Iceland.

Is the documented perception of stakeholder groups reflected in digital data?

Our methodological comparison indicated a mismatch between traditional and novel tools applied to explore perceptions towards European flounder in Iceland. When directly interacting with the targeted stakeholder group using online surveys, we documented highly negative perceptions. However, when we applied novel approaches to explore how European flounder has been communicated within the recreational angling community on social media, the most frequent words cannot be linked to a negative perception. The neutral tone in these communications is surprising. As most survey participants were targeted through the specific Facebook group, we expected to see the strongly negative perceptions captured in the surveys to at least be partially reflected in the results of the social media conversations. The common words and neutral topics notable in the newspapers are less surprising as they may just reflect the contrasting perceptions of the public and the stakeholders towards the European flounder. That is, the application of novel tools enables us to contrast potential differing perceptions between the general public and specific stakeholder groups.

Such comparative studies are needed to address the validity of results obtained applying conservation culturomics (Ficetola 2013; Correia et al. 2021; Jarić et al. 2021). Here, the case study of European flounder in Iceland represents a valuable opportunity for such methodological comparison to detect stakeholders' perceptions towards an alien species. Based on the surveys we have a thorough understanding of prevailing perceptions among the recreational angling community and due to the advantageous characteristics of questionnaires, especially the use of fixed answers and questions (Newing 2011), we were able to quantify them. Despite some great advantages, these traditional tools also come with certain limitations and shortcomings (Newing 2011). Factors such as limited geographic range and the potential bias of researchers as well as participants potentially influence the results (Newing 2011; Di Minin et al. 2015). However, we are confident that by advertising the online surveys not only via social media but also via channels such as newspaper articles and a podcast, we have captured the perception of a representative group of participants across the surveys conducted in 2019 and

2023. At the same time we have a holistic overview of how the arrival and spread of European flounder in Iceland has been communicated to the public via newspaper articles and within the stakeholder group over the past decade based on the data retrieved from a representative Facebook group.

Several factors could have contributed to the detected mismatch. One factor is a potential language bias that arises when utilizing textual data that is predominantly in Icelandic, a language currently spoken by less than 500.000 people globally. The use of non-English, non-major languages remains a challenge to these novel approaches (Funk and Rusowsky 2014; Ladle et al. 2016). It would have been preferential to apply sentiment analysis, a culturomics tool that has been increasingly used to highlight the perceptions and attitudes towards a specific topic across various forms of media (Lennox et al. 2020). As tools to conduct sentiment analysis on Icelandic texts are not yet available, we chose alternative approaches based on word frequencies. Both the unavailability of sentiment analysis of Icelandic texts as well as the translation work described previously could have contributed to the absence of negative perceptions in newspaper articles and social media conversations. Another potential factor is the scale of the case study, as Iceland is a small country. While this enabled us to capture a holistic picture of the communication of European flounder, the amount of data produced since the first documentation of European flounder might not have been sufficient to adequately capture the perceptions of the public and/or specific stakeholder groups through the analyses of digital data. Our results suggest that in the case of small-scale study systems, novel culturomics tools can provide valuable information, but should be applied complementary to traditional tools that directly interact with the target group to document prevailing perceptions and attitudes.

Linking communication to peaks in the public's interest in European flounder

Our results show fluctuations in the public´s interest in European flounder since its arrival in Iceland. While the term '*Platichthys flesus*' was among the three most frequent terms used in newspaper articles until 2013, a timeframe in which European flounder became increasingly present in Icelandic waters, it became much less frequently used in articles published between 2013 and October 2019. This development is in line with the transient nature of the public's attention towards conservation issues and many other global issues (Jarić et al. 2023), especially once the novelty of a topic wears off. However, following October 2019, the term became the most widely used term in the newspaper articles, potentially driven by the increased research and communication activities.

Public interest in Iceland, based on the temporal development of the number of times the Icelandic Wikipedia page for European flounder has been accessed, showed some distinct fluctuations over time that partially coincided with the current research being covered in Icelandic media. Both the newspaper article in September 2020 (Bjarnason 2020) as well as the coverage on national TV in October 2021 (Ólafsdóttir 2021) were followed by short-term elevations in public interest. Additionally, a prominent peak was documented in December 2021, following an episode of the flyfishing podcast *Hylurinn* where European flounder was discussed in an interview with a scientist at the Icelandic Marine and Freshwater Research Institute (MFRI) (Ólafsson and Harðarson 2021). While we could only identify potential triggers for a subset of the short-term peaks, these results indicate that public interest can be triggered by a variety of different platforms. This suggests that communication strategies could benefit from incorporating different communication platforms catering to different groups. By understanding the dynamics of the public‘s attention, we can not only learn how to trigger periods of increased interest, we can furthermore try to predict windows of opportunity where communication and outreach campaigns are likely to be most effective (Fink et al. 2020; Jarić et al. 2023). A popular tool to approximate public interest in a certain topic is Google Trends (Nghiem et al. 2016). However, in the case of European flounder in Iceland, Google Trends did not provide reliable results. The inconsistencies occuring between samplings are driven by the underlying characteristics of the analysis utilized by Google Trends, where only a subset of the total search queries are used to provide the Search Volume Index for the specific keywords and the subset used changes from day to day (Cebrián and Domenech 2024). These inconsistencies can be addressed for instance by drawing the average of repeated samplings which has been successfully applied in studies, indicated by cross-correlations of 79 – 99% between samplings (D'Amuri and Marcucci 2017; Cebrián and Domenech 2022). But the simulations carried out by Cebrián and Domenech (2024) further highlight that terms of low popularity produce a greater amount of variability, which would require a large number of repeated samplings to reduce the noise. European flounder in Iceland likely represents a low-popularity term, explaining the vast differences detected in the Google Trends results. Overall, this further highlights the limitations of conservation culturomic approaches in regards to small-scale studies.

Conclusion

Our results are consistent with the view that the social dimensions of biological invasions are crucial to obtain a holistic understanding of the impacts of alien species. The results of the current study highlight that perceptions of a species can profoundly differ between invaded and native range. While an alien species is perceived as highly negative in its introduced environment, the same species can be highly valued for its traits by a comparable stakeholder group in its native range. Furthermore, we show that stakeholders' perceptions and public interest in an alien species can fluctuate over time. Identifying potential triggers of these changes can represent a valuable lesson to design future outreach campaigns to increase public awareness and encourage the public to report their observations. In turn, those observations can contribute to early detections and monitoring of alien species. Finally, our study showcases the benefits of utilizing culturomics but also highlights limitations when applying some of these approaches on non-English text data in small countries.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: GÁÓ, AN, TH. Data curation: TH. Formal analysis: TH. Funding acquisition: TH, GÁÓ. Investigation: TH. Methodology: GÁÓ, AN, TH. Project administration: TH. Visualization: TH. Writing - original draft: TH. Writing - review and editing: GÁÓ, AN, HB.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Survey questions included in the three administered surveys

Authors: Theresa Henke, Ana Novoa, Hlynur Bárðarson, Guðbjörg Ásta Ólafsdóttir

Data type: pdf

Explanation note: A) Iceland 2019/2020, B) Iceland 2023, and C) native range.

Link: https://doi.org/10.3897/neobiota.93.117200.suppl1

Supplementary material 2

Statistical information on Facebook groups and media platforms

Authors: Theresa Henke, Ana Novoa, Hlynur Bárðarson, Guðbjörg Ásta Ólafsdóttir

Data type: pdf

Explanation note: Statistical information on Facebook groups and media platforms utilized to advertise surveys among recreational anglers in Iceland as well as institutions that were contacted in relation to advertising the survey throughout the European flounders´ native range.

Link: https://doi.org/10.3897/neobiota.93.117200.suppl2

Supplementary material 3

Descriptive statistics for the three administered surveys Iceland 2019/2020, Iceland 2023 and Native range 2021

Authors: Theresa Henke, Ana Novoa, Hlynur Bárðarson, Guðbjörg Ásta Ólafsdóttir

Data type: pdf

Link: https://doi.org/10.3897/neobiota.93.117200.suppl3

Supplementary material 4

Polarization scores for the responses to the four likert-style questions across all three surveys

Authors: Theresa Henke, Ana Novoa, Hlynur Bárðarson, Guðbjörg Ásta Ólafsdóttir

Data type: pdf

Explanation note: Low polarization scores indicate that responses are skewed to one side while a higher score suggests a more even distribution in the responses ranging from “strongly disagree” to “strongly agree”.

Link: https://doi.org/10.3897/neobiota.93.117200.suppl4

Supplementary material 5

Results of the Kendall Tau Rank correlation for all surveys

Authors: Theresa Henke, Ana Novoa, Hlynur Bárðarson, Guðbjörg Ásta Ólafsdóttir

Data type: pdf

Explanation note: We tested for potential relationships between the variables describing the perception of participants towards European flounder and selected explanatory variables. Significant results are highlighted in bold.

Link: https://doi.org/10.3897/neobiota.93.117200.suppl5

Supplementary material 6

Statistical comparisons of participants responses to the likert-style questions between surveys

Authors: Theresa Henke, Ana Novoa, Hlynur Bárðarson, Guðbjörg Ásta Ólafsdóttir

Data type: pdf

Explanation note: Wilcoxon rank test and Mann Whitney U test were employed to compare responses between the two Icelandic surveys and between the native range and Icelandic surveys, respectively.

Link: https://doi.org/10.3897/neobiota.93.117200.suppl6

Supplementary table 1. Survey questions included in the three administered surveys. A) Iceland 2019/2020, B) Iceland 2023, and C) native range.

A) Iceland 2019/2020
1. What option describes you best? (Choose 1 option) Options: recreational fisherman / landowner / lease holder / river manager / other
2. How many days do you spend fishing per season? (choose 1 option) Options: > 10 days / 6 – 10 days / 1 – 6 days / I don´t fish
3. In which region(s) do you spend the most time fishing. Please reply by regions as they are defined on the map (Can choose multiple options) Options: Northwest / Northeast / Southwest / Southeast
4. Before you responded to this survey, were you aware of the flounder in Icelandic waters? (Choose 1 option) Options: Have caught flounder / Have seen flounder / Have heard about flounder / No

5. How often do you catch these species when you fish? (5-point likert: Very often / Often / Occasionally / Rarely / Never) Options: Salmon / Anadromous brown trout / Anadromous Arctic char / Flounder
6. If you have caught flounder, what year did you first catch it? (Open text)
7. If you have caught flounder, can you name the site where you first caught it? (Open text)
8. Please indicate the locations where you have seen or caught flounder. (5 point likert: Very often / Often / Occasionally / Rarely / Never) Options: In the estuary / In river, < 50 m from estuary / In river, > 50 m from estuary
9. Can you name river/estuaries where you have seen or caught flounder? (Open text)
10. In the last 5 years .... (Choose 1 option) Options: I have caught more flounder / I have caught less flounder / No change / I have not caught flounder
11. In which month(s) do you go fishing? (Can choose multiple) Options: April – October
12. Please tick the month(s) when you have seen/caught flounder (Can choose multiple) Option: April – October
13. Please rate the following statements (5-point likert: Strongly agree / Somewhat agree / Somewhat disagree / Strongly disagree / I don´t know) Statements: The flounder could be a commercially valuable fish species in recreational fishing / The flounder negatively impacts my fishing experience / The flounder has negative impacts on other species in the river / The flounder is a pest
14. Please rate the following statements (3-point likert: No / Yes / I don´t know) Statements: Do you document your flounder catches? / Do you keep flounder if caught? / Have you prepared and cooked flounder? / Do you ever fish specifically to catch flounder? / Have you eaten flounder?
B) **Iceland 2023**
1. Did you take part in the survey about flounder in 2019/2020? (Choose 1 option) Options: Yes / No / I am not sure-I don´t remember
2. Have you caught or seen flounder? (Choose 1 option) Options: I have caught flounder / I have seen flounder / No
3. How many days do you spend fishing per season? (choose 1 option) Options: > 10 days / 6 – 10 days / 1 – 6 days / I don´t fish
4. How often do you fish for these species? (5-point likert: Very often / Often / Occasionally / Rarely / Never) Options: Salmon / Anadromous brown trout / Anadromous Arctic char / Flounder
5. Please rate the following statements (5-point likert: Strongly agree / Somewhat agree / Somewhat disagree / Strongly disagree / I don´t know) Statements: The flounder could be a commercially valuable fish species in recreational fishing / The flounder negatively impacts my fishing experience / The flounder has negative impacts on other species in the river / The flounder is a pest
6. Do you think it makes a difference whether the flounder arrived naturally or if it arrived due to human influence (for example with ships?) (Choose 1 option) Options: Yes / No / I don´t know
7. Please rank the following statements according to their importance in dealing with flounder in Iceland. The most important statement is placed on top and what you rank the least important should be at the bottom. (Ranking) Statements: Monitor the distribution of flounder in Iceland / Identify how the flounder arrived in Iceland / Try to prevent the arrival of other potential invasive species in the future / Explore

for potential options to restrict flounder from entering upper parts of river / Investigate the effects of flounder on other species / Develop methods to use the flounder
C) Native range
1. In which country do you fish? (Can choose multiple options) Options: Germany / UK / Sweden / Denmark / Estonia / Latvia / Finland / Lithuania / Faroese Islands / Poland / Russia / Norway / Other
2. How many days do you spend fishing per season? (choose 1 option) Options: > 10 days / 6 – 10 days / 1 – 6 days / I don´t fish
3. How often do you fish for these species? (5-point likert: Very often / Often / Occasionally / Rarely / Never) Options: Salmon / Anadromous brown trout / Anadromous Arctic char / Flounder
4. If there are more species that you target, that have not been listed above, please specify. (Open text)
5. Please indicate which of these 3 pictures shows a flounder? (Choose 1 option) Option: Common dab / European flounder / European plaice
6. Please indicate the locations where you have seen or caught flounder (5-point likert: Very often / Often / Occasionally / Rarely /Never) Options: marine waters / estuary / river within 1 km from estuary / river > 1 km from estuary
7. In the last 5 years .... (Choose 1 option) Options: I have caught more flounder / I have caught less flounder / No change / I have not caught flounder
8. In which month(s) do you go fishing? (Can choose multiple) Options: April – October
9. Please tick the month(s) when you have seen/caught flounder (Can choose multiple) Option: April – October
10. Please rate the following statements (5-point likert: Strongly agree / Somewhat agree / Somewhat disagree / Strongly disagree / I don´t know) Statements: The flounder could be a commercially valuable fish species in recreational fishing / The flounder negatively impacts my fishing experience / The flounder has negative impacts on other species in the river / The flounder is a pest
11. Please rate the following statements (3-point likert: No / Yes / I don´t know) Statements: Do you document your flounder catches? / Do you keep flounder if caught? / Have you prepared and cooked flounder? / Do you ever fish specifically to catch flounder? / Have you eaten flounder?
12. Before taking part in this survey, did you know about the introduction of flounder in Iceland? (Choose 1 option) Options: Yes / No / Other

Supplementary table 2. Descriptive statistics for the three administered surveys Iceland 2019/2020, Iceland 2023 and Native range 2021

	Iceland 2019/2020	**Iceland 2023**	**Native range 2021**
Participants			
Total	209	193	224
Included in analysis	**205**	**191**	**154**
Incomplete answers	4	2	20
Failed verification	-	-	50
Previous participation			
Yes	-	52 (27%)	-
Unsure	-	58 (30%)	-
No	-	80 (42%)	-
Fishing activity			
> 10 days annually	148 (72%)	136 (71%)	140 (91%)
< 10 days annually	57 (28%)	55 (29 %)	14 (9%)
Region fished (Iceland)			
Southwest	140 (50%)	-	-
Northwest	73 (26%)	-	-
Northeast	44 (16%)	-	-
Southeast	22 (8%)	-	-
Countries fished			
Germany	-	-	87 (36%)
Denmark	-	-	81 (34%)
Sweden	-	-	31 (13%)
Norway	-	-	31 (13%)
Ireland	-	-	4 (1.7%)
Faroe Islands	-	-	3 (1.2%)
Netherlands	-	-	2 (0.8%)
Poland	-	-	1 (0.4%)
Latvia	-	-	1 (0.4%)
Species targeted (very) often			
Atlantic salmon	80 (39%)	73 (38%)	23 (15%)
Brown trout	142 (69%)	122 (64%)	47 (31%)
Arctic char	135 (66%)	108 (57%)	6 (4%)
Other target species named			
n individual species	-	-	50
n species mentioned	-	-	439
Top 5			
Cod (*Gadus morhua*)	-	-	73 (17%)
Pike (*Esox lucius*)	-	-	43 (10%)
Perch (*Perca fluviatilis*)	-	-	32 (7%)
Mackerel (*Scomber scombrus*)	-	-	29 (7%)
Herring (*Clupea harengus*)	-	-	24 (6%)

Supplementary table 3. Polarization scores for the responses to the four likert-style questions across all three surveys. Low polarization scores indicate that responses are skewed to one side while a higher score suggests a more even distribution in the responses ranging from "strongly disagree" to "strongly agree".

	Iceland 2019/2020	**Iceland 2023**	**Native range**
Do you think the flounder could be an important recreational species?	0.1068	0.1749	0.2104
Does the flounder have a negative impact on your fishing experience?	0.2626	0.4061	0.0732
Do you think the flounder has a negative impact on other species?	0.1641	0.2091	0.2476
Do you think the flounder is a pest?	0.2031	0.3607	0.0622

Supplementary table 4. Statistical comparisons of participants responses to the likert-style questions between surveys. Wilcoxon rank test and Mann Whitney U test were employed to compare responses between the two Icelandic surveys and between the native range and Icelandic surveys, respectively.

	Iceland 2019/2020 - Iceland 2023	**Iceland 2019/2020 – Native range**	**Iceland 2023 – Native range**
	Wilcoxon rank test	Mann Whitney U test	Mann Whitney U test
Do you think the flounder could be an important recreational species?	W=10908 p=0.0202 *	W = 20614 p = < 2.2e-16 ***	W = 20978 p = < 2.2e-16 ***
Do you think the flounder has a negative impact on your angling experience?	W = 17754 p = 7.129e-055 ***	W = 1515 p = < 2.2e-16 ***	W = 2893.5 p = < 2.2e-16 ***
Do you think the flounder has a negative impact on other species?	W = 8387.5 p = 0.004445 **	W = 625 p = < 2.2e-16 ***	W = 864 p = < 2.2e-16 ***
Do you think the flounder is a pest?	W = 12549 p = 0.0001718 ***	W = 311 p = < 2.2e-16 ***	W = 1510 p = < 2.2e-16 ***

Supplementary table 5. Results of the Kendall Tau Rank correlation for all surveys. We tested for potential relationships between the variables describing the perception of participants towards European flounder and selected explanatory variables. Significant results are highlighted in bold.

Explanatory variables	Perception rec. Angling	Perception impacts angling	Perception impacts species	Perception Pest
Iceland 2019/20				
Angling activity	-0.1317 p=0.0954	0.0204 p=0.7807	0.0627 p=0.4722	0.04922 p=0.53
Salmon importance	-0.0949 p=0.1814	**0.1778 p=0.00695**	-0.0075 p=0.925	0.05558 p=0.4319
Trout/Char importance	-0.0538 p=0.4151	0.0538 p=0.4114	0.0192 p=0.8059	0.06704 p=0.3394
***P. flesus* experience**	0.0751 p=0.3029	-0.0392 p=0.5736	-0.0068 p=0.9323	0.01099 p=0.8789
Iceland 2023				
Angling activity	-1.154 p=0.2485	0.95239 p=0.3409	0.86283 p=0.3882	0.50852 p=0.6111
Salmon importance	-1.2955 p=0.1952	-0.48308 p=0.629	-1.331 p=0.1832	-0.1245 p=0.9009
Trout/Char importance	0.8663 p=0.05063	-0.8212 p=0.4116	-0.30664 p=0.759	**-2.4702 p=0.0135**
Native range				
Angling activity	-1.2738 p=0.2027	0.56569 p=0.5716	-1.5728 p=0.1158	-0.8755 p=0.3813
Salmon importance	0.13838 p=0.8899	**2.4041 p=0.01621**	-0.6942 p=0.4875	0.8785 p=0.3797
Trout/Char importance	0.86625 p=0.3864	-0.84338 p=0.399	0.78333 p=0.4334	-1.4744 p=0.1404
***P. flesus* experience**	**3.2528 p=0.00114**	**-3.5273 p=0.0004**	**-2.0508 p=0.0403**	**-2.469 p=0.01355**

8 Paper III

Have you seen this fish? Important contribution of stakeholder observations in documenting the distribution and spread of an alien fish species in Iceland

Henke T., Bárðarson H., Thorlacius M., Ólafsdóttir, G. Á. (accepted for publication in Neobiota)

Author contributions: T.H. and G.Á.Ó. conceptualized the study. T.H.conducted the data curation and H.B. and M.T. provided European flounder distribution data based on the MFRI databases. T.H. conducted initial analysis and G.Á.Ó. further contributed to it. T.H. wrote the original draft and G.Á.Ó., H.B., and M.T. provided revisions.

Title: Have you seen this fish? Important contribution of stakeholder observations in documenting the distribution and spread of an alien fish species in Iceland

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Abstract

To address the increasing global issue of biological invasions adequate long-term monitoring data is crucial. Due to substantial resource requirements such continuous monitoring remains largely underdeveloped across many countries. In recent years, experiential knowledge of the public, or specific stakeholder groups, has become increasingly popular to gather species' occurrence data. In the context of aquatic alien species recreational fishermen often represent a valuable stakeholder group. Using the case study of alien European flounder (*Platichthys flesus,* Linneaus 1758) in Iceland, we explore the benefits of incorporating stakeholder observation-based information with traditionally obtained data on the occurrence and distribution of an alien fish. We compiled records of European flounder reported by the recreational fishing community both when directly approached with an anonymous online survey as well as via social media conversations applying the approach of iEcology. We then contrasted this data to a compilation of European flounder records from databases at the Icelandic Marine and Freshwater Research Institute (MFRI). Our results show that including stakeholder-observation based distribution data in the monitoring of alien species offers significant advantage. While all data sources indicated similar patterns in the spread and distribution of European flounder in Iceland, they differed in the number of unique sites provided as well as their geographic distribution. Combining sources therefore allows to counteract inherent biases present across diverse sources. Our study furthermore indicates that interest to voluntarily report European flounder sightings decreased over time, but reemerged when stakeholders and/or the public were presented with an easily accessible opportunity to share information in the form of an online survey. We recommend implementing a monitoring approach for alien species that incorporates diverse sources of information and provides clear venues to report information for the public, and where possible involve stakeholders throughout the entire research process to holistically address biological invasions.

Keywords Biological invasions, Monitoring, iEcology, Stakeholder observations, Recreational fishermen; European flounder; Local Ecological Knowledge

Introduction

Biological invasions are an increasing global phenomenon (Seebens et al. 2017; Seebens et al. 2020) that can cause severe negative impacts on the recipient environment (IPBES 2023;

Schwindt et al. 2023) and result in substantial economic costs (Cuthbert et al. 2021). Managing the emerging alien species depends on the availability of timely data regarding their occurrence and spread (Groom et al. 2015; Cardoso et al. 2017; Latombe et al. 2017). Unfortunately, systematic management and monitoring of alien species is underdeveloped across many countries (Lehtiniemi et al. 2015; Latombe et al. 2017; Schwindt et al. 2023), often driven by the mismatch between the resources required for adequate monitoring and the funding available to the relevant management agencies and institutions (Piria et al. 2017; Robinson et al. 2020). As the detection rate of new aquatic alien species remains high (Bailey et al. 2020), diverse data sources are increasingly being used to refine distribution estimates (Hargrove et al. 2015; Jarić et al. 2020b; Robinson et al. 2020). These sources include public repositories, unpublished data and interviews with experts, such as those used by Ferreira-Rodríguez et al. (2020) to investigate the historical spread of the Asian clam *Corbicula* sp. in the Lower Danube region. Generally, it is increasingly recognized that collaborations between local stakeholders and researchers can greatly improve the collection of geospatial data (See et al. 2016). Information provided by the public or other stakeholders has often been utilized in invasion science for mapping and monitoring purposes, including studies on plants (Marchante et al. 2016; César de Sá et al. 2019; Gervazoni et al. 2023) and aquatic species (Ferreira-Rodríguez et al. 2020; Herrero et al. 2023).

Under the premise that people either possess valuable information based on their experiences and observations or are willing to learn new skills and contribute to the scientific process, the public can participate at various levels in survey projects (See et al. 2016). Local ecological knowledge (LEK) is defined as knowledge that has established within a specific group of people over time through their interactions with the local ecosystems and/or the utilization of local natural resources. It can be described as a knowledge-practice-belief concept (Olsson and Folke 2001; Löki et al. 2023). At a minimum this entails incorporating stakeholder observations as part of LEK in monitoring activities but ideally, stakeholders are involved throughout the entire research process, allowing them to holistically integrate their knowledge, experiences, and opinions to shape the process and outcome of projects beyond the simple provision of occurrence data. Information on stakeholder observations can be collected via a variety of sources and approaches, such as by directly interacting with target groups through interviews and online questionnaires (Löki et al. 2023) or accessing biodiversity platforms like iNaturalist (Howard et al. 2022). Finally, the emerging field of iEcology, defined as "the study of ecological patterns and processes using online data generated for other purposes and stored digitally" (Jarić et al. 2020a), offers promising, low-cost approaches to collect ecologically relevant data (Jarić et al. 2020a; Jarić et al. 2021). Following the approach of iEcology, data can be harnessed from various sources including social media platforms like Facebook (Pace et al. 2019).

European flounder (*Platichthys flesus,* Linneaus 1758) is a flatfish species that has been documented in Icelandic waters since 1999 (Jónsson et al. 2001) and is currently classified as potentially invasive (Gunnarsson et al. 2015). The species' native range is western Europe ranging from the Mediterranean Sea to the White Sea (Wilson and Veneranta 2019) where it is found in marine, estuarine and freshwater habitats (Skerritt 2010). The European flounder is catadromous (Summers 1979) but plasticity in life history and habitat utilization have been documented in several studies (Daverat et al. 2012; Le Pichon et al. 2014). Previous introductions of European flounder are known from the Great Lakes in North America, where it was introduced via ballast water but failed to establish (Cudmore-Vokey and Crossman 2000; Ricciardi and MacIsaac 2000). In the years following its first identification in Iceland, European flounder has rapidly spread throughout the country (Kristinsson 2011; Ragnarsdóttir and Metúsalemsson 2020) and while it is mostly encountered in nearshore habitats and estuaries (Henke et al. 2020), it also enters rivers and lakes (O´Farrell 2012; Hlinason 2013). Current information on the distribution of European flounder in Icelandic waters has accumulated through various sources, both formal (i.e. collected by scientific institutions) and informal (i.e. newspaper articles, interviews and similar) (Lúðvíksson 2013; Gunnarsson et al. 2015; NA 2017; Ragnarsdóttir and Metúsalemsson 2020), but there is no ongoing scientific monitoring program for this species. Investigations on the impacts of European flounder are limited but indicate potential competition with and direct predation on native fishes such as European plaice (*Pleuronectes platessa*) (Henke et al. 2020) and salmonids (O´Farrell 2012; Hlinason 2013). Furthermore, recreational anglers in Iceland perceive European flounder to negatively impact their angling activities (Henke et al. 2024). Globally, recreational fishermen have been successfully involved in various studies across different research fields (Löki et al. 2023) and the recreational fishing community in Iceland represents an important stakeholder group that frequently encounters the European flounder (Henke et al. 2024). In Iceland, recreational fishing is popular, with approximately 32.5 % of the population participating (Toivonen et al. 2000), and with a revenue of approximately 4.9 billion krona (37 million USD) in angling permits purchased for Atlantic salmon and brown trout (Institute of Economic Studies 2018).

The Marine and Freshwater Research Institute (MFRI) in Iceland conducts many annual surveys targeting native species, for example to evaluate commercial marine ground fish species, and to monitor salmonid stocks in fishing rivers (Jakobsdóttir et al. 2023; Helgason and Bárðarson 2024). Additionally, previous research has shown a high willingness among recreational anglers in Iceland to participate in and contribute to research (Henke et al. 2024). Considering these two aspects, the case study of European flounder in Icelandic waters offers a valuable opportunity to explore the potential of incorporating stakeholder observations in the monitoring of an alien fish species in countries that, despite developed surveying system for many aquatic resources, has no established approach for the monitoring of aquatic alien species.

In the current study we contrast occurrence data of European flounder based on stakeholder observations to data from monitoring and research programs of the MFRI with the goal of evaluating if stakeholder observation-based data can supplement alien fish species monitoring in Iceland. First, we specifically targeted the recreational fishing community in Iceland as a source for occurrence data of European flounder, both with an online survey and with an iEcology approach by mining Facebook posts for location data. Moreover, we use multiple data sources available from the MFRI, marine ground fish surveys and salmonid monitoring, but also logbooks from recreational fishing rivers and voluntary reports of unusual or occurrences of rare fishes received by the MFRI (rare fish database). Specifically, we ask 1) Does European flounder distribution and spread estimates differ by different data sources, that is, regular surveys vs. stakeholder observation-based methods?; and 2) Is stakeholder observation-based data, including MFRI data provided by the public (logbooks and rare fish), a viable option for monitoring alien fish species in Iceland? We discuss the findings in the context of strengths and weaknesses of different data sources as a tool for monitoring and how the data availability indicates public and stakeholder willingness to contribute data.

Methods

For the purpose of this study, we have obtained occurrence data of European flounder in Iceland from six different sources (Figure 1). In the following paragraphs we will introduce each source and provide additional information including how the data for each source was collected, indicate available parameters (i.e. time stamps and exact coordinates), as well as steps that have been taken to address differences in these available parameters. Furthermore, we outline the subsequent steps of analysis.

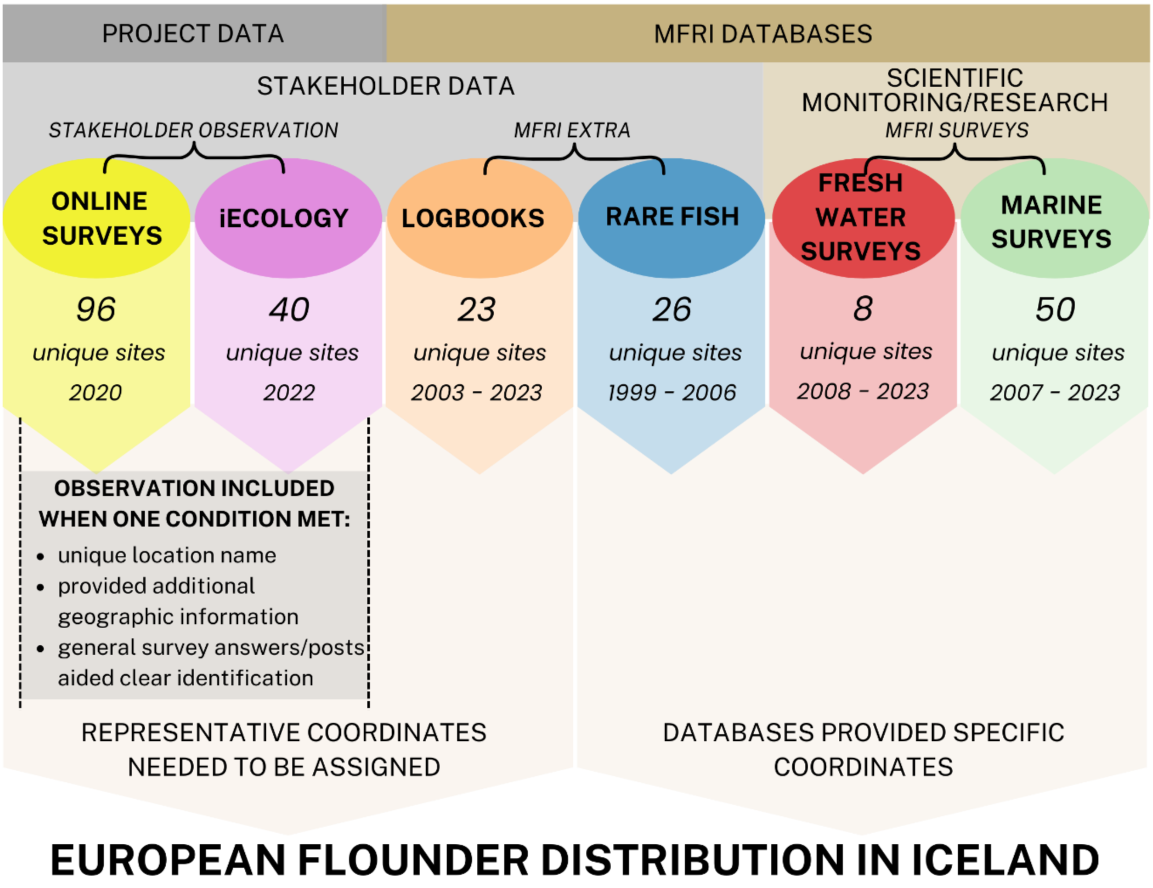

Figure 1 Overview of the six data sources incorporated in the current study.

Occurrence data collected from recreational anglers

First, we conducted an online survey targeting recreational anglers in Iceland to explore their experience with and perceptions of European flounder between October 2019 and June 2020. The anonymous survey, along with information about the aims of the scientific project, was predominantly shared through public Facebook pages of research institutions and a dedicated Icelandic recreational angling Facebook group (15.924 members as of November 2024). We chose Facebook as a tool to reach a wide range of potential participants, as this is a highly popular social media platform in Iceland that around 65 % of the population frequently use (Kemp 2024). In November 2019, an article published in a national Icelandic newspaper (Statistics Iceland 2024) that covered the research project (Jónsson 2019) further encouraged participation in the survey. In total, 209 people submitted responses to the survey.

In this survey we asked participants to provide locations where they encountered, either seen and/or caught, European flounder. The occurrence data from the survey was manually reviewed, removing those locations that we could not confidently assign to a specific waterbody. Due to the linguistic characteristics of the place names of Icelandic freshwater systems there are multiple rivers or lakes with the same name that can often only be differentiated when additional geographic indications are provided (e.g. the rivers “Varmá í Mósfellsbæ” and “Varmá í Hveragerði”). For each location provided by survey participants we checked whether at least one of the following conditions applied: 1) it is a recreational angling river/lake with a unique place name not requiring additional geographic information; 2) additional geographic information were provided allowing a clear identification; 3) additional information provided by the participant throughout the survey clearly identify the location such as through information on the region of Iceland they spent most of their time fishing. Locations were removed when none of these conditions were met.

Second, following the concept of iEcology (Jarić et al. 2021), we collected occurrence data from recreational fishermen in Iceland based on conversations within the Facebook group „Veiðidellan er frábær…“ [The fishing passion is great...], a group highly popular among the target group with 15.4 k members as of 02.05.2024. We evaluated different social media sources for their data availability on European flounder in Iceland as well as biodiversity platforms such as iNaturalist. While most platforms at the end of 2022 indicated a low number of data points relevant to this study (for example only three records had been submitted to iNaturalist prior to 2023) Facebook represented a popular tool among the Icelandic public (Kemp 2024) where European flounder has been frequently addressed. We manually identified Facebook posts and threads mentioning European flounder resulting in 50 recovered conversations occurring between 2013 and 2022 (see detailed information on the extraction and reach of the Facebook group in Henke et al., 2024). From those 50 conversations location reports of either catching or observing European flounder were extracted. Within this manuscript, this data is referred to as iEcology.

As neither the online survey nor the locations extracted from Facebook provided specific coordinates, we determined representative locations for each site. For rivers, representative locations were chosen near the lowest part of the river, for lakes near the mouth of the river through which European flounder most likely entered the lake, and for fjords within major estuaries. These locations were chosen under the assumption that they represent the minimum spread of the species. Where specific location names within habitats were provided, such as fishing beats within rivers, we pooled these locations together to create unique location records.

Occurrence data in the MFRI databases

Data on European flounder was extracted from all available data in the MFRI marine database resulting in European flounder occurrences from major annual surveys, such as, the spring groundfish survey (SMB), the autumn groundfish survey (SMH), and the gillnetting survey (SMN). The SMB and SMH are annual trawl surveys that sample widely around Icelandic waters in February-March and September-October respectively (Sólmundsson et al. 2022; Jakobsdóttir et al. 2023). The SMN is a spring gillnetting survey sampling inshore waters around Iceland (Bogason et al. 2024). There were also European flounder occurrences from less regular surveys, such as, a discontinued near-shore beam-trawl survey (2017-2022) (Thorlacius et al. 2024) and a demersal seine survey (1995-2013) (Pálsson and Sólmundsson 2017). In addition to these surveys, European flounder was also occasionally reported in marine research projects (Table 1). Survey- and research-based locations extracted from the MFRI marine database were pooled together under the group “marine surveys”.

Similarly, the freshwater MFRI records comprised European flounder location data from two sources. First, we extracted all locations where European flounder had been caught in freshwater surveys conducted by the institute. The MFRI sampled widely across recreational fishing rivers in Iceland with the main goal of annual salmonid stock assessment, this sampling is conducted at the same time of the year, usually in late summer. Second, we extracted flounder catches documented in logbooks from recreational fishing rivers, a database maintained by the Freshwater Division of the MFRI. Under the Law on salmon and trout fishing (Act 61/2006), fishing associations in Iceland are required to submit catch information on salmonids in their rivers. While catch information were traditionally submitted in the form of physical logbooks, the option of electronic submissions has been available since 2011 and in 2023 the MFRI established an online form allowing anyone to register their catches.

In addition to European flounder occurrence in surveys and logbooks we used data from the "rare fish database" managed within the Demersal Division of the MFRI. The rare fish database is an ongoing project logging reports and catches reported by stakeholders, often fishermen but anyone can report catches. In 2006, European flounder became part of regular surveying in MFRI marine surveys and was no longer reported to the rare fish database (personal communication Klara Jakobsdóttir, MFRI).

Location data from MFRI surveys provided specific coordinates of catches. For freshwater surveys locations within the same river were pooled together to represent unique sites. As the marine habitat cannot be divided by similar geographic boundaries, locations were treated as unique by default and only pooled when the differences in neither longitude nor latitude between two locations were greater than 0.01 (approx. 1.11 km). Logbook locations did not include specific coordinates and were therefore treated like the locations obtained from the online survey and Facebook. A full list of all data used is presented in Supplementary table 1.

Validating sites reported in the online survey

Three sites from each quadrant of Iceland (SW, NW, NE and SE) that had been reported in the online survey were selected and subsequently sampled using a beach seine (10 m long, 6 mm mesh) to confirm the presence of European flounder. Local landowners and/or river managers were contacted for recommendations on sampling sites to increase the likelihood of accessing likely areas of European flounder occurrence as well as to ensure safety during the sampling process. Where the safety of the scientists could not be guaranteed due to known, strong currents, we selected an alternative site nearby based on local recommendations. The sampling at these 12 sites took place between July and September 2020. Sites where not at least one European flounder was caught were considered as not validated and therefore excluded from further analysis.

Data analysis

All data handling, statistics and figures were done using R (version 4.3.2, (R Development Core Team 2023). First, we tested differences in the geographical representation of data sources by comparing both latitude and longitude between all data sources (marine surveys, freshwater surveys, logbooks, online survey and iEcology) using a pairwise Dunn test with Bonferroni correction implemented in the R package dunn.test (Dinno 2024).

To compare the annual detection of unique sites between data sources with time stamps available (rare fish, marine surveys, freshwater surveys and logbooks), we fitted a generalized additive model (GAM) to the number of unique sites per source using the *gam*() function of the *mgcv* package in R (Wood, 2017). The statistical family was zero inflated Poisson (-0.593, 1.903) and the link function identity. We fitted the model with year as fixed and a smooth term.

Individual locations per year ~ Year + s (Year, by = Source)

We furthermore examined how well these four sources documented the temporal spread of European flounder in Iceland. As European flounder was first detected in the southwest and southeast of Iceland (Jónsson et al. 2001), we used latitude to approximate the species' northward spread. We fitted a GAM to the latitude of documented European flounder sites using *gam()* to investigate for differences in the detection of the species' spread between the four sources. The statistical family was Gaussian with an identity link function. The model was fitted with year as fixed effect and a smooth term.

Latitude ~ Year + s (Year, by = Source)

For both models the smooth term was Year with source as an interaction term to account for the differences between sources. Smoothing parameters were estimated using restricted maximum likelihood. For the purpose of model diagnostics, we inspected fitted residuals and tested for autocorrelation using the functions *simulate.residuals()* and *testTemporalAutocorrelation()* of the *DHARMa* package (Hartig, 2022), respectively.

Results

The online survey (205 participants; see details in Henke et al. 2024) and the iEcology approach returned 97 and 40 individual locations, respectively, with the majority of sites located across western Iceland (Table 1, Supplementary table 1, Figure 2). In monitoring surveys and research activities, the MFRI recorded 50 unique locations in marine habitats and nine in freshwater habitats, which were all predominantly located in southwest Iceland (Table 1, Figure 2). European flounder was reported via logbooks for 23 individual sites mostly across western Iceland (Table 1, Figure 2). There were 26 unique site records stemming from the 'rare fish' project and these were widely recorded along the south and southwest of the country but also in the northwest of Iceland (Figure 2). These records date between 1999 and 2006 and represent the early spread of the European flounder before the species was no longer included in the rare fish database (2006/2007). The percentage of unique sites identified among the total records of European flounder differed widely between sources (Table 1). Among all records stemming from the online survey 32.8% were identified as a unique site. In comparison, the highest percentage was recorded for locations retrieved from the rare fish database, where 83.9% were unique sites.

Table 1. The number of unique sites where European flounder has been reported using different data sources. Numbers in brackets indicate the total number of recorded sites. For the MFRI sources the years of the first and the most recent record are listed as well as the number of individual European flounder reported in the records. For the marine surveys data,

we furthermore indicated how many of these unique sites were based on research activity or surveys.

Quadrant	SW	NW	NE	SE	**Total**
Online survey					
Unique sites	**36**	**39**	**10**	**11**	**96**
n records	(136)	(121)	(15)	(21)	(293)
iEcology					
Unique sites	**21**	**11**	**3**	**5**	**40**
n records	(31)	(30)	(5)	(7)	(73)
Logbooks					
Unique sites	**11**	**10**	**1**	**1**	**23**
n records	(17)	(24)	(1)	(1)	(43)
First record	2003	2012	2021	2018	2003
Most recent record	2023	2023	2021	2018	2023
n European flounder	29	434	1	1	465
Rare fish					
Unique sites	**15**	**1**	**0**	**10**	**26**
n records	(20)	(1)	(0)	(10)	(31)
First record	1999	2003	-	2000	1999
Most recent record	2006	2003	-	2006	2006
n European flounder	30	1	-	13	44
Freshwater surveys					
Unique sites	**5**	**3**	**1**	**0**	**9**
n records	(14)	(3)	(1)	(0)	(18)
First record	2008	2012	2023	-	2008
Most recent record	2023	2023	2023	-	2023

n European flounder	66	5	1	1	53
Marine surveys					
Unique sites	**34**	**13**	**1**	**2**	**50**
- research	9	4	0	0	- 13
- surveys	25	9	1	2	- 37
n records	(50)	(25)	(1)	(2)	(78)
First record	2007	2008	2018	2009	2007
Most recent record	2023	2023	2018	2021	2023
n European flounder	370	279	1	2	652

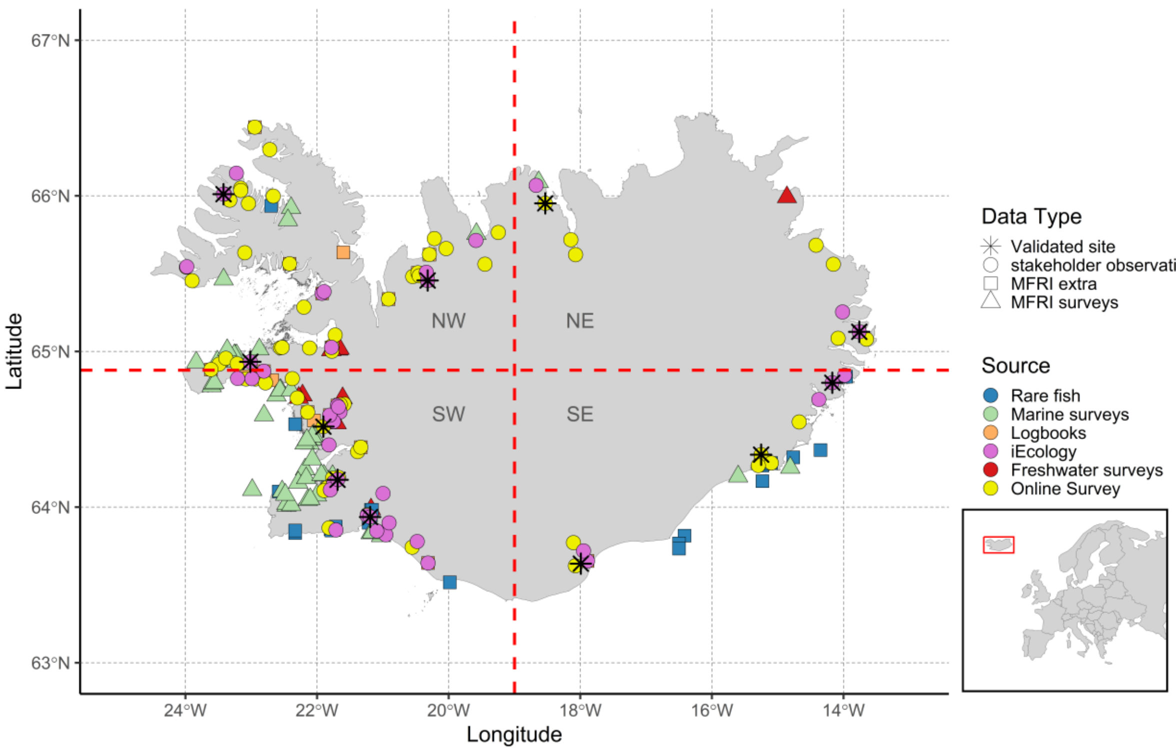

Figure 2 A map of Iceland showing all identified unique sites. For each site the color indicates from the six sources of European flounder locations while the shape highlights the

three different data types that we divided the sources into, namely stakeholder observations (Online survey & iEcology), MFRI extra (Logbooks and Rare fish), and MFRI surveys (including both marine and freshwater surveys). Locations validated by sampling are indicated with a black asterisk.

The various data sources differed significantly in their geographical representation (Figure 3). The marine surveys reported significantly more locations further west than the rare fish database, the iEcology approach and the online survey (all pairwise Dunn-tests $p < 0.01$). No other pairwise comparisons were significant for longitude. For latitude the marine surveys had a significantly higher representation of southern sites than the online survey (pairwise Dunn test $p = 0.0209$). Moreover, the rare fish database had significantly higher representation of southern sites than any of the other sources apart from marine surveys (pairwise Dunn-test all $p < 0.01$). No other pairwise comparisons were significant for latitude.

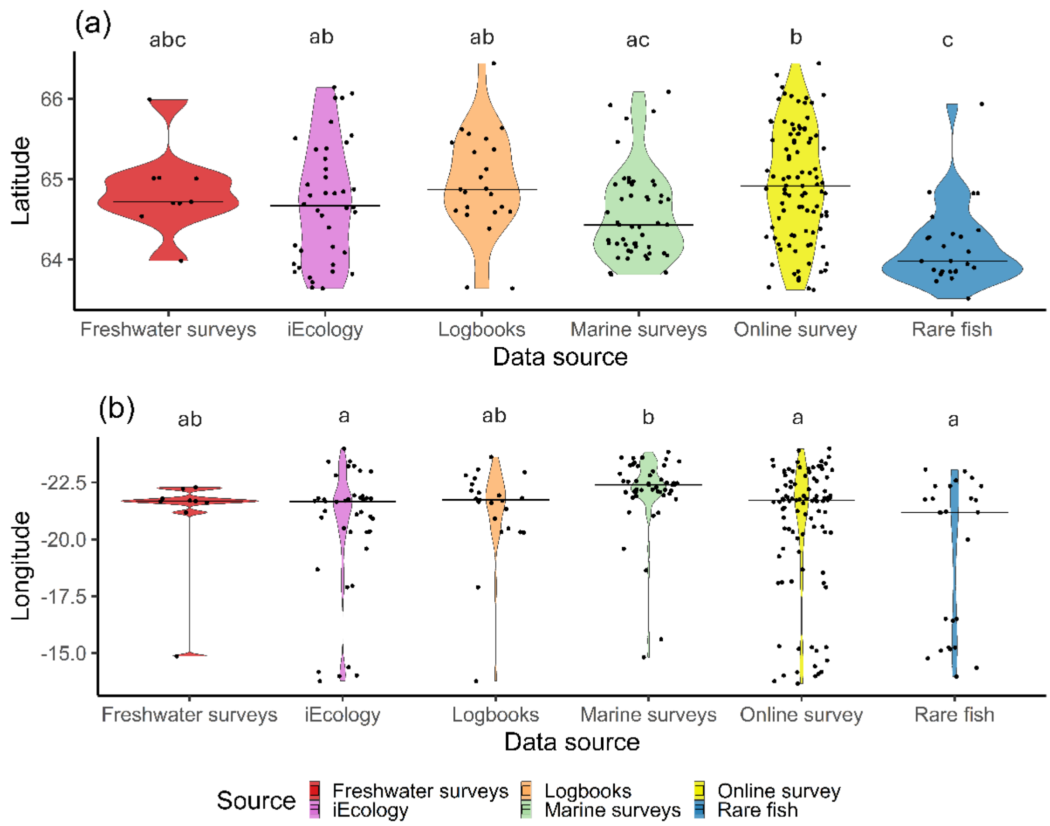

Figure 3. The geographical distribution of reported sites with flounder catches or sightings (note that the figure does not represent the number of fish caught). The figure highlights the geographical biases inherent to each survey method. The black points represent each site. Letters in the graph indicate the results of the pairwise Dunn test with Bonferroni correction where sources that share the same letter are not significantly different.

Between the four sources that provided distribution data with attributed time information, the annual detection and overall cumulated number of unique sites widely differed (Figure 4). The GAM smooths showed significant differences between all sources ($p < 0.05$ for all sources, Table 2). New sites recorded via logbooks increased the strongest in 2016 when nine new sites were added (Figure 4). In the rare fish database, the highest number of new sites (n = 8) was recorded in 2002 (Figure 4). While the number of new sites detected in marine surveys peaked in 2017 with 11 new sites, freshwater surveys recorded the highest number of new sites in 2012 and 2023 with three sites each (Figure 4).

Within each of the four MFRI sources, the first record was documented in the southwest of Iceland but the year of first record ranged from 1999 (rare fish) to 2008 (freshwater surveys) but the pattern (Figure 5). The geographic distribution of records in the subsequent years differs between sources. Most notably here is that within four years (2000 – 2003) the rare fish data indicated European flounder distribution ranging from northwest to southeast Iceland (Figure 5). However, statistical tests revealed no significant differences between sources in capturing the northward spread of European flounder approximated by latitude (Supplementary table 2, Supplementary Figure 1). It should be noted that the number of available data points for this analysis is low.

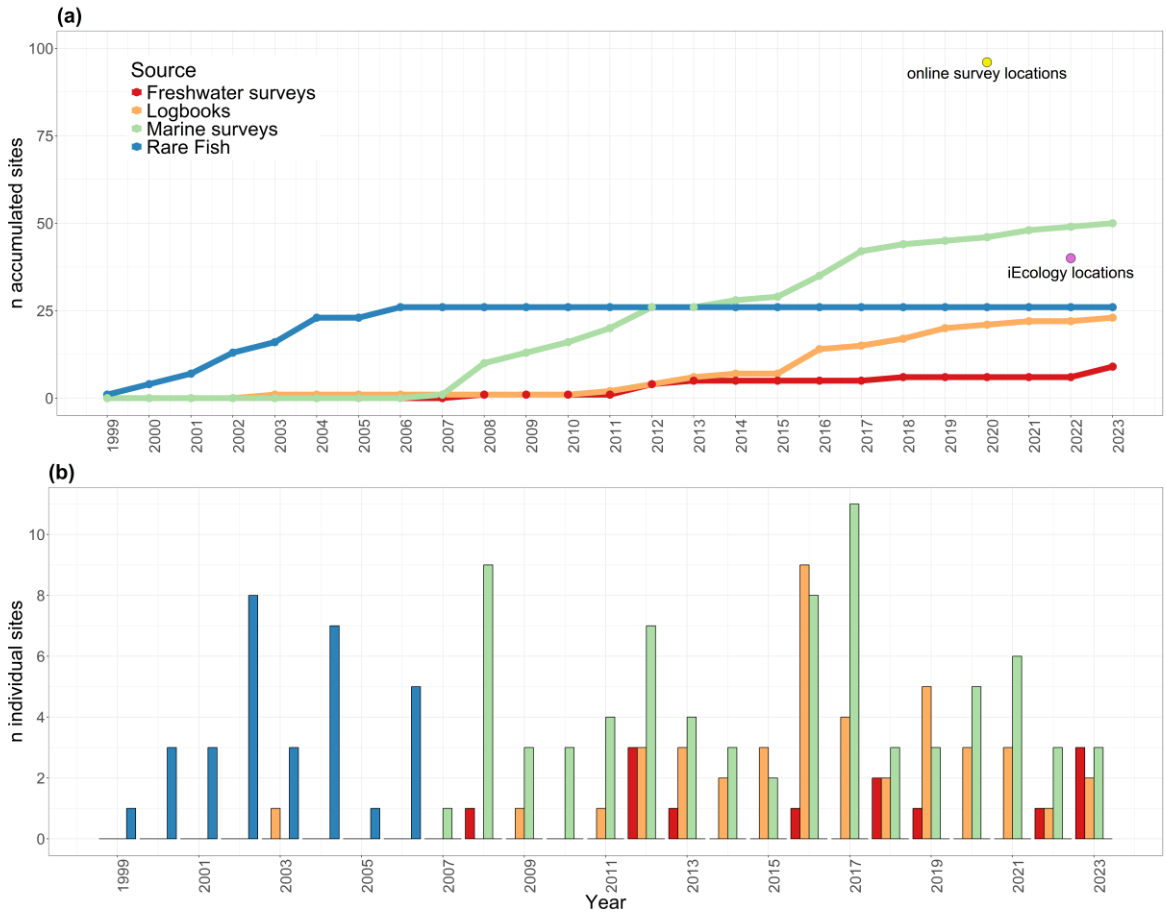

Figure 4. (a) Cumulated number of unique sites per source with time stamped data available. For comparison, the number of sites collected by online survey and iEcology are indicated (b) Barplots showing the number of unique sites recorded annually per source.

Table 2. Estimated parameters based on the generalized additive model (GAM) highlight the differences between data sources in recording unique sites of European flounder in Iceland.

Parametric coefficient	Estimate	Standard error	z value	Pr (>|z|)	
Intercept	0.000	0.000	NaN	NaN	
Year	-1.163 e^{-04}	7.749 e^{-05}	-1.501	0.133	
Smooth term	**Source**	**Edf**	**Ref. df**	X^2	**p value**
s(Year)	Freshwater surveys	1.000	1.001	6.593	0.0103
s(Year)	Logbooks	3.064	3.757	45.073	< 2 e^{-16}
s(Year)	Marine surveys	4.888	5.826	86.387	< 2 e^{-16}
s(Year)	Rare fish	3.861	4.732	51.607	< 2 e^{-16}

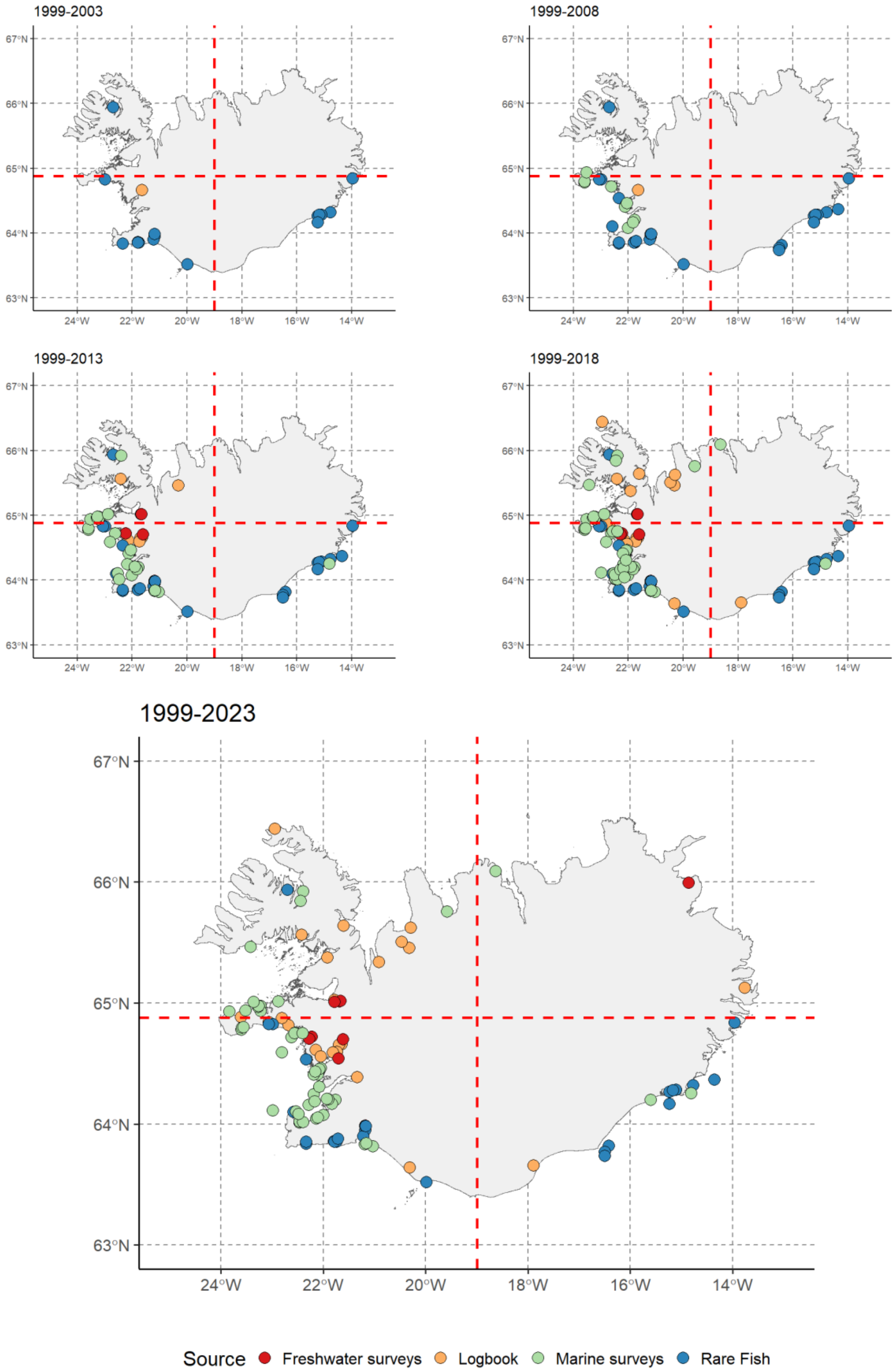

Figure 5. European flounder records mapped for each source that had time stamped data available. The five maps indicate the proceeding spread of European flounder throughout

Iceland in five-year increments, with the final map showing all records documented in the MFRI sources until 2023.

The ground truthing of online survey sites confirmed the presence of European flounder in 11 out of 12 sites around Iceland. Despite considerable sampling effort, the sampling at one site in the NE did not capture any European flounder and the record was consequently excluded from further analysis. Interestingly, one additional site in the NE was later confirmed by a MFRI freshwater survey in 2023. Therefore, the lack of validation by independent sampling of the NE sites does not necessarily confirm that European flounder is absent from these sites but is likely rarer in the NE than in other quadrants (Figure 2).

Discussion

The current case study of European flounder in Iceland shows the benefits of stakeholder observation-based approaches, in addition to existing aquatic surveys, to document both the distribution and the spread of alien fish species. Although the different data sources showed similar distributions and indicated a similar geographic pattern in the spread throughout Iceland, combining sources counteracted the inherent biases of using methods not specifically targeting European flounder. Furthermore, we show that stakeholders are willing to share their knowledge when directly approached with an opportunity such as the online survey, but also based on personal initiative and effort as seen by the occurrences in the rare fish database collected in the early stages of the European flounder spread in Iceland.

Stakeholder observations to document the occurrence of European flounder

The results of the online survey targeting recreational fishermen generated 96 unique locations and therefore provided a higher number of occurrence locations than the previously available survey data based on the MFRI databases, which delivered 50 marine, and nine freshwater locations. Efforts to sample European flounder at 12 representative sites around Iceland named in the online survey showed a high validation rate of over 90 % as the sampling at 11 out of 12 sites resulted in at least one individual. While the remaining site was consequently omitted from further analysis, the absence of European flounder in the river Hofsá in northeast Iceland is likely explained by the overall scarcity of European flounder in the northeast region of the country as its presence was confirmed in 2023 during monitoring of salmonid stocks in the same area. The knowledge of recreational fishing communities has previously proven valuable in addressing conservation issues in aquatic environments (Giovos et al. 2019; Löki et al. 2023). Recreational fishers spend substantial time in the aquatic environments gathering experiential knowledge, beyond what is often available to scientists, and can therefore be more likely to encounter rare or new species (Silvano and Begossi 2012; Löki et al. 2023). The quantitative advantage of stakeholder observation-based data we documented in the current study on European flounder is in accordance with the results of these earlier case studies. While scientific surveying can maximize data quality by strategic sampling plans, stakeholder observation-based data are less predictable. In the current study, stakeholders reported unique sites at a lower ratio than scientific surveys, but the overall higher number of locations provided as well as the confirmation of persistent flounder occurrence provided by repeated reporting of some sites, is advantageous to monitoring activities. An additional advantage of stakeholder observation-based approaches is the increased awareness among stakeholders, which is crucial in addressing biological invasions especially at early stages (Dehnen-Schmutz et al. 2018). The advantages of stakeholder observation-based data were also supported by comparison of the different data sources available within the MFRI. Specifically, large parts of the previously available distribution data on European flounder were already based on stakeholder knowledge, in the form of logbook entries and voluntary submissions to the rare fish database. These submissions were predominantly by recreational anglers and commercial fishermen.

When directly targeting stakeholders or local knowledge holders is not feasible, for example, because of cost, need for prior training etc., iEcology can offer additional approaches to utilize already existing stakeholder observations stored in the form of web-based data such as social media conversations (Jarić et al. 2020a). In the current study the locations scraped from Facebook did not provide the same number of occurrences as the online survey, but it still exceeded the previously documented distribution data based on the freshwater records of the MFRI. Many challenges and limitations have been noted for iEcology approaches, such as, potential spatiotemporal biases and validation of data accuracy (Jarić et al. 2020a; Jarić et al. 2021). However, in the current study 80% of the locations extracted from social media were also named in the online survey, and the approaches produced a comparable distribution pattern, validating iEcology as a tool in the current case study. Overall, in combination with other sources of information and under considerations of potential limitations and biases, social media data can be of great value when addressing conservation issues (Toivonen et al. 2019) as well as recording new species (Cresson et al. 2021).

Despite the apparent advantages of stakeholder observation-based approaches for documenting European flounder occurrence it should be noted that they provided only presence data while data collected as part of scientific surveys most often provides both presence and absence as well as potential information on size, age, diet and environmental variables at the catch site, i.e. salinity, water depth, etc., as well as co-occurring species. These data are all needed to accurately estimate distribution and habitat suitability as well as the ecological impacts of alien species (Robinson et al. 2020). Conversely, involving stakeholder observation-based data in monitoring activities can enable scientists to obtain large amounts of data in a short amount of time, requiring less resources (Cardoso et al. 2017) and it may be particularly suitable to document early stages and spread of invasions.

Stakeholder observations to document the temporal spread of alien species

In addition to documenting occurrences and spread, public and stakeholder observations are often the first records of an alien species (Thomas et al. 2017; Epanchin-Niell et al. 2021; Kousteni et al. 2022; Pocock et al. 2024). The first official documentation of European flounder in Iceland was based on the submission of a specimen to the MFRI by a member of the public after it was caught at the mouth of the river Ölfusá in southwest Iceland (Jónsson et al. 2001). As shown in this study, stakeholder observation-based sources remain better in reporting European flounder at sites where this species is still rare. Where preventing the arrival of alien species, the most desirable scenario (Browne et al. 2009; Pyšek and Richardson 2010; Schwindt et al. 2023), fails, early detection of alien species becomes crucial (Pyšek and Richardson 2010; Schwindt et al. 2023) but often depends on the premise that the public recognizes and reports unusual observations. Dehnen-Schmutz et al. (2018) identified raising awareness as one of the main topics that should be prioritized in policies addressing biological invasions.

Following the first detection of an alien species, the experiential knowledge of stakeholders can contribute to the reconstruction of the species' temporal spread (Latombe et al. 2017). While there was overall no significant difference in the documentation of the European flounders' northward spread, the voluntary records submitted to the 'rare fish' project already indicated a distribution expansion ranging around half of the country in the early 2000s. While the records of European flounder catches in MFRI's marine surveys generally suggest a similarly fast expansion northward, note that the surveys only officially started recording European flounder after 2006. The recent catch of European flounder during routine freshwater surveying in 2023 provided the first confirmation of the species in the northeast corner of Iceland and the first contribution of formal freshwater surveys to the reconstruction of the temporal spread.

Maintaining stakeholder willingness to report observations

Stakeholder observations-based data highly depends on the willingness of the public and other stakeholders to share their knowledge. The comparably high number of documented locations of European flounder shown in this study indicate that there is quite some willingness among stakeholders, specifically, the recreational fishing community in Iceland to contribute their experiential knowledge for monitoring purposes. Globally, recreational fishermen have been increasingly involved in management and conservation (Granek et al. 2008) and the results of Copeland et al. (2017), suggest that among other incentives there are social factors providing motivation to get involved.

Our data indicates fluctuations in the number of observations submitted to the MFRI by fishermen, which has also been reported by Cresson et al. (2021), who suggest that the reporting of rare species is not only strongly linked to personal motivation and interest of the fisherman but is also likely to decline once the familiarity with this species increases. The reporting of European flounder catches to the MFRI were mostly initiated by stakeholders' personal motivation although in the years following the first documentation of European flounder news items and reports discussing its status as a new species were relatively common (Henke et al., 2024). The willingness to report could potentially be linked to the general awareness of the public and their interest in the topic of alien species, which for the European flounder in Iceland has been fluctuating over the years (Henke et al., 2024), as well as perceptions of European flounder as novel and "rare" and thereby of interest. In the years following the first official documentation of European flounder in Iceland (Jónsson et al. 2001) when it was still a novelty, occurrences were predominantly recorded as part of the 'rare fish' project, but these reports stopped after 2006. The public's attention towards conservation issues such as biological invasions is generally rather transient (Jarić et al. 2023). The current results suggest that public interest in an alien species is unlikely to be maintained at a level necessary to document spread after initial establishment. However, when stakeholders were approached with an opportunity to share their knowledge and opinions, along with information on the objectives and the anticipated value of their participation, they provided many more locations of European flounder occurrences.

It has been recommended that at a minimum, countries should obtain updated occurrence records of alien species every five years and make these publicly available (Latombe et al. 2017). In this study, we have shown that stakeholder observation-based tools, when designed accordingly, can offer a great contributary source of data where resources for alien species monitoring are limited. Latombe et al. (2017) further suggests that national monitoring of alien species could be improved by building upon already existing structures. In line with previous studies (Jarić et al. 2020a; Löki et al. 2023), we show that there are many ways to collect stakeholder observation-based data, including logbooks, online questionnaires and iEcology. However, there are certain considerations on how to foster a continuous two-way knowledge exchange between stakeholders and scientists to be considered when designing such approaches (Courchamp et al. 2017). Here it can be beneficial to create platforms that are readily accessible and easy to use for the targeted stakeholder group. Recreational anglers in Iceland are required by law to submit catch reports of salmonids (Act 61/2006) and the electronic logbook of the MFRI offers an existing structure to submit catches of Atlantic salmon, brown trout and Arctic charr. A fourth option ("other") allows the records of other caught species, most applicable to catches of European flounder or pink salmon (*Oncorhynchus gorbuscha*), an invasive salmonid species that has shown strongly increasing abundances not only in Iceland but many other northern European countries (Lennox et al. 2023). Simply providing options specific to European flounder and pink salmon could raise awareness of this information being both officially recorded and important for management, thereby encouraging anglers to report catches. In turn, the resulting data could greatly improve the monitoring of the overall spread of alien fish species in Iceland and provide indications of abundance at very low cost. However, these considerations regarding accessible platforms for data collections should not end at the public and stakeholder level. It should be noted that while we are confident that the underlying data for this study represents the bulk of the available data on European flounder catches in Iceland, we are aware that other institutions and/or scientists may have collected additional catch data. A holistic database that keeps updated records across institutions would greatly benefit not only the monitoring of alien species in Iceland but also other conservation efforts.

Building upon stakeholder observation in the monitoring of alien species

We have shown that stakeholder observations can represent a valuable, complementary source in the monitoring of an alien species. However, considering the context dependency of biological invasions (Robinson et al. 2017; Catford et al. 2022) approaches involving stakeholders need to be carefully designed on a case-by-case basis to appropriately address each invasion individually. In the case of European flounder in Iceland, we selected Facebook over other social media or biodiversity platforms that are more commonly used in similar studies (Pace et al. 2019; Jaric et al. 2021) as Facebook was much more frequently used in this specific case. In addition to choosing the most appropriate data source(s), the reliability of observations regarding the correct species identification needs to be evaluated as this is a crucial aspect of gathering distribution data. In our case, we rated the reliability of stakeholder observations as high based on the fact that European flounder is easily distinguishable from other species in rivers and lakes as it represents the only flatfish species entering these habitats. This was further reinforced by successfully conducted site validation. We recommend that the approach implemented in this study, can be highly valuable and applicable in small nations where resources for formal, scientific monitoring of alien species is limited but collaborations between research institutions, management parties and stakeholder groups are easier to establish.

We acknowledge that, while stakeholder observations are part of Local ecological knowledge (LEK), to holistically incorporate the knowledge of stakeholder groups in the monitoring of alien species, their involvement must be established throughout the entire research process. As the phenomenon of biological invasions is inherently of interdisciplinary and complex nature, embedding LEK in the necessary research and management approaches is becoming increasingly recognized (Caceres-Escobar et al. 2019;

McElwee et al. 2020). While the current study shows the benefits of including stakeholder observations in monitoring it does not fully integrate the available LEK. We recommend broadening the approaches to the monitoring of European flounder in Iceland as well as of other alien species, to include LEK where the context allows, for a more holistic understanding of the alien species and their impacts.

Conclusion

Our results show that even with active aquatic surveying, designed to monitor commercially and recreationally important species, there can be a significant advantage to including stakeholder observation-based data sources to monitor alien species. In the case of the European flounder in Iceland, diverse sources based on stakeholder observations, ranging from logbook entries to online questionnaires and social media data, notably improved the information available from surveys carried out by the national marine and freshwater institute. Based on these results and the observation that interest in reporting European flounder as a novel species decreased over time, we therefore recommend monitoring approaches that build upon existing structures providing a clear venue for reporting European flounder occurrences and increased efforts to increase awareness about the issue of biological invasions as well as the value of their contribution. We further recommend expanding on the approach of stakeholder observations and integrate the full scope of LEK embedded in the involved stakeholder group.

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9 Paper IV

Floundering in-between definitions – Expert and stakeholder views on addressing an alien species with uncertain introduction pathway

Henke T., Ólafsdóttir G. Á. (in preparation)

Author contributions: T.H. and G.Á.Ó. conceptualized the study. T.H. compiled the data and conducted the initial analysis. T.H. wrote the first draft and G.Á.Ó. provided revisions.

Title: Floundering in-between definitions – Expert and stakeholder views on addressing alien species with uncertain introduction pathway

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Abstract:

Biological invasions are known to have detrimental impacts on the recipient ecosystem, representing one of the leading threats to global biodiversity. The study of species introductions is often marked by strong context-dependencies and a high level of uncertainties which is reflected in the diverse terminology and numerous definitions used to categorize alien species. In addition to the uncertainty inherent to the scientific field, there is often an additional source of uncertainty associated with specific cases of invaders such as their origin and introduction pathway. Using the case study of European flounder in Iceland, we assessed the views of specialists and a representative stakeholder group on addressing alien species with remaining uncertainty regarding its introduction pathway. European flounder (*Platichthys flesus*) is a flatfish species native to the central European coasts and has been documented in Iceland since 1999. While its origin has been genetically identified as the Faroe Islands, it remains unclear whether the species arrived due to natural dispersion or was introduced via ballast water. We used two anonymous online surveys to assess the views of specialists, represented by both international invasion scientists as well as a broader group of scientists based in Iceland (either aquatic or invasion science background), and the recreational angling community in Iceland as an important stakeholder group. Our results show that while specialists displayed high confidence in applying terminology to the case of European flounder, the terms used varied widely. In total of 26 different terms were listed with 'Invasive species', 'Non-native species', 'Alien species', and 'Cryptogenic' being the most frequent. In contrast to the widely differing views on terminology, specialists largely agreed that in cases of uncertainty regarding an alien species' arrival, the introduction pathway should be identified but its identification should not be prioritized over assessing impacts. The stakeholder group prioritized impact assessment as well as establishing preventative measures towards future invasions over the identification of the European flounder's introduction pathway.

Keywords: biological invasions, terminology, uncertainty, stakeholder, European flounder

Introduction:

Biological invasions are one of the top threats to global biodiversity and have garnered the interest of scientists for the last decades (Simberloff et al. 2013; Bellard et al. 2022; IPBES

2023). There is a consensus that introduced species can cause detrimental negative impacts on the fauna and flora of the recipient ecosystem, including ecological and socioeconomic impacts (Simberloff et al. 2013; Hawkins et al. 2015; Bacher et al. 2017). However, as biological invasions are often context dependent (Catford et al. 2022), uncertainty at varying levels can complicate actions to address the issues inherent to invasions (Liu et al. 2011; Latombe et al. 2019). Invasive species have historically been defined by multiple criteria, including ecological and socioeconomic impacts, but also by their spread and the introduction pathway. This inherent complexity, and more specifically, the consequent intricacy of the language used to characterize invasions, may contribute to uncertain definitions and thereby actions (Latombe et al. 2019). Terminology used in invasion science does not only vary widely, but there are also stark variations in the understanding of concepts and definitions linked to specific terms (Russell and Blackburn 2017; Kapitza et al. 2019; Latombe et al. 2019; Shackleton et al. 2022). It has been shown that some of the driving forces of these divergent terminologies can be related to the taxon addressed (e.g. plants and mammals), geographic locations (e.g. North America vs. Europe), as well as the field of work (e.g. academics, practitioners) and the underlying discipline (e.g. natural science vs social science perspective) (Humair et al. 2014; Shackleton et al. 2022).

The recently published IPBES report, representing the most holistic assessment to date, is using the terminology and definitions: ‘native species’ (defined as “A species (animal, plant or other organism) within its natural range, including shifting its range, without human involvement”), ‘alien species’ (defined as “A species whose presence in a region is attributable to human activities that have enabled it to overcome the barriers that define its natural range”), ‘established alien species’ (defined as “A subset of alien species that have produced a viable, self-sustaining population and may have spread”), and ‘invasive alien species’ (defined as “A subset of established alien species that spread and have a negative impact on biodiversity, local ecosystems and species. Many invasive alien species also have impacts on nature’s contributions to people (embodying different concepts, such as ecosystem goods and services and nature’s gifts) and good quality of life”) (IPBES 2023). However, there are numerous terms used that address specific aspects and contexts of biological invasions beyond those addressed in the definitions provided by IPBES. Examples of such terms include ‘neonative’, concerning species introductions that are not linked to human assistance but have been associated with environmental change induced by anthropogenic factors (Essl et al. 2019), and ‘cryptogenic’, addressing species where the native status and origin is unclear (Carlton 1996). While such wide-ranging terminology offers the chance to address different facets of the context-dependency that inevitably emerges when addressing biological invasions, it can also hinder the reporting of alien species (Castro et al. 2023), as well as for the development of management approaches (Richardson et al. 2011; Essl et al. 2019). It can furthermore fuel the ongoing criticism towards the field of invasion science (Richardson and Ricciardi 2013). Despite several attempts to unify the use of terminology such as Colautti and MacIsaac (2004) and (Blackburn et al. 2011), and most recently (Soto et al. 2024), no one all-encompassing solution has been suggested.

European flounder (*Platichthys flesus*) was first documented in Icelandic waters in 1999 (Jónsson et al. 2001) and has rapidly spread throughout most of Iceland in subsequent years (Henke et al. 2024a). Since the species’ first documentation in Iceland, there have been opposing hypotheses regarding its introduction pathway suggesting that it either arrived from the Faroe Islands potentially due to natural dispersion (Jónsson et al., 2001, Thorainsdóttir et al., 2014) or was introduced via ballast water from the western European coast (Thorarinsdóttir et al. 2014; Gunnarsson et al. 2015). Recent genetic research has identified the Faroese population as most likely source of the European flounder found in Iceland (Henke et al. unpublished manuscript). Therefore, and although a Faroese origin does not rule out human mediated introduction via ballast water, it opens the option of natural dispersal due to the geographical proximity of the Faroe Islands to the southeast coast of Iceland (see (Henke et al. unpublished manuscript) . Limited research has been conducted on the ecological impacts of this species on the native environment, although small-scale studies have indicated competition with and direct predation on native species such as the European plaice (*Pleuronectes platessa*) (Henke et al. 2020) and salmonids (O´Farrell 2012; Hlinason 2013). Due to the spatial overlap and potential competition with the native Atlantic salmon (*Salmo salar*, Linnaeus 1758), brown trout (*Salmo trutta*, Linnaeus, 1758) and Arctic char (*Salvelinus alpinus*, Linnaeus, 1758), the recreational angling community targeting these highly sought-after species has been identified as an important stakeholder group in the case of European flounder in Iceland (Henke et al. 2024b). Angling activities are not only highly popular among the Icelandic public (Toivonen et al. 2000), they are also of great economic value with the sale of angling permits totaling at an expenditure of approximately 4.9 billion krona (37 million USD) in 2018 (Institute of Economic Studies 2018). Previous research among the Icelandic recreational angling community has shown highly negative perception towards European flounder (Henke et al. 2024b).

Given the uncertainties inherent to the case of European flounder (*Platichthys flesus*) in Iceland coupled with high stakeholder interest and awareness (Henke et al. 2024b), we use the case study of European flounder to explore how specialists evaluate the status and potential management approaches of an introduced species with undetermined introduction pathway. We moreover explore to what extent such uncertainty matters to stakeholders. Utilizing two anonymous online surveys addressing international and national specialists as well as the recreational angling community in Iceland, we first document specialists' views on how to address species with uncertain introduction pathways in general, and more specifically, how they would use terminology to categorize the invasion status of European flounder in Iceland. Second, we examine if an uncertain introduction pathway is relevant to how recreational anglers in Iceland perceive the European flounder and how they would prioritize determining introduction pathways relative to other actions.

Methods:

Survey design and administration

An anonymous online survey, hereafter referred to as specialist survey, was created to target the international community of scientists working in the field of invasion science. The survey was first opened in September 2022 where it was advertised at 12th International Conference on Biological Invasions (Neobiota) held in Tartu, Estonia in September 2022 (https://www.elus.ee/index.php/en/neobiota-tartu-2022/). In the subsequent months, the survey was advertised via social media, international email lists specifically addressing specialists in the field of invasion science, as well as opportunistic personal advertisement. Due to the limited size of the scientific community in Iceland specifically working with biological invasions, we encouraged a broader group of Icelandic scientists from either aquatic or invasion science background to participate in the survey. Within Iceland the survey was therefore additionally advertised among scientists working at the Marine and Freshwater Research Institute of Iceland (MFRI). While most participations took place until the end of 2022, the survey remained open for participations and received occasional submissions until August 2024 without additional advertisement.

Secondly, an anonymous online survey targeting the recreational fishing community in Iceland, hereafter referred to as stakeholder survey, was administered in February 2023 as part of a larger project. We embedded the data collection for this present study within a larger survey in order to avoid survey fatigue among the target group (Sinickas 2007). The survey was closed for participations in March 2023 after a sufficient number of participants was reached (see details in Henke et al., 2024). Of the nine questions included in the survey, two questions were relevant for the present study (Supplementary Table 1). We mainly advertised the survey to the target group via social media and additionally presented it in an episode of an Icelandic podcast popular among the recreational fishing community (Ólafsson and Harðarson 2023). We manually scanned the answers to both surveys for missing data and where necessary excluded submissions when the information provided was not sufficient. In both surveys, participants were informed about the background and goals of the respective survey and the research project (Supplementary Table 1).

Data analysis

All data analysis was conducted in R (version 4.3.2, R Development Core Team (2023)).

We applied a two-step analysis to the answers provided by participants of the specialist survey when asked for the terminology they deem most appropriate in the case of European flounder in Iceland (Supplementary Table 1B Question 6). To assess the participants' confidence in providing terminology, we classified the answers into six categories using a classification scheme (Supplementary Figure 1). These categories were comprised of "No answer/expressed hesitation", "Multiple distinct terms", "Conditional term(s)", "descriptive", "distinct term(s) with modal qualifiers", and "one distinct term". While we considered the categories "No answer/expressed hesitation" and "one distinct term" to indicate no confidence and strong confidence, respectively, we considered the remaining categories collectively to represent limited confidence without specific, inter-categorical hierarchy. We created a Sankey diagram using the *plotly* package (Sievert 2020) to display the classification progress and outcome. In the second step, we recorded the terms listed by participants and their frequency. If participants listed multiple terms, all terms were counted. Results were displayed in barplots using the *ggplot* (Wickham 2016) and *ggpol (Tiedemann 2020)* packages. We tested for a significant difference in the answers between the international group of invasion scientists and the aquatic scientists based in Iceland using Fisher's exact test embedded in the *stats* package (R Development Core Team 2023).

We graphed the responses to the likert-style perception questions in the specialist survey (Supplementary table 1 B questions 4,5, and 7) using the *likert* package (Bryer and Speerschneider 2016). To indicate the level of separation among the answers to each likert item, we calculated the polarization score using the *agrmt* package (Ruedin 2021). The polarization score can range from 0 (all responses fall in the same category) to 1 (responses evenly distributed between opposing categories (van der Eijk 2001). We applied the Mann-Whitney U test using the *stats* package (R Development Core Team 2023) to assess whether the opinions of scientists based in Iceland, regardless of whether they work in invasion science differed significantly from the international group of invasion scientists. All graphs for the results of the stakeholder survey were produced using *ggplot* (Wickham 2016).

Results

Survey participation

A total of 83 scientists took part in the specialist survey stemming from 24 countries (Supplementary Table 2). Participating scientists were most commonly based in Iceland, or 22 participants of which 9 indicated having been involved in invasion science. The second largest participant was USA (16) followed by the UK and Canada (7 each) (Supplementary Table 2). A total of 193 responses were received in the stakeholder survey among recreational fishermen in Iceland of which 191 were retained for analysis.

Determining terminology for a species with uncertain introduction pathway

There was a high confidence level among participants of the specialist survey in listing terminology regarding European flounder in Iceland with most of the responses classified as one distinct term, both by the international group of invasion scientists as well as scientists based in Iceland (Figure 1; Supplementary Table 3). This was followed by responses classified as conditional term(s) or distinct term(s) with modal qualifiers, indicating more limited confidence (Figure 1; Supplementary Table 3). There was generally a similar pattern in the frequency of the classifications between the two groups and no statistically significant difference in the distribution of answers among the six categories (Fisher's exact test, p = 0.06667).

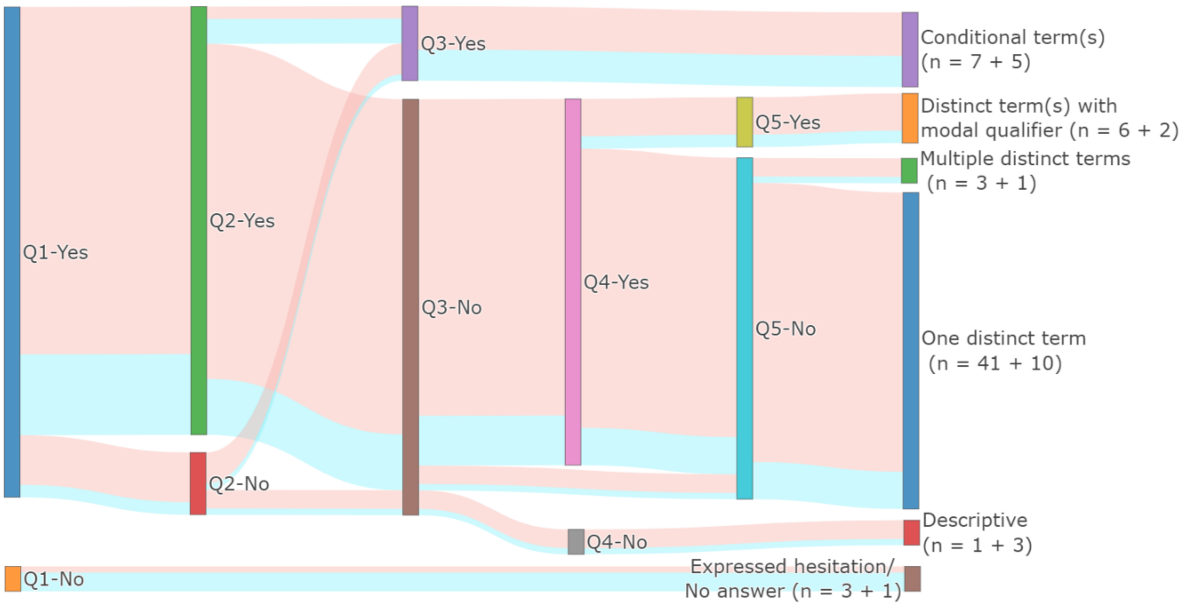

Figure 1 Sankey diagram displaying the distribution of responses throughout the classification process as well as the eventual distribution among the six categories. Responses submitted by international invasion scientists are displayed in red and those of aquatic scientists based in Iceland in blue. The questions used in the classification process are "Did the participant provide a classification?" (Q1), "Did the participant provide one single term?" (Q2), "Did the participant provide a conditional term?" (Q3), "Did the participant use one distinct term?" (Q4), and "Did the participant use modal qualifiers?" (Q5) (Supplementary Figure 1).

Between both groups, a total of 26 different terms have been listed (Figure 2). Among the international invasion scientists, 21 terms were provided where the terms “invasive species” (n = 18), “non-native species” (n = 14), and “cryptogenic species” (n = 6) were the three most frequently named terms (Figure 2). Among aquatic scientists based in Iceland, 10 different terms were used of which “non-native species” (n = 6), “invasive species” (n = 4), and “alien species” (n = 4) were the most common (Figure 2). The distribution of responses among the 26 unique terms was significantly different between the two groups (Fisher’s exact test p = 0.0006).

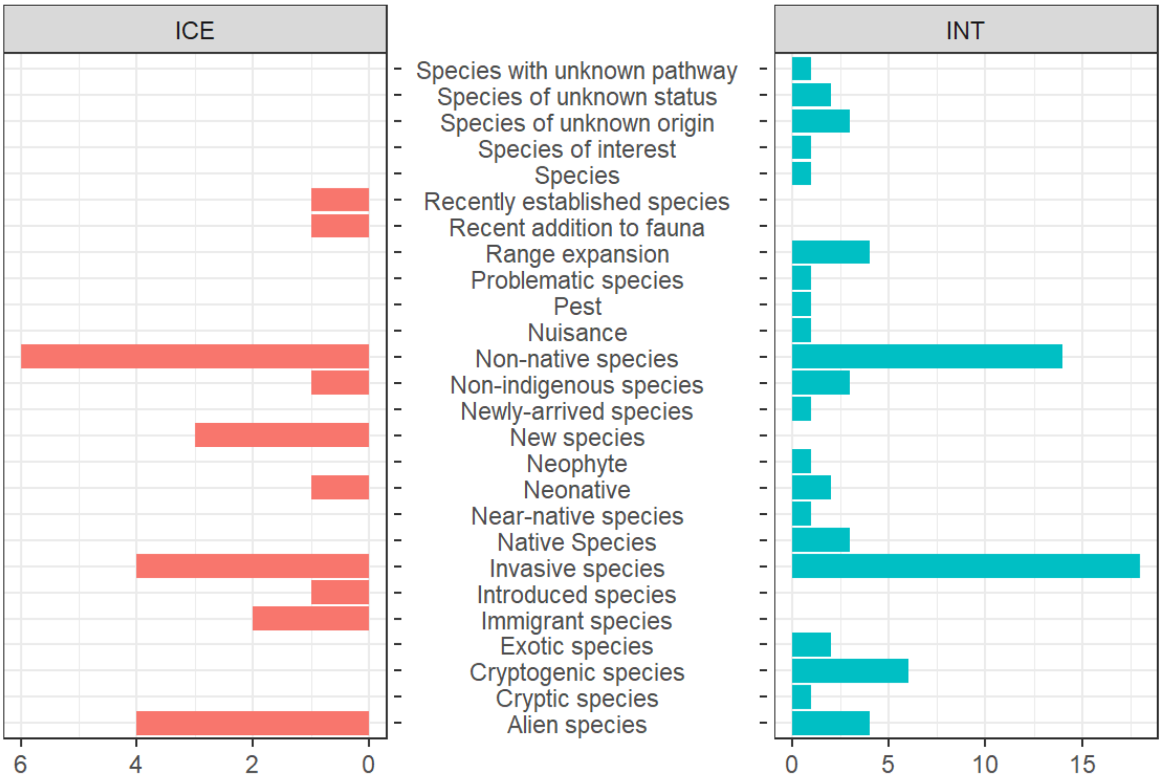

Figure 2 Barplots indicating the frequency in which terms were used by international invasion scientists (blue) and aquatic scientists based in Iceland (red) to describe European flounder in Iceland.

Perceptions of scientists on handling uncertainty in invasion science

Concerning the actions that should be done if uncertainty remains whether a species arrived naturally or was (un-)intentionally introduced, participants generally agreed that identifying the introduction pathway should be of high priority (International: 89%; Iceland: 86%) and that it is more important whether the species shows negative impacts on the new environment (International: 95%; Iceland: 86%) (Figure 3). While they generally don´t think that natural dispersal should be assumed until proven otherwise (International: 68%; Iceland: 50%) nor that the origin of a species is irrelevant (International: 72%; Iceland: 71%), they were of mixed agreement whether species should be considered as introduced until proven otherwise (Figure 3). There was no significant difference in the pattern of responses of international invasion scientists and scientists based in Iceland (Supplementary Table 4). Polarization scores to these questions ranged from 0.137 and 0.155 regarding question Q4.3 (“It is more important whether the species shows negative impacts”) to 0.328 and 0.404 regarding question Q4.4 (“Species should be considered as introduced until proven otherwise”) for the international invasion scientists and the Iceland-based scientists, respectively (Supplementary Table 4).

Assuming the theoretical case of a species with uncertain introduction pathway where mitigation actions could be successful, participants generally agreed that the examination of potential introduction pathways should be conducted simultaneously (International: 82%; Iceland: 70%), they overall did not agree with the statement that no mitigation should be applied if the possibility of natural dispersal remains (International: 74%; Iceland: 55%). Responses were mixed with a tendency towards agreeing regarding mitigation actions being implemented despite remaining uncertainty (International: agreement 61%; Iceland: agreement 53%) and mitigation actions being implemented only when negative impacts are evident (International: agreement 54%; Iceland: agreement 60%) (Figure 3). We detected a significant difference in the responses of participants regarding the simultaneously examination of introduction pathways and the implementation of mitigation actions with international invasion scientists agreeing more strongly than scientists based in Iceland (792.5, $p = 0.03164$; Supplementary table 4). For both groups, polarization scores were lowest for question Q5.2 ("Introduction pathways should be examined in PARALLEL to implementing mitigation actions") (Internation: 0.172; Iceland: 0.25) and highest for question Q5.4 ("Mitigation actions should be implemented ONLY when negative impacts are evident") (International: 0.45; Iceland: 0.468) (Supplementary table 4).

Focusing specifically on the case of European flounder in Iceland, participants generally agreed that resources should be focused on identifying whether it arrived naturally (International: 77%; Iceland: 81%) and that management should be developed based on scientific indications of negative impacts (International: 95%; Iceland: 90%). However, they overall disagree with no mitigation actions being implemented (International: 65%; Iceland: 56%) and potential management being based on stakeholders' negative perceptions (International: 51%; Iceland: 60%) (Figure 3). We detected no significant differences between answers provided by international invasion scientists and scientists based in Iceland (Supplementary Table 4). For both groups the polarization scores were lowest for question Q7.3 ("Potential management should be developed based on scientific indications of negative impacts") (International: 0.126; Iceland: 0.179). For international invasion scientists, polarization scores were highest with 0.343 concerning question Q7.4 ("Potential management should be based on stakeholders' negative perception" and for scientists based in Iceland concerning question Q7.2 ("No mitigation actions should be implemented") with 0.384 (Supplementary Table 4).

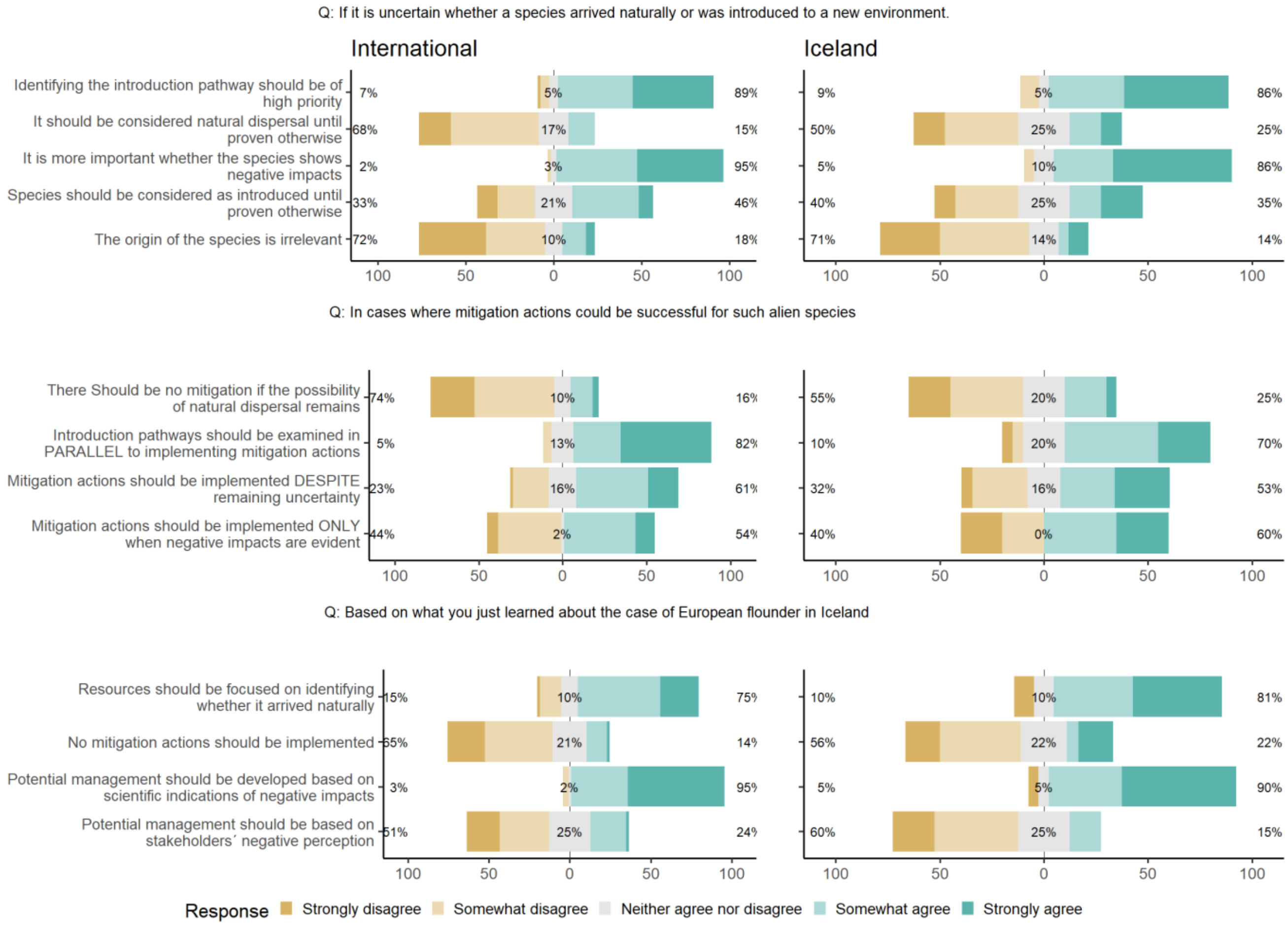

Figure 3 Perceptions of participants in the specialist survey regarding the handling of uncertainty when dealing with biological invasions in general as well as European flounder in Iceland specifically. Displayed likert graphs indicate participant's answers to the questions "If it is uncertain whether a species arrived naturally or was introduced to a new environment", "In cases where mitigation actions could be successful for such alien species", and "Based on what you just learned about the case of European flounder in Iceland" (Supplementary table 1 B questions 4,5, and 7). The five potential response levels ranged from "Strongly disagree" in orange to "Strongly agree" in green. Responses are shown for international invasion scientists on the left and (aquatic) scientists based in Iceland on the right.

Perceptions of recreational fishermen in Iceland based on online survey

When provided with six different, potential future steps concerning the European flounder as well as alien species in Iceland in general, participants gave highest priority to investigating the effects of European flounder on other species in Iceland followed by the prevention of the arrival of potential future alien species and the monitoring of the European flounder in Icelandic waters (Figure 4 A). While 52.4% of the participants indicated that it does not matter to them whether European flounder arrived naturally or was un(intentionally) introduced, 36.7% stated that it is indeed important to them (Figure 4 B).

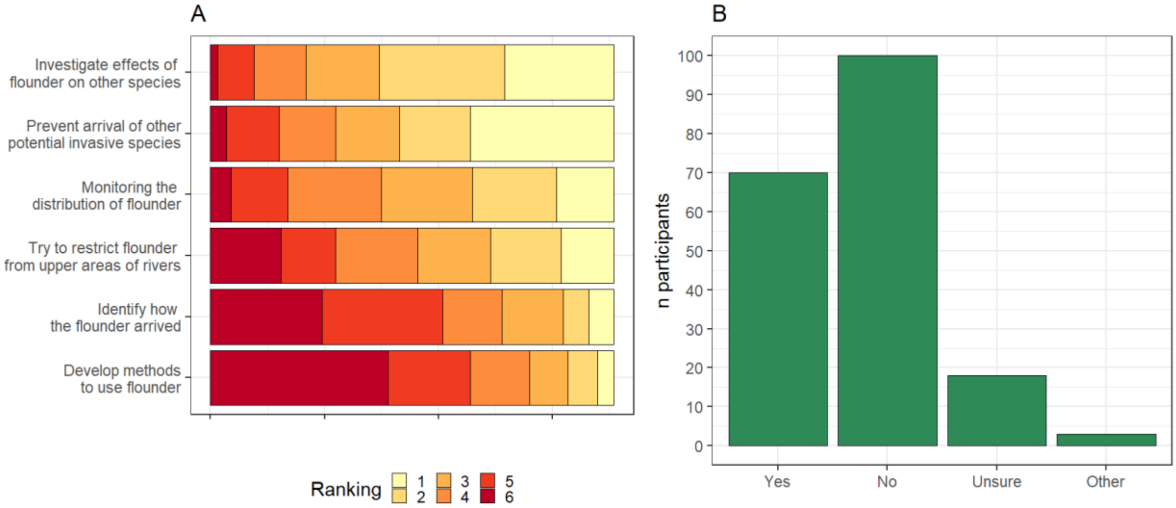

Figure 4 Results of the stakeholder survey. A) Barplot indicating the ranking of six potential future steps regarding participants' prioritization (Supplementary Table 1 A question 2). Participants ranked the options from 1 (highest prioritization, displayed in yellow) to 6 (lowest prioritization, displayed in dark red). B) Participants' responses when asked whether it makes a difference to them if the flounder was introduced due to human influence or not (Supplementary Table 1 A question 1).

Discussion:

In the present study, we show diverse expert views on the most applicable terminology to use in the case of an alien species with uncertain introduction pathway, here the European flounder in Iceland. However, their views generally aligned in the importance of conducting pathway identification simultaneously to assessing potential impacts and evaluating management approaches. The recreational angling community in Iceland prioritized assessment of the species' impacts as well as the prevention of future arrivals of invaders over eliminating uncertainty regarding the European flounder's arrival. Nevertheless, many expressed that the introduction pathway influenced how they perceive the flounder.

Terminology to classify alien species with uncertain introduction pathway

The results of this study highlight the persistent dissensus regarding the terminology used in invasion science. Soto et al. (2024) identified 59 terms used to classify the invasion status of a species, which represents a steep increase to earlier studies that identified 25-30 different terms (Colautti and MacIsaac 2004; Falk-Petersen et al. 2006; Lockwood et al. 2013). In the current study, survey participants provided a multitude of different terms to label European flounder in Iceland under consideration of the uncertainty regarding the species' introduction pathway. Like the results of previous studies (e.g. (Kapitza et al. 2019; Golebie et al. 2022; Soto et al. 2024), "invasive" was the term most frequently listed. Often interchangeably used terms such as 'alien', 'exotic', 'introduced', and 'non-native' appear in varying order of frequency following 'invasive' in these studies. In the current study, the term 'invasive' was followed by the common terms 'non-native' and 'alien'.

However, our results further highlight a difference in the use of terminology between the international group of invasion scientists and scientists based in Iceland. While the general pattern of ‘invasive’ being the most frequent and the terms ‘non-native’ and ‘alien’ ranking highly remained among the international group of invasion scientists, an additional term emerged among the top 4 terms used. The term ‘cryptogenic’ was the third most frequent term. ‘Cryptogenic’ refers to species where the native status and origin is not definitely resolved (Carlton 1996) and represents one of the terms that includes certain context dependent aspects in its definition. In comparison, the list of terminology listed by aquatic scientists in Iceland did not include this term at all, and further differed as the most frequently used term was ‘non-native’ instead of ‘invasive. Golebie et al. (2022) showed that in literature reporting on aquatic alien species, published between 2008 and 2018, the term ‘invasive’ was most commonly used with the exception of studies addressing early-stage invasions where ‘non-native’ was the most frequently used. A potential reason for the difference of the most frequently used term between these two groups could be that the invasion of European flounder in Iceland is perceived by local scientists as still being at a rather early stage, driven by the limited scientific attention this species’ introduction has received in the early years after its first documentation.

Even though the views on what terminology is most suitable to classify the European flounder in Iceland differed widely among participants, there was generally a high confidence to provide a term, regardless of what group they belonged to. Previous studies have pointed out that differences in the view and application of terminology have been linked to the specialists’ taxa of interest, discipline, position (academic vs practitioners) and geographic location (Humair et al. 2014; Shackleton et al. 2022). These factors, or a combination of them, could be the reason for the high confidence and large number of terms present among our results. While we are able to confirm that there was a wide range of geographic backgrounds among the applicants, the data collected in the current survey does not provide sufficient information to make any claims regarding other potential drivers.

Addressing alien species with uncertain introduction pathways

Overall, specialists agreed that for alien species where the introduction pathway has not been confidently identified, resources should be invested to resolve this uncertainty. Knowledge on how alien species have arrived in recipient environments is not only important for the specific case addressed but can deliver valuable information in a more general context as it can help identifying potential pathways that require management to prevent future invasions (Carlton and Ruiz 2005; Pyšek et al. 2013; Genovesi et al. 2014; Chapman et al. 2015). In the case of European flounder in Iceland, resolving the question around the species’ arrival has even further implications as it can influence the classification of its invasion status. One of the hypotheses on the European flounder’s arrival has been the introduction via ballast water from the western European coast (Thorarinsdóttir et al. 2014; Gunnarsson et al. 2015). Ballast water is known to be a viable pathway for European flounder introduction as it was introduced to the Great Lakes in North America via ballast water, although failed to establish a population and spread in the new environment (Cudmore-Vokey and Crossman 2000; Ricciardi and MacIsaac 2000). However, due to the geographic proximity of its source population in the Faroe Islands (Henke et al. unpublished manuscript) natural dispersion cannot be ruled out for European flounder in Iceland (Jónsson et al. 2001; Thorarinsdóttir et al. 2014). If the European flounder’s arrival in Iceland occurred by natural dispersal, the discussion regarding its classification would be further complicated in the absence of human assistance in the process.

Specifically addressing the European flounder in Iceland, views did not differ significantly between the two expert groups. Participants generally agreed that potential management measures should be developed based on scientific indication of negative impacts rather than stakeholder perceptions. Due to the limited scientific attention towards the European flounder since its arrival in Iceland, information on impacts on the environment can currently only be derived from a few small-scale studies (O´Farrell 2012; Hlinason 2013; Henke et al. 2020). These studies suggest potential ecological impacts on native species due to competition for resources as well as direct predation. Therefore, in addition to dedicating resources to the identification of the European flounder’s introduction pathway as suggested by the majority of participants, resources should also be spent on determining the extend of the indicated ecological impacts imposed by the species.

While considered as important, specialists did not prioritize the identification of the introduction pathways over addressing potential impacts of the species and rather suggest conducting both simultaneously. It should be highlighted though that this is the only aspect where the views between the two groups differed significantly with international invasion scientists showcasing stronger agreement on the simultaneous addressing of pathways and impacts. Pathways are a crucial component of addressing biological invasions, especially considering that the increasing number of emerging pathways is among the driving forces of the escalating number of species introductions (Pyšek et al. 2020). However, another crucial consideration is the limited time to respond to emerging invaders and for management measures to grasp. While the prevention of future invaders arriving is the most desirable management option, countries should be prepared to rapidly respond if a new introduced species emerges (Simberloff et al. 2013; Genovesi et al. 2014; Woodford et al. 2016). If time is spent on clearly identifying the species’ pathway before assessing the need of developing management approaches, the window where actions tackling the spread of the species, if deemed necessary, are feasible, rapidly reduces (Simberloff 2014). There is no one-size-fits-all solution to managing especially established invasions and therefore each case should be assessed individually (Simberloff 2014). In the case of European flounder in Iceland, population eradication or control is unlikely to be a viable option as it is now widely established throughout the country (Henke et al. 2024a).

Stakeholder views on the uncertainty of the European flounder’s introduction pathway

The identification of the European flounder’s introduction pathway appeared to play a minor role for the recreational angling community in Iceland as most participants attributed low priority to identifying whether the species’ introduction derived from natural dispersion. Instead, they clearly prioritize assessing the impacts of European flounder on native species. Considering the strong monetary value of recreational angling of Atlantic salmon, Arctic charr and brown trout in Iceland (Institute of Economic Studies 2018), it is likely that they are primarily concerned about the impacts on these species. The prioritization of impact assessment is not surprising as previous research has highlighted a strongly negative perception of this stakeholder group towards European flounder, indicating a perceived negative impact on their angling (Henke et al. 2024b). However, the group’s high ranking of preventing future species introductions is more surprising as it indicates an established, future oriented awareness of the risks imposed by biological invasions as well as the necessity of preventative measures that goes beyond their immediate environment. In contrast, Sutcliffe et al. (2017) suggested that there is often disparate prioritization between nationwide preventative measures to counteract arrival of future invasions and the perceived stronger need of prioritizing the response to immediate threats on a local scale.

To tackle biological invasions, it has been recognized that a multitude of perspectives on perceptions, priorities and goals across academic, management and stakeholder players are incorporated (Vaz et al. 2017; Garcia-Diaz et al. 2022). And though the aspect of what the stakeholder group prioritizes in future steps regarding the European flounder and biological invasions in Iceland has only been explored on a surface level within this study, it provides valuable information. Previous research has already highlighted this group's great willingness to participate and provide information in research projects on European flounder regarding it´s perceived impacts (Henke et al. 2024b) and its distribution (Henke et al. 2024a). On the other hand, the results indicate that the uncertainty around the European flounder's introduction pathway is of lesser concern to the stakeholder group.

Conclusion

Classifying the invasion status and labeling an alien species using the large pool of terminology available in invasion science becomes even more complicated when the specific case entails further uncertainties. In our study we have shown that while there is high confidence among specialists to assign terminology to the case of European flounder in Iceland, there is low consensus on the specific term that should be applied. While the specialists generally agree that the identification of the European flounders' introduction pathway should be among the priorities going forward, the selected stakeholder group of recreational anglers indicate that addressing the impacts of this species and the prevention of future arrivals of alien species are more important than identifying how the European flounder arrived. Our results highlight the need for a unified set of terminology in invasion science but also recommend the incorporation of stakeholder views when evaluating priorities in the addressing of biological invasions.

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Supplementary files:

Supplementary Table 1 List of questions included in the survey among Icelandic recreational fishermen, scientists as well as in the semi-structured interviews

A) Anonymous online survey among recreational fishing community in Iceland

Introduction: Hi everyone, I am a PhD student at the University of Iceland and have been researching flounder in Iceland for the last few years. The flounder was first found in Iceland in 1999 and is now found around most of Iceland, both in estuaries but also up in rivers and lakes. 3 years ago, I did an online survey, asking recreational fishermen about

their experiences and opinions about the flounder. Now, that new results have come up, I am doing a follow-up survey, asking the recreational fishing community once again about their experience and opinions. Although this survey is open to anyone, I particularly hope that those that answered the survey in 2019/2020 will participate. Part of my PhD is genetic research to look at where the flounder has come from. The results of that study show that the flounder has most likely arrived from the Faroe Islands. This means that the flounder could both have colonised Iceland naturally or been introduced by one of many ships moving between countries.
Many definitions of invasive species state that the species has been introduced by human action, such as shipping, but that does not necessarily change how the species is viewed by the public or should be managed. With this follow-up survey, I would like to find out what the opinion currently is about flounder in Iceland and whether it makes a difference to you that the flounder could have come here naturally.
The survey takes around 5-10 minutes to fill out and is available in Icelandic and English. The data will be handled anonymously. If you would like to receive an update on the results of this study, please provide an email address at the end of the survey. If you have any further questions, please send me an email at thh183@hi.is

Question 1: Do you think it makes a difference whether the flounder arrived naturally or if it arrived due to human influence (for example with ships)? (Choose one option) Options: Yes / No / I don't know

Question 2: Please rank the following statements according to their importance in dealing with flounder in Iceland. The most important statement is placed on top and what you rank the least important should be at the bottom. (Rank the six provided statements) Statements: Monitor the distribution of flounder in Iceland / Identify how the flounder arrived in Iceland / Try to prevent the arrival of other potential invasive species in the future / Explore for potential options to restrict flounder from entering upper parts of rivers / Investigate the effects of flounder on other species / Develop methods to use the flounder

Question 3: Do you have any other comments? (Open text)

B) Anonymous online survey among specialists

Introduction: My name is Theresa Henke and I am a PhD student at the University of Iceland. I am doing research on the European flounder (Platichthys flesus) in Icelandic waters. Flounder is not a native species in Iceland, it was documented for the first time in 1999 and has since been classified as "potentially invasive" based on an assumed introduction by ballast water, rapid spread to most regions of Iceland and some scientific results that indicate negative impacts on native species via competition and direct predation. My own research has shown impacts on stakeholders, especially the recreational fishing community, that perceive the flounder as highly negative and have strong concerns about impacts on the native salmonids.
As part of my research, I have also investigated the most likely place of origin of flounder in Iceland, using genetic analysis to compare samples collected all around Iceland to reference data from all over Europe. The results strongly indicate the Faroe Islands as the most likely place of origin. Based on the proximity of the Faroe Islands to Iceland, approximately 400km, these results open the question of whether flounder was introduced via the considerable boat traffic between countries or colonized by natural

dispersal.
It is likely that dispersal of marine species to subarctic and even arctic regions will increase in the next decades and it is important to consider how these species should be classified and managed. In terms of perceptions I would like to understand if the origin of the flounder influences the perception of stakeholders, for example, by making them less negative.
To be able to place the perceptions of stakeholders in context I plan to also document the perceptions and viewpoints of the scientific community, both within and out with Iceland. Therefore, I would highly appreciate your participation in this survey as a representative of the invasive science community. The survey is completely anonymous and takes ~ 5 minutes to finish. If you have any further questions or comments, please contact me via email (thh183@hi.is) or Twitter (@TheresaHenke2).

Question 1: Are you actively involved in invasion science? (Choose one option) Options: Yes / No / Other

Question 2: In which country are you based? (Open text)

Question 3: How do you personally define an invasive species? (Open text)

Question 4: If it is uncertain whether a species arrived naturally or was introduced to a new environment. Please rank your agreement to the following statements (6-point likert: Strongly agree / Somewhat agree / Neither agree nor disagree / Somewhat disagree / Strongly disagree / I don´t know)
Statements: Identifying the introduction pathway should be of high priority / It should be considered natural dispersal until proven otherwise / It is more important whether the species shows negative impacts / Species should be considerd as introduced until proven otherwise / The origin of the species is irrelevant for decision making

Question 5: In cases where mitigation actions could be successful for such alien species. Please rank your agreement to the following statements (6-point likert: Strongly agree / Somewhat agree / Neither agree nor disagree / Somewhat disagree / Strongly disagree / I don´t know)
Statements: There should be no mitigation if the possibility of natural dispersal remains / Introduction pathways should be examined in PARALLEL to implementing mitigation actions / Mitigation actions should be implemented DESPITE remaining uncertainty / Mitigation actions should be implemented ONLY when negative impacts are evident

Question 6: Knowing that the flounder could have either been introduced to or arrived naturally in Iceland, what term would you use to describe the flounder? (Open text)

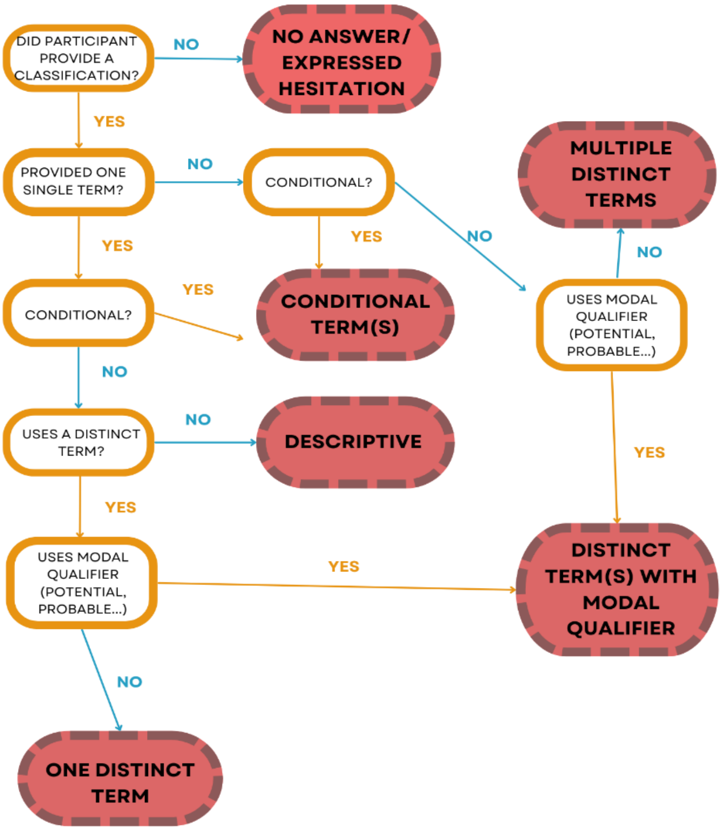
Question 7: Based on what you just learned about the case of the European flounder in Iceland. Please rank your agreement to the following statements (6-point likert: Strongly agree / Somewhat agree / Neither agree nor disagree / Somewhat disagree / Strongly disagree / I don´t know)

Statements: Resources should be focused on identifying whether it arrived naturally / No mitigation actions should be implemented / Potential management should be developed based on scientific indications of negative impacts / Potential management should be based on stakeholders´ negative perception **Question 8:** Do you have any further comments? (Open text)
C) Semi-structured interviews **Question 1:** When you hear the term "invasive species", what does it mean to you? **Question 2:** How and when did you become aware of the flounder in Iceland? **Question 3:** When you talk to friends, customers, other fishermen, researchers, and the topic flounder comes up in the conversation, what is often talked about? **Question 4:** When you are out fishing and you end up catching a flounder, what would you do with it? **Question 5:** What would like to see being done about the flounder in the future? **Question 6:** In what ways do you think the flounder could be used? **Question 7:** How would you describe the current status of management of flounder in Iceland? **Question 8:** Do you think a management strategy for flounder is necessary in Iceland?

Supplementary Table 2 List of countries represented in the international survey among scientists and the according number of participants per country

Country	N participants
Australia	1
Belgium	2
Brazil	1
Canada	7
Chile	1
Denmark	1
Estonia	2
France	2
Germany	5
Hungary	1
Iceland (Invasion scientists – non-invasion scientists)	22 (9 – 13)
Ireland	3
Malta	2
Netherlands	1
Northern Ireland	1

Norway	2
Poland	1
Portugal	1
South Africa	1
South Korea	1
Spain	1
Switzerland	1
UK	7
USA	16
Total	**83**



Supplementary Figure 1 Classification scheme used for categorizing the confidence in which participants provided a response when asked what terminology they deem most appropriate to the case of European flounder in Iceland.

Supplementary Table 3: Number of participants' answers classified into each of the six categories. Participants were asked what terminology they would apply to the case of European flounder and the categories indicate the level of confidence with which

terminology was suggested. Listed are the total number of participants per category as well as the numbers per group (International v. Iceland).

Confidence classification	All	International	Iceland
One distinct term	51	41	10
Distinct term(s) with modal qualifier	8	6	2
Conditional term(s)	12	7	5
Multiple distinct terms	4	3	1
Descriptive	4	1	3
No answer/ expressed hesitation to classify	4	3	1

Supplementary Table 4: Polarization scores for answers stemming from specialists working in invasion science (excluding Iceland) as well as from scientists based in Iceland. The table additionally provides the results of the Mann Whitney U test comparing the results between the two groups.

	Polarization International	Polarization Iceland	Mann Whitney U test
If it is uncertain whether a species arrived naturally or was introduced to a new environment			
Q4.1 Identifying the introduction pathway should be of high priority	0.1844262	0.1969697	654.5 p = 0.856
Q4.2 It should be considered natural dispersal until proven otherwise	0.2416667	0.35	485 p = 0.1765
Q4.3 It is more important whether the species shows negative impacts	0.1370056	0.1547619	622.5 p = 0.8348
Q4.4 Species should be considered as introduced until proven otherwise	0.3278689	0.4041667	632 p = 0.8081
Q4.5 The origin of the species is irrelevant	0.2944444	0.2896825	586 p = 0.6222
In cases where mitigation actions could be successful for such alien species			
Q5.1 There should be no mitigation if the possibility of natural dispersal remains	0.2568306	0.35	502.5 p = 0.2147
Q5.2 Introduction pathways should be examined in PARALLEL to implementing mitigation actions	0.1721311	0.25	**792.5 p = 0.03164**
Q5.3 Mitigation actions should be implemented DESPITE remaining uncertainty	0.3114754	0.4298246	601.5 p = 0.7998

Q5.4 Mitigation actions should be implemented ONLY when negative impacts are evident	0.4497354	0.4680556	575.5 p = 0.6933
Based on what you just learned about the case of European flounder in Iceland			
Q7.1 Resources should be focused on identifying whether it arrived naturally	0.240113	0.2698413	506 p = 0.1845
Q7.2 No mitigation actions should be implemented	0.2719298	0.3842593	437.5 p = 0.3291
Q7.3 Potential management should be developed based on scientific indications of negative impacts	0.1263889	0.1791667	641 p = 0.6044
Q7.4 Potential management should be based on stakeholders' negative perception	0.3432203	0.275	646 p = 0.5168