Master's thesis

Sprat (*Sprattus sprattus*) in Iceland

What do we know and what can we predict about the future?

Nicholas Matthew Hoad

Advisors: Jón Sólmundsson, MSc.
Hjalti Karlsson, BSc.

University of Akureyri
Faculty of Business and Science
University Centre of the Westfjords
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Supervisory Committee

Advisors:
Jón Sólmundsson, MSc
Hjalti Karlsson, BSc

External Reader:
Haseeb Randhawa, PhD

Program Director:
Verónica Méndez Aragón, PhD

Nicholas Matthew Hoad
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What do we know so far and what can we predict about the future?

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Declaration

I hereby confirm that I am the sole author of this thesis and it is a product of my own academic research.

Nicholas Matthew Hoad

Abstract

Sprat (*Sprattus sprattus*) (Icelandic: brislingur) is a small clupeid fish superficially similar in appearance to a small herring. It is widely dispersed in shallow waters in Europe from the North and Baltic Seas to the Mediterranean with separate subspecies occurring in each of these three subregions. Sprat was unreported in Icelandic waters until 2017, when a single individual was caught in a research trawl off the south coast. Since then, further records have been reported in coastal waters south and west of the country. It is probable that sprat entered the Icelandic marine zone as pelagic eggs or larvae which were carried from elsewhere in Europe, such as the Faroe Islands, although isolated incidents of sprat being found in ballast water have been reported. New species entering marine ecosystems deserve attention as to whether or not a species could be high or low impact within a system and be of consequences for marine managers. This thesis aims to summarise much of the data that has been collected to date, from secondary data as well as primary data collected in partnership with the Icelandic Marine and Freshwater Research Institute. Weight, length, maturity class, and age data from subsets of samples collected are presented and species distribution models produced to predict current habitat suitability and potential future habitat suitability under four different climate scenarios. It is confirmed that sprat spawns in Icelandic waters and reaches at least four years of age. Species distribution models suggest habitat suitability will continue to be present under all modelled climate scenarios for the years 2050 and 2100. It is suggested that future investigation of the species' behavioural ecology in Iceland, particularly feeding preference and ecological niche overlap with other species, may be a valuable route for further research.

Útdráttur

Brislingur (*Sprattus sprattus*) er smávaxinn fiskur af síldaætt, svipaður útlits og ung síld (*Clupea harengus*). Brislingur finnst víða í innhöfum og við strendur Evrópu frá Eystrasalti, Norðursjó og suður í Miðjarðarhaf og eru aðskildar undirtegundir á hverju þessara svæða. Brislingur fannst fyrst við Ísland árið 2017 þegar einn fiskur fékkst í rannsóknavörpu. Síðan hafa nokkur hundruð brislingar fengist við sunnan- og vestanvert landið. Líklegt er að brislingur hafi borist til Íslands með hafstraumum sem sviflæg egg eða lirfur frá öðrum svæðum við Evrópu, t.d. Færeyjum, þótt ekki sé hægt að útiloka að tegundin hafi borist með kjölfestuvatni skipa. Mikilvægt er, t.d. vegna veiðistjórnunar, að fylgjast vel með tegundum sem berast nýjar í vistkerfi hafsvæða, þannig að hægt sé að meta hve mikil áhrif þær hafa á lífríki nýrra heimkynna. Markmið þessarar ritgerðar er að taka saman gögn um brisling sem safnað hefur verið hingað til, bæði eldri og ný gögn sem safnað var vegna þessa verkefnis í samvinnu við Hafrannsóknastofnun. Kynnt eru gögn um lengd, þyngd, kynþroskastig og aldur brislings og útbreiðslulíkön gerð til að meta líkleg útbreiðslusvæði í nútíð og framtíð miðað við fjórar sviðsmyndir loftslagsbreytinga. Rannsóknin staðfestir að brislingur hrygnir við Ísland og nær a.m.k. fjögra ára aldri. Útbreiðslulíkön benda til að brislingur muni geta lifað við Ísland árin 2050 og 2100, sama hvaða sviðsmyndir loftslagsbreytinga voru skoðaðar. Mælt er með að komandi rannsóknir á brislingi á Íslandsmiðum beinist að fæðuvistfræði og vistfræðilegri skörun við aðrar tegundir.

In memory of Hewart Jeffries.

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1 Introduction

The distribution of species in both terrestrial and marine realms is dependent upon a complex suite of biotic and abiotic variables which define the organisms' niche (Holt, 2009). The concept is described by Holt (2009) as an abstract space bounded by axes representing the biotic and abiotic factors which affect an organisms' or species' fitness. Changes in these factors, therefore, have the potential to impact fitness in this space, but the entry of species into an environment in which environmental factors are optimal can allow also for the successful colonisation of this new geographical space. Ecosystems are dynamic environments which respond to changes in a host of variables. Naturally occurring fluctuations in the environment have impacts on species at both fine and coarse resolutions. For instance, in aquatic and marine systems, diurnal fluctuations in riparian water temperature impact Atlantic salmon (*Salmo salar*) standard metabolic rate and the North Atlantic Oscillation (NAO), fluctuating on a decadal level during the early 20th century, appears to influence the recruitment of Atlantic cod (*Gadus morhua*, hereby referred to as cod) recruitment due to the impacts on sea temperatures (Enders & Boisclair, 2016; Lehodey *et al.*, 2006).

A species which encounters a new environment which provides a suitable niche may be able to colonise this new space. A species may enter new environments that present conditions favourable to growth and reproduction, known as extra-range dispersal. This may occur naturally (for example through oceanic rafting of terrestrial organisms) or through movement by humans whether deliberate or otherwise (e.g. Keller *et al.*, 2011). Furthermore, the influence of human activity, such as fishing, and anthropogenically induced warming on land and in the oceans, has demonstrable impacts on a species' ability to survive, both positively and negatively, resulting in altered ranges of species (e.g. Valdimarsson, Astthorsson, & Palsson, 2012; Oguz, Fach, & Salihoglu, 2008). New species in an environment may cause little or no perceivable impacts beyond their presence, or they can alter food webs and ecosystems posing a risk to native species and ecosystem services for human populations (e.g. Molnar *et al.*, 2008; Pimentel, Zuniga, & Morrison, 2005).

The Arctic region is at the forefront of climate change and has been shown to have warmed at up to four times the rate of the global average (Rantanen *et al.*, 2021). Changes to sea ice extent have potentially important knock-on effects on primary and secondary production, physical habitat requirements of birds and mammals, as well as the physical attributes of marine waters due to meltwater input (IPCC, 2014a; Laidre *et al*., 2008; Perrette *et al*., 2011; Wassmann *et al*., 2011). The Arctic can be viewed as a sink destination for invasive species due to the generalized movement of species away from the equator due to warming temperatures, towards the poles and habitats that more closely match the thermal regimes for which they are adapted (Kourantidou, Kaiser, & Fernandez, 2015). Shifts in the ranges of species have been observed in both the marine and terrestrial realms, as new habitats in historically thermally limiting environments become warmer and more optimal. For instance, sea lamprey (*Petromyzon marinus*) were observed for the first time in 2008, and bluefin tuna in 2012, off the east coast of Greenland, likely due to observed temperature increases opening up new viable habitat for these generally more southern species (Emblemsvåg *et al*., 2020; Mackenzie *et al*., 2014). Depending on the species, range shifts in the Arctic may be less due to thermal tolerance and more as a result of changes to the physical environment as a result of climate change. For example, populations of polar bears (*Ursus maritimus*), have been observed to become isolated as a result of declining sea ice in the Baffin Bay area, with a decrease in connectivity with other populations (Laidre *et al*., 2018).

The subarctic environments, while less ice-dominated, are also experiencing many of the challenges of the Arctic resulting from climate change and human activity. The invasion of species into subarctic freshwater environments is likely facilitated by climate change (Rolls, Hayden, & Kahilainen, 2017). For instance, in northern Sweden, it was noted that the invasion of Northern pike (*Esox Lucius*) into a freshwater lake system coincided with increasing summer temperatures. In this case, the pike became dominant over the native Arctic char populations, for which it is a competitor and predator (Byström *et al*., 2007). Shifts in the range of species have also been observed, as new habitats in historically thermally limiting environments become warmer and more optimal, an example being the northern limits of sport fish ranges in Ontario, Canada, which have demonstrated a shift of 12.9 to 17.5 km per decade, attributed to observed warming of freshwater environments (Alofs, Jackson, & Lester, 2014). The introduction of species by humans has also occurred. For instance, the Arctic fox (*Alopex lagopus*) was introduced to the Aleutian Islands to supplement the dwindling fur trade in the late 19th and early 20th centuries (Croll *et al*., 2005). Some islands received these introductions, however, some did not, with the result that the impacts of the species can be readily observed. In this case, the Arctic fox, which is a predator on seabirds, caused a marked shift in nutrient transport from the marine to terrestrial zones, thus causing a significant reduction in soil quality and altering the terrestrial plant communities from grasslands to maritime tundra (Croll *et al.*, 2005).

Iceland, which lies just below the Arctic circle, has experienced these changes in species compositions and distributions, much like many other high-latitude areas. Since the settlement period, around the end of the 9th century, terrestrial species composition has changed markedly (Alsos *et al.*, 2021; Streeter *et al.*, 2015; Sveinbjörnsdóttir, Heinemeier, & Gudmundsson, 2004). The influence of human activity and climatic changes have been felt in the terrestrial and marine environments. Human settlement in Iceland caused significant changes in plant species communities due to the utilisation of trees such as *Juniperus communis* as well as potential pressure from grazing (Alsos *et al.*, 2021). The Arctic fox, once the only native land mammal, has been joined by a host of introduced mammalian species, including grazing mammals, particularly sheep (*Ovis aries*) and the mouse (*Mus musculus*) which have impacted the landscape and vegetation communities of Iceland (Dugmore *et al.*, 2005). In the marine environment, the seaweed *Fucus serratus* was probably introduced around the 19th century and recent warming temperatures have seen the increased biomass of several fish species, once only seen in low numbers but now with significant population sizes. For example, the European flounder (*Platichthys flesus*) and pink salmon (*Oncorhynchus gorbuscha*) were first recorded in Icelandic waters in 1999 and 1960, respectively (Coyer *et al.*, 2006; Guðjónsson, 1961; Henke, 2018; Henke, Patterson, & Ólafsdóttir, 2020). New species which establish and expand in range within an environment (here termed invasive species) may be benign, with limited to no impact on the existing ecosystem, or they may be in direct competition with (and begin to outcompete) native organisms or communities, (Henke, Patterson, & Ólafsdóttir, 2020). At their most damaging, they may displace native organisms or fundamentally alter the dynamics of the local system, including changes to community structure or ecosystem processes and services such as nutrient cycling (Molnar *et al.*, 2008). In the case of the European flounder, the species has been shown to have a high trophic overlap with the native European plaice (*Pleuronectes platessa,* herby referred to as plaice) (Henke, Patterson, & Ólafsdóttir, 2020). Pink salmon have been shown to pose significant hazards to Atlantic salmon, both in the wild and in aquaculture facilities in Norway, and with the recognition that the species is spawning in Icelandic waters, potential impacts on Atlantic salmon in Iceland may well be a pressing consideration for future research (Elliot, 2022; Hindar *et al.*, 2020).

European sprat (*Sprattus sprattus*), hereby referred to as sprat, was first recognised in Icelandic waters in 2017 and since then has been identified more frequently in research trawls (Pálsson *et al.*, 2022). Understanding the biology of a new species in an ecosystem is a priority. With the potential that the sprat could become either or both commercially exploitable or an invasive species, knowledge of where the species is, how it is utilising the Icelandic marine environment, as well as its spawning potential allows for more effective management decisions as or when deemed necessary.

This thesis aims to begin to address aspects of sprat biology in Iceland, as well as predict where the suitable habitat for the species is currently located and how this may change under future climate scenarios.

1.1 Aims and objectives

Due to the limited biological and ecological information on the current distribution of sprat in Iceland or research on the potential impacts of the species, there is a clear need to fill some of these knowledge gaps.

This thesis aims to provide information about the current status of the species in Ísafjarðardjúp, Northwest Iceland, to model potential distributions in the future as well as to provide data and information which can be used to assess the ecological impacts of this new species.

Research questions:

1. What is the abundance of sprat occurring as bycatch in the shrimp fishery or within survey trawls in the Westfjords of Iceland?
2. In which specific areas are sprat occurring as bycatch or within survey trawls within the Westfjords?
3. Of which maturity and age classes are sprat caught in the Westfjords?
4. What could the potential distribution of sprat be around Iceland today and under future climate scenarios?

1.2 Thesis layout

Due to the aims of this thesis, the theoretical background in chapter two gives an overview of some of the concepts potentially relevant to understanding the mode and consequences of the establishment of sprat in Icelandic waters. Section 2.1 discusses marine systems' response to change and gives an overview of some of the key processes and examples which have been shown to alter community composition and structure on a global scale. Section 2.2 gives background on the Icelandic marine ecosystem and its importance to the Icelandic economy with regard to fisheries. Section 2.3 gives an overview of sprat, highlighting key characteristics of the species, its importance as a fisheries resource, as well as examples of its impact in a number of ecosystems experiencing various pressures. In section 2.4, current knowledge about the state of sprat in Icelandic waters is given alongside the potential impacts of its presence. To answer research question four, this thesis will look at the potential distributions of the species as a result of climate change and as such, section 2.5 gives a brief background on relevant processes used in climate predictions. Finally, as species distribution models (SDMs) are utilised, section 2.6 gives a background of methodologies and applications of SDMs and Maxent, used in this thesis. The methods and results are given in chapters three and four. Finally, the discussion in chapter five, draws together some of the current knowledge on sprat in Icelandic waters, linking to the key themes highlighted in chapter two.

2 Theoretical Background

2.1 Marine ecosystem response to change

The multitude of processes, changes and pressures placed on marine and coastal areas can fundamentally alter systems. Understanding the capacity of these systems to buffer these, with limited alteration of key ecosystem processes, structure, and function, is a critical element in creating management plans which support sustainable marine and coastal zones.

The responses of ecosystems to changes in a diverse range of variables such as climate, chemistry or the harvest of species can be gradual or profound. In some cases, the ecosystem response curve can be said to be ‘folded back’ suggesting two altering ‘stable states’ with an unstable intermediary. When environmental conditions pass a certain threshold there can be a dramatic shift from one stable state to another. It may not be possible to simply reverse this shift through the re-establishment of conditions from the past (with regards to temperature, chemistry or fishing pressure, for example) as the alternative stable state has already been established. The pattern of switches within an ecosystem at critical conditions is referred to as ecosystem hysteresis (Scheffer *et al*., 2001).

The result of the entry of sprat into Icelandic waters is likely determined by external forces acting on this system and it is, therefore, important to understand the situational context of this. Here, the broad concepts of several forces are described which may be relevant context for the status of sprat over time.

2.1.1 Overfishing

Fish accounted for about seven percent of all protein consumed globally in 2017 and 17 percent of all animal protein (FAO, 2020). For around 3.3 billion people, fish accounted for 20 percent of protein consumption (FAO, 2020). Capture from marine fisheries frequently exceeds 80 million tons and around 39 million people are involved directly in capture fisheries internationally (FAO, 2020). The link between fisheries and livelihoods is inescapable, however, as is the potential pressure exerted on to target species.

Industrial and commercialised fishing techniques which support these livelihoods date back centuries, however, in many cases this has had consequences on the stocks of targeted species. In England and Wales, steam powered vessels were first introduced in the 1880s, allowing for a great expansion in fishing power (Thurstan, Brockington, & Roberts, 2010). This rapid increase in fishing pressure has been shown to have corresponded with an equally rapid decline in the availability of benthic fish species, measured in landings per unit of fishing power (LPUP). In the case of England and Wales, LPUP has dropped by 94% between 1889 to 2007, highlighting the pressure put on marine ecosystems by the industrialisation of the fleet (Thurstan, Brockington, & Roberts, 2010).

It has been observed that overfishing of predators can cause marked changes in system dynamics (Frank *et al*., 2005; Österblom *et al*., 2007). In the North Atlantic and the Baltic Sea, the shift from predator-dominated systems with a high density of species such as cod and haddock (*Melanogrammus aeglefinus*) can experience a shift towards a system dominated by small pelagic species following intense fishing pressure (Lindegren, Diekmann, & Möllmann, 2010). Under the hypothesis of ecosystem hysteresis, predator-dominated systems will regulate their recruitment by the suppression of small pelagic foragers which prey upon their eggs and larvae. Following the 'artificial' suppression of predators by selective fishing pressure, small pelagic species can maintain dominance in a system through their increased recruitment (due to reduced predation) as well as their increased predation of predator eggs and larvae (Scheffer *et al*., 2001). This principle would also hold in a shift from small pelagic-dominated systems toward a predator-dominated system under the influence of high pelagic fishing pressure. Importantly, this system shift is not maintained by fishing pressure. Even in the event of a cessation of all fishing activity, the shift has taken place and is often self-maintaining. Targeting fishing pressures may alleviate some pressures on exploited stocks. For example, it has been shown that where cod are heavily exploited, controlled additional fishing of clupeids may support predator stocks. This is largely due to the reduction in adult clupeid biomass and a subsequent increase in juvenile biomass as a result of the release from density dependence. This increase in juvenile biomass provides a greater abundance of potential prey for cod (Soudijn *et al.,* 2021*)*.

Even in the absence of ecosystem hysteresis, recovery of systems under a reduction in fishing pressure may not be predictable. The Firth of Clyde, Scotland, has historically been an area of intense fishing pressure. Herring (*Clupea harengus*) was a targeted species as early as the 16th century and depletion in stocks was recognised as early as the late 19th century, with laws put in place in Scotland preventing trawling within three nautical miles of the shore as well as closing the whole Firth of Clyde to trawling (Thurstan & Roberts, 2010). Following a reduction of herring catch in the seine net fishery in the 1950s and 1960s industry pressure rose to the point where the Clyde was re-opened to trawling, with the demersal trawl subsequently becoming the dominant method of fishing by the local industry (Thurstan & Roberts, 2010). Demersal fisheries expanded, with high catches in the 1960s and 1970s, however, landings once again dropped which, in turn, led to the repeal of the three nautical mile limit to try and maintain the industry. What followed has been called a 'terminal decline' of demersal landings leading to the 'endpoint of overfishing', where no stocks were able to support a sustainable fishery (Thurstan & Roberts, 2010). In an ecosystem of previously high species evenness with large maximum lengths, community structure changed to the point where whiting (*Merlangius merlangus*) dominated the system, representing about 90% of biomass (Heath & Speirs, 2012). The Clyde was seen by some to be a prime example of "fishing down the food web," a term made popular by Pauly *et al.* (1998), describing the process by which higher trophic level organisms are fished to the point that they become unsustainable, either ecologically, economically or a combination of the two. As this happens, the fishing industry overwhelmingly tends to then turn towards newer profitable species. With the continuation of this process, a trend appears over time of fisheries gradually moving towards lower-trophic organisms such as crustaceans, as other species are lost to the industry (Pauly *et al*., 1998). In the context of the Firth of Clyde, fishers had exploited demersal species as well as Norway lobster (*Nephrops norvegicus)* since the 1950s to diversify from herring. Following the expansion of the demersal fleet and the subsequent crash in demersal stocks, *Nephrops* became the dominant fishery species by 2008, representing 84% of landings by weight, followed by other invertebrate species (Thurstan & Roberts, 2010). Where profitable demersal and herring fisheries had once dominated, but collapsed, the industry had turned almost entirely to crustaceans. Fishery recovery in the Clyde, in general, has been seen by some to be a successful example of ecosystem recovery, with biomass increasing by around 100% since the 1980s, measured through acoustic surveys (Lawrence & Fernandes, 2021). However, sprat have become the most abundant forage fish species in this area once dominated by herring (Lawrence & Fernandes, 2021).

Fisheries are integral to livelihoods as well as local and national economies around the world, however, the harvesting of species from the marine environment needs to be managed with care to avoid unintended consequences. Efforts are in place internationally to implement best practice solutions in the fisheries sectors. The Code of Conduct for Responsible Fisheries, for example, was adopted by FAO members in 1995, following a period of multiple fish stock collapses in the 1980s (FAO, 1995). The code sets responsible practice from extraction through to consumption, promoting conservation and an ecosystem-based approach while recognising the importance of the sector to societal needs. The fisheries policies and management frameworks of the majority of nations are compliant with this code (FAO, 2020).

2.1.2 Introduction of novel species

The introduction of novel species to marine ecosystems is increasingly well documented on a global scale, although research is lacking across taxa as well as on the consequences of introductions (Watkins *et al.*, 2021). The boundaries of a species range can "leak", with expansion or contraction of ranges based on a number of factors such as changes in the extent of suitable habitat or dispersal patterns (Dunstan & Bax, 2007). Species' also may "jump" into new habitats outside of their established ranges. Focussing on marine systems, the modes by which these species enter these new environments or change their distribution patterns may be governed by a range of forces. Species may enter new areas, simply as a result of the stochastic processes by which species have always moved, such as egg dispersal, while anthropogenically-induced movement of species may also occur, for instance, through transport in ballast water (Wonham *et al.*, 2000). These anthropogenically-mediated forms of range shift may include the deliberate introduction of species to new environments or accidental transport of organisms. The latter could occur in several ways, such as through ballast water or the escape of organisms from captivity. Animals may also change their distribution patterns as a response to changing environmental conditions (Campana *et al.*, 2020b). In this thesis, two terms are used to distinguish organisms which establish in a new area independently of human activity (immigrant), or those which arrive and establish through anthropogenic means (non-native) (Falk-Petersen, Bøhn, & Sandlund, 2006). Although these terms are useful for discussion, in reality it may be difficult to distinguish between the two terms. For instance, defining if a species moves due to warming waters counts as independent from, or as a result of, human activity.

The impacts of immigrant/non-native species on the local environment may be ecological or socio-economic. As mentioned, some species pose a low/no perceivable threat to extant systems, however, others thrive and may reach extreme population densities (1000 s m^{-2}) and outcompete other species in the local environment, otherwise termed invasive (Bax *et al.*, 2003). This has been seen in the San Francisco Bay area in which the majority of habitats are dominated by at least one non-native species (Bax *et al.*, 2003). Across the United States, Pimentel, Zuniga, & Morrison (2005) reported 138 non-native fish species with an associated loss estimated at over $1 billion per annum, however, introductions have benefitted some sectors, particularly sport fishing.

The comb-jelly (*Mnemiopsis leidyi*), native to North and South America and introduced into the Black Sea region in the 1980s, was noted to be increasing in biomass at a considerable rate in the 2000s, partly because of the lack of fish predators present which specialise on *Mnemiopsis* in the region, in contrast to their native range. The invasion of *Mnemiopsis* in the Baltic region coincided with the collapse of an important fishery species the anchovy (*Engraulis encrasicolus*) and a shift in dominance towards *Mnemiopsis*. In trying to understand this reversal in dominance, Oguz, Fach, & Salihoglu (2008) modelled the lower trophic level and bioenergetics of anchovy populations and connected predation, fishery pressure, climate and food competition in a framework describing shift. What they found was a combination of factors which ultimately led to the change observed within the Black Sea ecosystem. From 1970 to 1984, anthropogenic nitrate loading had increased production to the point where eutrophication began to occur in the euphotic zone, during this period the comb jelly was also first introduced to the Black Sea. From 1985-1987 climate change continued to enrich the euphotic zone while the *Mnemiopsis* was able to acclimatise to the new environment as well as have a competitive advantage in prey consumption under the high levels of secondary production. Concurrent with this, the anchovy was experiencing a decrease in spawning stock biomass through fishery pressure. From 1988, favourable temperatures for *Mnemiopsis* growth and the subsequent enhanced predation of the species on anchovy eggs and larvae ultimately resulted in the sustained population growth of *Mnemiopsis* and the suppression of the anchovy (Oguz, Fach, & Salihoglu, 2008). While this is just one example of the establishment of dominance of a non-native, it is demonstrative of the non-linear pathways of such an invasion and the multiple factors which may facilitate the process.

There are fundamental challenges to the management of marine immigrant and non-native species, whether invasive or otherwise. Such challenges include the perception of the public and marine managers over the nature of marine systems. Often, marine systems are perceived as inherently open systems even though, at least for some species, this is proven otherwise (Thresher & Kuris, 2004). This can lead to a defeatist attitude towards the management of non-natives. Furthermore, the technical nature of managing marine species is an added barrier to the control of non-natives. This includes the need for often limited knowledge of marine taxa, as well as more challenging techniques in, for instance, the removal of organisms (Thresher & Kuris, 2004). A further challenge to the management of invasive species comes from monitoring. Initial detection of marine invasive species may be relatively slow, compared to terrestrial invasions, due to the added complexity in monitoring marine areas. In many cases of biological invasions citizen science may be able to reduce some of these challenges, with the potential to plan co-ordinated surveys or simply have irregular but widespread reporting as or when a species is found and data collection and management may be driven by researchers or the public (Danielsen *et al.*, 2009). In aquatic systems, the first observations may well be made by fishers rather than researchers. This was the case for the weakfish (*Cynoscion regalis*), which was introduced to the Iberian peninsula around 2012, where the detection of the species was made possible due to the actions of fishers (Morais & Teodósio, 2016). Citizen science has the potential to support a range of issue pertinent to marine management. Focussing on invasive or novel species, these include raising awareness amongst stakeholder groups, the inclusion of knowledge from multiple and disparate sources, the provision of long-term datasets and sustainability in the monitoring of specific sites (Cigliano *et al.*, 2015). In instances where funding for marine research is limited or reduced, citizen science also poses a potential tool to ensure continued monitoring effort, at least to some degree (Hyder *et al.*, 2015).

2.1.3 Climate change and water temperature

Fish are ectothermic organisms, making the temperatures of their environments critical for the regulation of physiological functions. To understand the physiological basis behind realised thermal tolerances, hypotheses such as the oxygen- and capacity-limited thermal tolerance (OCLTT) paradigm have been suggested. The OCLTT concept utilises a range of indicators to understand the key processes which limit thermal tolerance and the active range within which organisms are able to maintain aerobic performance and metabolism (Pörtner, Bock, & Mark, 2017). In theory, it seems rational to link aerobic capacity to fitness, although it is pointed out by Lefevre, Wang, & McKenzie (2021) that direct evidence of this is lacking and fitness is the result of the interplay of numerous factors not limited to aerobic capacity. Regardless, temperature has a critical influence on physiology in fish species which is a result of a combination of temperature and time. For example, short exposures to temperatures at the upper range of a species' thermal tolerance can result in loss of equilibrium and death in a matter of hours, due to effects on the nervous system and cardiovascular system and the denaturation of enzymes and other proteins, whereas reduced health or fitness, ultimately leading to death, can also occur at the lower end over a matter of weeks due to increased susceptibility to parasites and bacteria, impacts on swimming performance and resulting predation (Lefevre, Wang, & McKenzie, 2021).

Temperature has been shown to be significant in predicting the abundance and distribution of fish species (Keyl, 2017). The impact of temperature on fish growth and reproductivity is profound suggesting that fish are particularly vulnerable to shifts in distribution as a result of climate change (Campana, *et al.*, 2020b; Campana *et al.*, 2020a). This is demonstrably the case for both freshwater and marine species (Engelhard, Righton, & Pinnegar, 2014; Frainer *et al.*, 2017; Jeppesen *et al.*, 2010; Lema *et al.*, 2019; Perry *et al.*, 2005). This said, not all species will respond in the same way to temperature change. For instance, broadly speaking, temperate species tend to have a higher tolerance for temperature fluctuations, potentially due to the wider range of temperatures experienced on a seasonal basis. However, these species will have lower critical thermal maxima (CT_{max}) compared with tropical species. In contrast, due to the reduced tolerance to thermal fluctuations, tropical species have a much higher sensitivity to sea temperature change (Comte & Olden, 2017; Nati *et al.*, 2021). There are many forces acting on populations at any one time including predation and fishing and Campana *et al.* (2020b) note that while the principle of temperature-induced distribution shifts is clear, it can still be difficult to identify the occurrence of such shifts as a result of this signal factor alone. They attempted to quantify the three-dimensional shifts in species distribution under increases in temperature around Iceland. Through linear modelling, they found fish species have kept pace with changing temperatures around Iceland and predicted that, around Iceland, a net movement of 72% of species would occur under a future 1°C rise (Campana *et al.*, 2020b).

Water temperatures also influence indirect factors relating to fish ecology. In particular, the impact on lower trophic levels such as phytoplankton and zooplankton abundance caused by increasing water temperatures will influence primary and secondary productivity resulting in altered prey abundance for higher-trophic organisms. For example, *Calanus finmarchicus*, a planktonic copepod, population structure and abundance are influenced highly by temperature near Spitzbergen. As a prey species of Norwegian summer-spawning herring, Atlantic mackerel (*Scomber scombrus*) and blue whiting (*Micromesistius poutassou*), increased abundance of *C. finmarchicus* in northern waters due to increased temperatures could facilitate a northward shift in the distribution of these predators if the copepod prey species is able to thrive further north (Weydmann *et al*., 2018).

Changes in distribution of fish (or other marine species) as a result of changes in temperature could be through the movement of individuals or spatial variation in survival rates or recruitment or a combination of these factors (Campana, *et al*., 2020b). As discussed earlier, the impacts associated with the introduction of new species to an environment are variable and may be benign or pose serious problems for the ecological communities already present there. Predicting how changes in the environment may impact immigrant/non-native species distribution is therefore of importance for informing potential management strategies.

2.2 Icelandic marine ecosystem

2.2.1 Icelandic fisheries

Fisheries have been important to the Icelandic economy since around the fourteenth century, when a move was made from fishing to supplement an agricultural economy to fisheries taking on a far greater value with cod, caught by handline in small boats, being an important export commodity for a European market (Valtýsson, 2020). In recent decades, total catch from fisheries has been between one and two million tons annually, usually with a value of over USD 1000 million (OECD, 2021; Valtýsson & Jonsson, 2018). In 2018, the seafood sector was responsible for 4524 jobs involving 1148 vessels (OECD, 2021). There have been many changes over time to the Icelandic fisheries sector. Notably, the introduction of quota systems and especially the individual transferable quota (ITQ) system introduced in 1990, while being criticised by some for its failures in supporting small rural communities, has been widely seen as successful in enhancing economic efficiency and creating a sustainable fisheries economy (Knútsson, Kristófersson, & Gestsson, 2016; Kokorsch & Benediktsson, 2018). Icelandic fisheries management (both demersal and pelagic) has been widely accepted as being economically successful. For instance, Arnason (2008), while mindful of not conflating correlation and causation, points to Iceland's growth in GDP from the early 1990s to the mid to late 2000s as evidence of the success of the ITQ system, highlighting that it had caused an increase in the availability of capital which was instrumental in feeding the rise of the successful pre-crash Icelandic financial sector.

Demersal species, particularly cod, have always been of high economic significance to the Icelandic fisheries sector. While the economic dominance of the demersal fishery over the pelagic fishery is undisputed, the significance of the pelagic sector in terms of catch is greater (Statistics Iceland in Saevaldsson & Gunnlaugsson, 2015). For many years, the only pelagic fishery was that of herring. In Iceland, as in many Northern European nations, herring (which comprised of three separate stocks; the Icelandic summer-spawning, Icelandic spring-spawning and Norwegian spring-spawning herring) was highly significant for coastal communities when present, yet collapsed across much of the North Atlantic in the 1960s (Óskarsson, 2018; Sigurdsson, 2006). Following the collapse of the stock in the 1960s, attention turned to capelin (*Mallotus villosus*) which quickly grew to around 1 million tons per annum and often constituted over 80% of annual catch from the 1980s through to 1995 (Saevaldsson & Gunnlaugsson, 2015; Valtýsson & Jonsson, 2018). Capelin was mainly used for fishmeal, rather than for human consumption. Since its peak in the late 1990s, capelin catches experienced a decline, with four years (1982, 2009, 2018/2019 and 2019/2020) in which quota was unissued for the species due to low spawning stock biomass. Populations do seem to have recovered to some extent, with the highest Total Allowable Catch (TAC) recommendation in 2021/2022 since at least 2010/2011 (Hafrannsóknastofnun, 2022; Saevaldsson & Gunnlaugsson, 2015). Spawning stock biomass of Icelandic summer-spawning and Norwegian spring-spawning herring recovered through the 1970s and the herring fishery expanded again over this period (Jakobsson & Stefánsson, 1999). However, the Icelandic spring-spawning herring has not recovered in line with the other two exploited stocks demonstrating an example of recruitment overfishing, where the stock is reduced to such an extent that it is no longer able to revive (Óskarsson, 2018).

In summary, the fishing sector is of great importance to Iceland and the Icelandic economy. Understanding changes to the marine systems on which it depends is, therefore, key to identifying opportunities, challenges and threats to this resource. From a management perspective, having access to data early on is therefore essential for implementing control measures if necessary.

2.2.2 Anthropogenically-induced marine introductions, climate change and range shifts in Iceland

Iceland has had several cases of non-native species entering its waters, confirmed both through observation and genetic analysis, with the number of cases of introductions increasing over recent decades, numbering 22 in 2021, including obscure species and those of unknown origin (ICES, 2021; Thorarinsdottir, Gunnarsson, & Gíslason, 2014). Taxa that have been introduced include phytoplankton, macroalgae, crustaceans, molluscs, tunicates and fish which have entered the Icelandic marine zone either through anthropogenically-mediated transport or via movement of plankton or planktonic stages through passive transport via oceanic currents and some of which have become invasive (Thorarinsdottir, Gunnarsson, & Gíslason, 2014). A summary of immigrant/non-native species recognised by Thorarinsdottir, Gunnarsson, & Gíslason (2014) can be seen in Table 1. Since the work of Thorarinsdottir, Gunnarsson, & Gíslason (2014), further species have been observed. These include *Schizymenia jonssonii*, a red algae observed in 2020; and pink salmon, observed spawning in Icelandic waters in 2022 (Elliot, 2022; MFRI, 2022).

Table 1. *Summary of marine immigrant/non-native species recognised in Iceland in 2014. Modified from Thorarinsdottir, Gunnarsson, & Gíslason (2014).*

Taxa	**First Record**	**Mode of Introduction**
Phytoplankton		
Heterosigma akashiwo	1987	Shipping
Stephanopyxis turris	1997	Shipping
Mediopyxis helysia	2007	Shipping
Neodenticula seminae	2002	Currents
Macroalgae		
Fucus serratus	1900	Shipping
Codium fragile	1974	Shipping
Bonnemaisonia hamifera	1978	Shipping
Crustacea		
Cancer irroratus	2006	Shipping
Crangon crangon	2003	Shipping/Currents
Mollusca		
Mya arenaria	1958	Shipping
Cerastoderma edule	1948	Shipping

Tunicata		
Ciona intestinalis	2007	Shipping
Fish		
Platichtys flesus	1999	Shipping/Currents
Oncorhynchus mykiss	1983	Aquaculture

A long-established non-native in Icelandic waters is the seaweed *F. serratus* commonly found across the shores of Northern Europe and most likely introduced to Iceland between the settlement period (~900 AD) and the 19th century, when it was first recorded (Coyer *et al.*, 2006). For seaweeds, canopy-forming species have the potential to impact community structure in the local environment (Eriksson, Rubach, & Hillebrand, 2006; Jenkins, Norton, & Hawkins, 2004). In one study in the Southwest of Iceland, Ingólfsson (2008) found that there was a low abundance of the barnacle *Semibalanus balanoides* in an area dominated by *F. serratus* for > 20 years in comparison with an area where *F. serratus* was absent. This is in line with previous studies on the interaction between these two species, namely the impacts of whiplash by *F. serratus* on *S. balanoides* (Ingólfsson, 2008; Jenkins, Norton, & Hawkins, 1999). It was also found that *Fucus distichus* cover was also reduced in an area dominated by *F. serratus*. These two species share a similar vertical distribution. Finally, grazer abundance was also higher where *F. serratus* was present, thought to be due to the higher attractiveness of this species to grazers (Ingólfsson, 2008).

The European flounder is a demersal species which has been observed in Iceland since 1999 (Thorarinsdottir, Gunnarsson, & Gíslason, 2014). The process by which this species reached Iceland is not well understood although it is thought to be either through natural dispersal from the Faroe Islands or through ballast water (Thorarinsdottir, Gunnarsson, & Gíslason, 2014). The European flounder poses potential risks to local fish populations through competition with other species such as plaice for prey species (Farrell, 2012; Henke, 2018).

A notable pelagic species to enter both Icelandic waters and Icelandic fisheries as a target species is the Atlantic mackerel (Astthorsson *et al.*, 2012; Hannesson, 2013). The first confirmed record of the species was recorded in 1895, although species referred to as mackerel were reported as early as the 1640s (Hermannsson, 1924 in Astthorsson *et al.*, 2012). Sporadic reports are available from throughout the 20th century through a period of warmer and colder periods until in 1987 and 1991 when schools were reported (Astthorsson *et al.*, 2012). Around 220 t of Atlantic mackerel were caught as bycatch in 2000 and increasing records of bycatch were reported through the 2000s. From 2007, a direct fishery for the species was introduced. The increasing abundance in Icelandic waters is attributed to species range shifts under warming waters around Iceland, particularly since 1996 (Astthorsson *et al.*, 2012). As a valuable pelagic target species, the incentive to utilise this resource was clear. However, it did not come without some controversy internationally. Historically co-managed by the European Union, the Faroe Islands and Norway, the entry of Atlantic mackerel into Icelandic waters (and the subsequent exploitation of the stock) initially caused considerable friction and diplomatic tension between Iceland and these other stakeholders (Hannesson, 2013).

Water temperatures around Iceland are not constant and have shown roughly bi-decadal oscillations in sea surface temperatures over the past 2000 years (Sicre *et al.*, 2008). This variability is linked to the North Atlantic Oscillation (NAO), driven by the high-pressure system near the Azores and the subpolar low-pressure system near Iceland. During positive NAO years, well-developed pressure systems in both regions result in strong westerly winds, with negative NAO years driven by less well-developed pressure systems and a reduction in westerly winds. A result of these positive and negative NAO fluctuations are variations in precipitation and temperature patterns on a seasonal and decadal cycle (Sicre *et al.*, 2008; Wanner *et al.*, 2001). Bottom water temperatures and salinities also show variability, although seemingly not connected to processes such as the NAO and more connected to finer-scale forces such as storms and ice melt (Jochumsen, Schnurr, & Quadfasel, 2016).

This variability in seawater temperatures and salinities over annual and decadal timescales is reflected in the distribution of fish stocks in Iceland. Since 1996, waters to the south and west have increased by 1-2 °C. This has led to increased catches of warmer water species such as haddock, Atlantic mackerel and monkfish (*Lophius piscatorius*) to the north of the country in recent years (Valdimarsson, Astthorsson, & Palsson, 2012). Vagrant species such as twaite shad (*Alosa fallax*) and ocean sunfish (*Mola mola*) have been observed more frequently in the past few decades (Valdimarsson, Astthorsson, & Palsson, 2012).

Alongside distribution shifts and the increasing abundance of species such as Atlantic mackerel in Icelandic waters, the impacts of climate and seawater temperature changes can be observed for other species. In Iceland, following a warming in temperatures since the 1980s, there has been a collapse in the Icelandic scallop (*Chlamys islandica*) and northern shrimp (*Pandalus* *borealis*) stocks (Jonasson *et al.*, 2007; Jónsdóttir, Magnússon, & Skúladóttir, 2013). However, it is suggested that these collapses are not the direct result of warming temperatures combined with species thermal tolerance, but rather indirect consequences of the warmer environment. In the case of the Icelandic scallop, the population collapse was due primarily to disease which may have been more able to propagate due to more favourable temperatures, in addition to high fishing mortality (Jonasson *et al.*, 2007). On the other hand, the northern shrimp experienced enhanced predation by cod, especially in inshore areas where higher water temperatures were observed, which in turn suggested an enhancement in food requirement (Jónsdóttir, Björnsson, & Skúladóttir, 2012; Valtýsson & Jonsson, 2018).

2.3 *Sprattus sprattus*

2.3.1 Introduction to the species

The sprat, is a small (rarely over 16 cm), pelagic, shoaling fish belonging to the family Clupeidae (Bucholtz, Krüger-Johnsen, & Tomkiewicz, 2011). It occurs as three subspecies and has historically been known to be present in the North-East Atlantic Ocean (*Sprattus sprattus sprattus*), the Baltic Sea (*Sprattus sprattus balticus*) and the Mediterranean Sea (*Sprattus sprattus phalericus*) (Bucholtz, Krüger-Johnsen, & Tomkiewicz, 2011; FAO, 2022) (Figure 1).

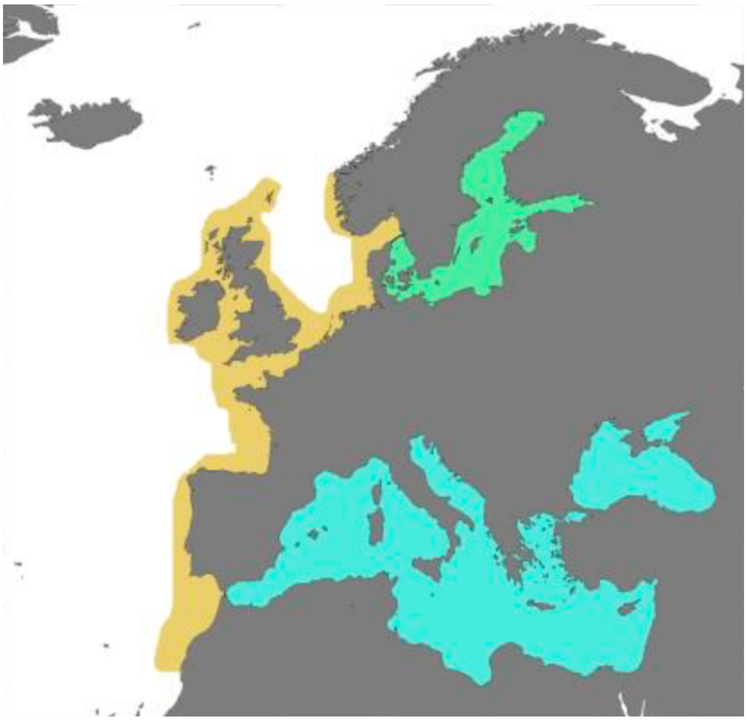


***Figure 1**. Historically recognised distribution of sprat (*Sprattus sprattus*). Yellow indicates the distribution range of *Sprattus sprattus sprattus*, green represents the range of *Sprattus sprattus balticus* and blue represents the range of *Sprattus sprattus phalericus*. Taken from Haslob (2011), redrawn after Whitehead (1985).*

The sprat is a planktivorous species, preying on zooplankton including the eggs of species such as cod and plaice, as well as being an important prey species for several higher trophic taxa including cod and haddock as well as mammals such as grey seals (*Halichoerus grypus*), and birds such as common terns (*Sterna hirundo*), among others (Casini *et al.*, 2014; Dänhardt & Becker, 2011; Lundström *et al.*, 2010; Plirú *et al.*, 2012; Solberg, Røstad, & Kaartvedt, 2015).

Sprat is found in coastal waters and estuaries and up to 100 km from shore and at depths down to around 150 m while largely remaining within the 50 m depth contour (Whitehead, 1985, Muus & Dahlstrøm, 1989 from Binohlan, n.d.). Bottom temperature and sea surface salinity have also been shown to be significant factors controlling the distribution and abundance of the species (Keyl, 2017). The species is tolerant of hypoxic waters of around 7% O_2 saturation and within Norwegian fjords, this allows it to utilise deeper waters (within the 150 m depth contour), potentially as an avoidance mechanism against predators such as gadoids which seem to avoid waters below around 15-20% O_2 saturation (Kaartvedt, Røtad, & Klevjer, 2009).

Spawning takes place between spring and late summer in the North Sea (ICES, n.d.; Wahl & Alheit, 1988). Temperature is a limiting factor with a minimum temperature of 6°C and a maximum of 12°C required for spawning (Morawa, 1954 in Wahl & Alheit, 1988). In the Baltic Sea, sprat utilise shallower waters for feeding while spawning areas are in deeper basins or marginal slopes with spawning duration longer in the south than the north (Aro, 1989). It is considered an r-selected species as a short-lived (rarely over five years) multiple batch spawner (Bailey, 1980; Bucholtz, Krüger-Johnsen, & Tomkiewicz, 2011; Peck *et al.*, 2012). Spawning can take place around 10 times in a spawning season (Alheit, 1988 in Wahl & Alheit, 1988).

Morphological characteristics of sprat are superficially similar to those of juvenile herring. They are small-bodied and mainly silver in colouration. The dorsal area has a similar iridescence to that of the herring. In herring this is bluish in colour, however, in sprat, the colouration has more green lending it an olive tone. Sprat have also, commonly, a more pronounced keel in comparison to herring, with discernible serrations, or scutes, along the ventral margin. The major diagnostic difference between herring and sprat is found in the relative positions of the dorsal fin origin and the pelvic fin origin. In herring, the dorsal fin origin is found anterior to the pelvic fin origin, while in sprat this positioning is reversed (Figure 2). These morphological characteristics are used to speciate between sprat and herring in the field, however, the differences are not always clear for one or more of the characteristics.

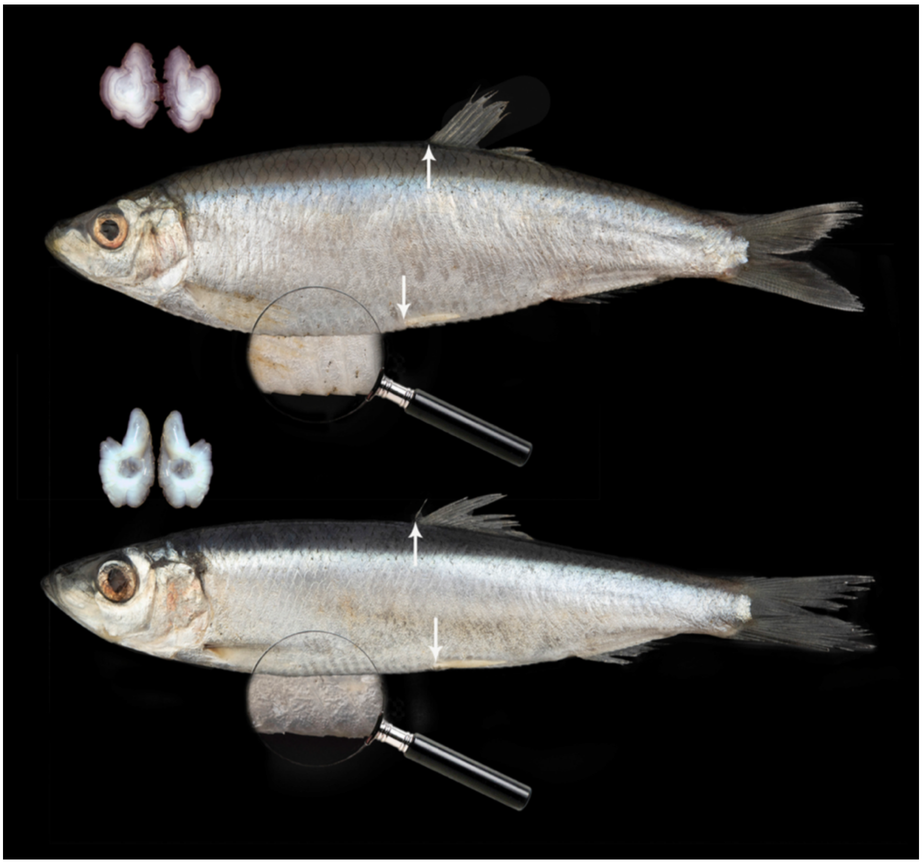


***Figure 2**. Morphological differences between sprat (<u>Sprattus</u> <u>sprattus</u>, above) and Atlantic herring (<u>Clupea</u> <u>harengus</u>, below), displaying the differences between the location of the dorsal fin origin in relation to the pelvic fin origin, the scute formation on the ventral margin, colouration and shape differences as well as differences between otolith shape. Taken from Pálsson* et al. *(2022).*

2.3.2 Management of the species in Europe

Each of the three sprat subspecies is a commercially valuable fishery species in their respective geographic areas. Since the 1990's global catch has been routinely over 500 thousand tonnes in live weight per year supplying both the demands for direct consumption of fish products as well as fish meal processing (FAO, 2022; Kasapoğlu, 2018).

The International Council for the Exploration of the Sea (ICES) provides catch advice on sprat in the North-East Atlantic and Baltic Sea. For *S. s. sprattus*, the subspecies were previously divided by ICES into four management units, which may be termed as stocks although the stock structure is under continued investigation (Quintela *et al.*, 2020). These management units are the North Sea (Area IV), Skagerrak and Kattegat (Area IIIa), the English Channel (Areas VIId and VII and the Celtic Seas (Areas VI and VII although without VIId and VIIe) (ICES, 2013). In 2018, the North Sea and Skagerrak and Kattegat sprat were merged into one stock assessment unit based on otolith shape, genetics and cohort analyses. There is genetic homogeneity between the English Channel and North Sea sprat, however, the stock has remained as two management units (ICES, 2018). Management of the sprat fishery is based on an 'escapement strategy' used to maintain the population above a critical level by implementing a cap on fishing mortality. This cap (F_{cap}) is currently set at 0.7 (Quintela *et al.*, 2020).

2.4 Establishment of sprat in Icelandic waters

During an Marine and Freshwater Research Institute (henceforth referred to as MFRI) research cruise in August 2017, the first sprat was identified in Icelandic waters off the south coast of the country with two more individuals identified in the Westfjords in 2019 (Pálsson *et al.*, 2022). Since then, there have been increasing reports of sprat identification on MFRI surveys (Pálsson *et al.*, 2022). While little is known about the mode of original transport of sprat into this new habitat, it is theorised that eggs or larvae may have drifted on ocean currents from spawning grounds elsewhere, such as the Faroe Islands or North Sea (Pálsson *et al.*, 2022).

The sprat arriving in Iceland is not necessarily surprising. As discussed, new species have established in the Icelandic marine zone numerous times over the past decades. Although the species probably lacks the long-distance swimming capacity required for it to arrive from an established population (such as in the Faroe Islands or Norway), other species such as the European flounder have been recorded doing so, with arrival likely to be a result of the drift of eggs or larvae. Previous species distribution models (SDMs) have shown Iceland to be a potentially suitable habitat for sprat. Schickele *et al.* (2020), in their study modelling a range of European small pelagic fish, using an ensemble model approach, demonstrated regions of the southern and western coasts of Iceland to be potentially suitable habitats, albeit with a low suitability index, even with the absence of records from Iceland itself.

How the sprat arrived in Iceland is currently unknown. One theory is that eggs or larvae drifted to Icelandic coastal waters from another established population, such as the Faroes (Pálsson *et al.*, 2022). However, it is not inconceivable that the species arrived through inadvertent human intervention. Records of sprat entering new ecosystems by any means are scarce; however, Wonham, Carlton, Ruiz, & Smith (2000) record sprat identified from ballast water on two occasions. On one occasion, at least one sprat was found in ballast water in a ship from Ireland when sampled in Baltimore (U.S.A) in ten-day-old ballast water. On another, at least one sprat was found in ballast water in a ship in Germany (from an unknown port with unknown ballast water age) (Wonham *et al*., 2000). No further information could be found recording sprat transfer or survivability in ballast water, however, while this may be an unlikely mode of transport of the species to Iceland, it cannot be entirely ruled out.

With the identification of sprat in Icelandic waters occurring for the first time in 2017, there has been little opportunity to investigate the current or projected status of the species or the potential impacts of its establishment. Within the literature, there are some lessons which can be drawn from observing the behaviour of the species in geographically comparable environments, or in environments in which the species assemblages mirror, to some degree, those of Icelandic waters. Furthermore, as discussed, this species introduction is not occurring within a theoretical static system. Rather, it is within a dynamic marine ecosystem experiencing pressures such as those outlined in sections 2.1 and 2.2. It is therefore important to try to predict impacts with reference to these other forces.

The potential impact of sprat on currently exploited fish stocks in Iceland is an area which may have important repercussions for Icelandic fisheries. In the central Baltic, there was a shift from a cod-dominated to a sprat-dominated system in the late 20th century. High fishing mortality and recruitment failure of cod, as well as high recruitment and low fishing pressure of sprat, led to a high sprat abundance. Importantly, sprat are predators of cod eggs, especially during periods of low zooplankton availability (Köster & Möllmann, 2000). With the increase of sprat and a decrease in cod, which became unable to keep sprat populations from growing, there is a potential for a role reversal and in the Baltic, sprat begin to limit cod recruitment (Parmanne *et al*., 1994 in Köster *et al*., 2003). In another example from the Baltic, herring growth has been demonstrated to be limited by a combination of salinity and competition with sprat. Following the increase in sprat abundance in the Baltic, as discussed, the interplay between these two limiting factors has had a detrimental impact on herring stock size (Casini *et al*., 2010). However, it is also worth noting that the Baltic is a relatively unique region due to its brackish nature, which causes increased sensitivity of species to salinity fluctuations as well as sprat and herring having a large diet overlap (Casini *et al*., 2010). Despite this, and due to the importance of both cod and herring to the Icelandic fishing sector, such interactions could be an area which would need further investigation in Iceland, particularly if sprat biomass increases.

As discussed in section 2.3.2, sprat is of commercial value to many nations. The potential establishment of a commercially viable stock of sprat within the Icelandic EEZ would present both opportunities and challenges to the fishery sector if the choice is made to exploit this stock. Opportunity is clearly linked to the opening of a new fishery resource as has been seen in the case of the Atlantic mackerel. In the case of the sprat, there may be less difficulty in terms of international management and cooperation. In much of Europe, sprat stocks transcend the boundaries of national EEZs as well as exist within the area covered by the Common Fishery Policy (Quintela *et al*., 2020). With Iceland both geographically and politically distant from the European continent, management of the stock may pose fewer challenges and sprat would not pose challenges in terms of active migration in and out of the Icelandic EEZ into those of other nations or unions.

Understanding how sprat may utilise Icelandic marine ecosystems is a key aspect in predicting future impacts from their establishment. Solberg, Røstad, & Kaartvedt (2015) attempted to assess the ecology of overwintering sprat in a fjord environment in Norway, which may present similar conditions to some Icelandic fjords, giving potential insight into how the species may respond to the conditions presented in the country. Both biotic and abiotic variables were incorporated into the study which was done using echo-sounding and acoustic surveys, to assess how sprat responded behaviourally to variables such as the presence/absence of ice and hypoxic waters, as well as an assessment of prey and predator abundance, diversity and distribution. The study site presented variable levels of oxygenation in deep water over the study period (four separate winters from 2005 to 2010), with times of hypoxia and anoxia as well as oxygenation through to the bottom of the water column (about 150 m). These periods of oxygenation occurred roughly every 2-3 years. The fjord also often became ice-covered in winter and sprat were able to exploit this environment by changing behavioural strategies with regards to their vertical distribution. Sprat were seen to utilise shallower depths, forming dense layers below the surface at night and utilising the middle of the water column (rather than deep waters). The move from rise and sink behaviours to enhanced use of the mid-waters is thought to be due to the reduction in light, making schooling behaviour a more viable anti-predator strategy (Solberg, Røstad, & Kaartvedt, 2015).

Sprat are generally tolerant of warmer water temperatures than many species native to Icelandic waters. Serpetti *et al.* (2017) used an integrated ecosystem model to investigate the impact of both increasing temperatures and fishing pressure on a range of species on the west coast of Scotland, with blue whiting as one of the focus study species. Under each future climate scenario modelled, blue whiting demonstrated an increase in biomass as a response to temperatures becoming more optimum for the species as well as reduced pressures from predators, for whom the temperatures were becoming less optimum (Serpetti *et al.*, 2017). The authors reported sprat as being similar to blue whiting in terms of the species temperature tolerance and it could follow that sprat has the potential to mirror some of the results of the blue whiting in terms of response to warming temperatures in this and similar contexts. With increasing water temperatures, it seems likely that sprat may be one of the many species which experience a northwards range shift towards regions of more optimum thermal regimes. In their study investigating the impacts of projected climate change scenarios on the distribution of small pelagic species in Europe, Schickele *et al.* (2021) found habitat for most of the species modelled has the potential to decrease in the North and Mediterranean Seas while increasing in the Baltic and Black Seas. The notable exception to this general rule were the Icelandic shelf area as well as the arctic regions of Scandinavia. Under the most extreme scenario, RCP 8.5 (RCPs are described in the following section), the Environmental Suitability Index (ESI) for sprat was modelled to increase by around 0.2 to 0.4 by the end of the 21st century while decreasing by around the same factor in the species current range.

It has not been suggested that sprat has undergone a northwards expansion in Iceland as a response to warming waters *per se*. However, the outcome of sprat establishing in Icelandic waters may end up facilitating a similar result. As discussed, sprat are able to utilise a wide range of environmental conditions from ice-covered fjords to waters of warmer temperatures. Over the coming decades, with potentially increasing warming of waters, modelling has shown that habitat suitability may well increase in the country. When considered in relation to the sprats' higher optimum and maximum temperature tolerance compared to commercially valuable fish species native to Iceland, the long-term implications of the species' presence may become important management considerations. Interactions between sprat and species such as, for example, cod and herring, which have been observed in other marine ecosystems have the potential to become factors which need further study within Iceland.

2.5 Predicting climate change

As of the previous United Nations Intergovernmental Panel on Climate Change (IPCC) assessment report, the organisation stated itself as being 95% certain that humans are the main cause of observed warming trends globally (IPCC, 2014b). The IPCC produces periodical reports on the current state of understanding of the physical science basis behind and predictions of future climate change as well as pathways and guidance towards effective mitigation. The World Climate Research Programme Working Group on Coupled Modelling has been responsible for a series of coordinated climate model experiments and simulations at both long-term (a period of a century) and near-term/decadal (10-30 years) timescales. The Coupled Model Intercomparison Project (CMIP) utilises atmosphere-ocean global coupled models within this series of experiments (Taylor, Stouffer, & Meehl, 2012). Now in its sixth phase, the CMIP is one of the foundations of the IPCC reports assessing the scientific basis, impacts and mitigation of climate change (IPCC, 2014b; World Climate Research Programme, 2021).

Representative Concentration Pathways (RCPs) were used within the IPCC fifth assessment report, describing four projections of greenhouse gas emissions, atmospheric concentrations of these emissions, pollutants and land usage under various mitigation measure applications. The four projections describe a scenario of extensive mitigation with low emissions (RCP 2.6) and a scenario of continued heavy emissions (RCP 8.5) as well as two which fall in between these extremes (RCP 4.5 and RCP 6.0) (Moss *et al*., 2010). The RCPs were created as an alternative to traditional scenario models, which tended to predict socio-economic and environmental change before bringing these together to estimate the impact in terms of radiative forcing. The RCPs were designed, instead, by identifying key outcomes in terms of radiative forcing, before researching potential pathways by which the planet may reach these. As such, the RCPs, as the name implies, are representative pathways, with each radiative forcing outcome having a range of possible pathways that could ultimately meet it (Moss *et al*., 2010). One of the benefits of this approach is time, where climate modellers and integrated assessment modellers (focussing on socio-economic and emission scenarios) are able to work in parallel, rather than sequentially (Moss *et al*., 2010). Within the IPCC sixth assessment report, RCPs were supplemented by Shared Socio-Economic Pathways (SSPs) (Arias *et al*., 2021). The fundamental differences between the two are in the pathway rather than the outcome. As such, comparisons between RCPs and SSPs can be made, as the RCP simulations provided climate information toward the

SSPs. Regional differences between the two may not be identical, however, these would likely be small and the use of both sets of information may be useful in analysis (O'Neill *et al*., 2016).

The impacts of change in marine ecosystems have been discussed in part in sections 2.1 and 2.2. Understanding how potential future scenarios model change in the marine realm is therefore of great value. The fifth assessment report of the IPCC on climate change discusses several impacts of climate change on terrestrial, freshwater and marine ecosystems. Focussing on the marine realm, key challenges identified include the inability of organisms to move with warming temperatures (medium confidence), increased extinction risk from climate change (high confidence), changes in marine ecosystems challenging the sustainable provision of ecosystem services including fisheries (high confidence) and risks to coral reef and polar ecosystems from increased ocean acidification (medium to high confidence) (IPCC, 2014b).

While this thesis is not focussed on climate change as such, the context of climate change cannot be overlooked. Changes to ecosystems, such as the establishment of new species, may occur independently of climate impacts but happen within systems which are all experiencing some level of anthropogenically induced stress. It is therefore important to acknowledge the environmental changes that have happened, are happening now and may happen in the future, when studying such establishments.

2.6 Species Distribution Modelling

2.6.1 Overview

SDMs have been used in numerous studies with the aim of modelling the distributions of taxa in the present and under future climate scenarios (Robinson *et al.,* 2017). They function by modelling geo-referenced observations of species presence and/or absence according to bio-geographic predictor variables using a variety of statistical methodologies (Franklin, 2013). The model can be used to plot predicted species presence or suitable habitat according to known predictor variable values making the tool useful in cases where bio-geographic data is known but species survey data is limited or lacking. In the marine environment, SDMs are extensively and increasingly used for purposes such as conservation planning, estimating the impacts of climate change and answering theoretical questions (Robinson *et al*., 2017). Two examples of SDM application include studies modelling the previous ranges of sperm whales (*Physeter* *macrocephalus*) in Indonesia and freshwater fish response to climate change (Bond *et al*., 2011; Sahri *et al*., 2020 respectively).

According to Robinson *et al*. (2017), there are six key steps to SDM design:

1. **The selection of species or taxa and research goals**: The species or taxonomic groups of interest are identified and research goals and questions are defined. Common research goals include those in the fields of theoretical ecology, climate change, planning and impact assessments (Robinson *et al*., 2017).
2. **The selection of species or taxa data**: A database of species occurrence is compiled through primary data collection, secondary data compilation or a hybrid approach. Absences and pseudo-absences are also compiled. The quality of the data is evaluated to check for issues such as geographic accuracy and sampling bias.
3. **The manipulation of biogeographical predictor variable data**: Environmental predictor variables are downloaded in a raster format. The quality of environmental predictors is evaluated according to relevance to the model species/taxa ecology, resolution, projection, collinearity and the temporal distribution of environmental layers in relation to the occurrence data.
4. **The running of the model**: The chosen model is run using the appropriate algorithm.
5. **The calibration of the model**: Occurrence and predictor variables are integrated for calibration. These are used to evaluate the model internally, through subsampling or substitution methods, for example. Independent datasets can be used to evaluate the model externally. Model fitness can be identified by measures such as goodness-of-fit, residual plots, variable importance, covariate response curves, correlation scores and model quality.
6. **The validation of the model**: The model projections are mapped in geographical space. Prediction accuracy should be measured through the ecological realism of the output, the model fit of test data, precision, specificity, sensitivity, Area Under the ROC Curve (AUC) score, and the percentage of variance explained, among others.

Robinson *et al*. (2017) also lay out a checklist of aspects key to effective reporting on SDMs for researchers. These are:

1. General features to be reported.
    - Description of the species being studied.
    - The goal of the study.
    - The geographic area of study.
    - The methodological approach.
2. Data and deficiencies.
    - If predictor layers are missing which may have an impact on the model.
    - The errors within the utilised predictor layers.
    - The sample size.
    - Sample effort.
    - Absences points or the approach to dealing with lack of absence data
3. Model parameters.
    - The training and testing models and their relationship.
    - How probability of presence is affected by predictor variables.
    - Interactions between data and model and model robustness as a result.
    - Selection of the most appropriate explanatory model
4. Model validation.
    - Results of model evaluation using different methods.
    - How the model functions over space and time.
    - How the model functions when tested with independent data.
    - If results from other models agree or disagree.

2.6.2 Maxent

Of the many methods of performing SDMs available to ecological researchers, the Maximum Entropy (henceforth referred to as Maxent) model, a correlative approach, has been a consistently popular choice and has seen steadily increasing use since its development (Elith *et al*., 2011; Kearney, Wintle, & Porter, 2010; Merow, Smith, & Silander, 2013; Nabout *et al*., 2012). One of the benefits of Maxent models is the fact that they function well even with low sample sizes. For instance, Wisz *et al*. (2008), found Maxent to outperform many other models at low (n = 30) as well as high (n = 100) sample sizes. Maxent is available for use through dedicated software or the *dismo* package in R, the language and environment for statistical computing (Hijmans *et al*., 2021; S. J. Phillips *et al*., 2017; S. J. Phillips, Dudík, & Schapire., n.d.; R Core Team, 2021).

The goal of Maxent is to estimate the unknown probability distribution of a species (π) based on Presence-Only (PO) points in which a species is found ($x_1, \dots, x_m$) within a finite geographic space (x). Pseudo-absences, randomly sampled points from the geographic space of the model, are also used in place of the true-absence data used in many other modelling approaches. The model aims to create a distribution with the greatest (MAXimum) spread (ENTropy) throughout the region of study, given the input data and parameters. The approach assumes initially that the probability of distribution relates to the researchers' concept of the species distribution and that presence records come from a random sample from across the geographic space x, in proportion to population size (Merow, Smith, & Silander, 2013). However, it does not take into account sampling bias that may arise from this pre-existing concept (i.e. it may be easier to access some areas) (S. J. Phillips, Dudík, & Schapire, 2004). Environmental predictor variables, across the geographic space ($f_1, \dots, f_n$) are defined by the user and split into grid cells.

With regards to the mentioned issue of the often-unknown nature of the sampling method of PO data, it should also be noted that sample selection bias can have a significant impact on model output if pseudo-absence data does not reflect the sampling effort of the presence data. Many datasets are compiled through non-random or stratified sampling efforts. As an example, herbarium collections are often collected from regions where the species is known to be present and is easily accessible, such as near roads. For the purposes of SDMs, this poses challenges and forms biases between habitats near to and far from roads within a model if pseudo-absences are not selected carefully. Phillips *et al.* (2009), instead of generating pseudo-absences randomly within a defined area, used target-group data for each of the species for which they had presence points. For instance, if studying a bird species, the target group presences would be all birds within the study area. This relies on a slight assumption that sampling effort for all species of the same target group has a similar bias, but was shown to increase model performance.

From a Maxent model (among other SDM modelling approaches), presence can be estimated from the probabilities of occurrence using threshold values which state the point at which a probability of an occurrence is considered suitably likely to represent the presence of a species in that geographic area or cell. Setting the threshold value is up to the user with a number of options to choose from. Within the *dismo* package in R, the functions for setting a threshold value are as follows (Hijmans *et al*., 2021):

1. kappa: the threshold at which kappa is highest ("max kappa")
2. spec_sens: the threshold at which the sum of the sensitivity (true positive rate) and specificity (true negative rate) is highest
3. no_omission: the highest threshold at which there is no omission
4. prevalence: modelled prevalence is closest to observed prevalence
5. equal_sens_spec: equal sensitivity and specificity
6. sensitivity: fixed (specified) sensitivity

Previously, there has been a tendency within the research community to defer to the kappa maximisation approach to define the threshold value. This was questioned by Liu, Berry, Dawson, & Pearson (2005), who found, through a comparison of 12 approaches using two species distributions, that the presence, average predicted probability/suitability and three sensitivity-specificity-combined approaches were favourable. Conversely, it is recommended by Merow *et al*. (2013) that thresholding is often not necessary within many studies. Furthermore, identifying a threshold value which is biologically meaningful poses problems in many applications since prevalence or population density may be required, a metric which is often unknown. They also argue that specificity thresholds rely on the assumption that background points are equal to absences, which is not the case. For these reasons, they suggest that continuous predictions which are interpreted by the researcher are often more appropriate and may even be less impacted by pre-existing assumptions of the researcher with regard to what an appropriate threshold may be (Merow, Smith, & Silander, 2013).

Up to this point, presence data are also referred to as training data, or data used to create the model. In validating a Maxent model, testing data, presence points not used within the modelling process, are used. In testing a model, the fraction of test points which are located within a cell which was predicted as being suitable is equated across all thresholds, known as the training omission rate. The fraction of all pixels predicted as being suitable is also found, known as the predicted area. Together, these values as well as the omission rate on both training and testing data are used to validate the model. Training data can be created in multiple ways and partitioned depending on the aims of the researcher. In particular, partitioning approaches may be selected due to the desire to reduce spatial autocorrelation of data, which has been shown to be valuable for models with few presence records (Radosavljevic & Anderson, 2014; Shcheglovitova & Anderson, 2013; Veloz, 2009).

As discussed by Merow *et al*. (2013), while the Maxent approach was designed with certain assumptions in mind, the real-world application of a Maxent model may not always meet core assumptions. Knowing the size of the population allows the model to predict the occurrence rate within a cell. Where population size is unknown, relative comparisons between the occurrence rates are the only meaningful results in what are termed Relative Occurrence Rates (RORs). The ROR is the core output from Maxent and describes the relative probability that a cell is contained in a collection of presence samples. Alternatively, it can be assumed that the grid cells themselves have been sampled randomly rather than individuals leading to a model that predicts the probability of presence within each cell. Maxent is able to predict the probability of presence using a transformed ROR called logistic output, although the assumptions within this process are strong and have been criticized.

It may be difficult for a Maxent user to decide if they should assume that PO data is a random sample of individuals and predict RORs or assume that data is from a random sample in space and predict the probability of presence. The former is the intended purpose of Maxent but relies on questionable assumptions about PO data, while the latter relies on a questionable reading of Maxent outputs but a reasonable assumption on PO data. This said it is still possible to use Maxent outputs as indices of habitat suitability (Merow, Smith, & Silander, 2013).

In SDM methods, the Area Under the ROC Curve (AUC) is the probability that a random presence site will rank above a random absence site. On an AUC plot, the *x-axis* represents the sensitivity, or the number of true positives, which are the values of presence predicted correctly. The ROC curve plots these two values against each other at different classification thresholds. The *y*-axis represents the specificity of the model, or the number of true negatives, which is the number of absence values predicted correctly (Lobo, Jiménez-valverde, & Real, 2008). A random ranking is demonstrated by an AUC of 0.5 with a perfect ranking demonstrated by an AUC of 1.0 (S. J. Phillips & Dudík, 2008). However, AUC requires absence points which seems in contradiction to the fact that Maxent is frequently referred to as a PO approach. Despite the potentially misleading description, absence points are still required within the Maxent process. This reflects an understanding that pure PO approaches tend to underperform in predictive accuracy in comparison to Presence-Absence (PA) approaches (Barbet-Massin *et al*., 2012; Elith *et al*., 2006). These absences are the pseudo-absences mentioned earlier. This has implications for the reading of the result, with the AUC then representing the probability of a random presence site being ranked higher than a random background site (S. J. Phillips & Dudík, 2008). Pseudo-absences are taken from across a defined area of predictor variable data. These points should be taken from an ecologically realistic area and one within which the species in question should be capable of dispersing (Merow, Smith, & Silander, 2013).

Before running the model, certain parameters can be set by the user. Of note are features, or the statistical models used to fit the prediction. Options for features are linear, quadratic, product, threshold, and hinge or hybrid models (Merow *et al*., 2013). Feature selection is of importance in designing a model and can depend on multiple factors. For instance, it is suggested by some that, due to the fact that if response to an environmental gradient is unimodal, then quadratic features are more suitable (Merow, Smith, & Silander, 2013). It is also suggested by Merow *et al*. (2013) that complex models may create "noise" from non-linear responses to predictor variables. Feature regularization multipliers (RMs) can also be set. Although Maxent aims to create a model of maximum entropy, some constraints on this are set to prevent overfitting the model. Regularization limits entropy to a certain range around the mean in order to do this (Warren & Seifert, 2011). By setting RMs, Maxent users have some control over the range around the mean the model is constrained. These solve some issues of complexity in the model by controlling the selectivity with regards to the predictor layers used. High RMs "smooth" the model, selecting the layers of the most value, while low RMs are less selective. Low RMs have the possibility of over-fitting models. In selecting modelling parameters, there are two broad groupings of methodologies: data modelling (DM) and algorithmic modelling (AM). As discussed by Warren & Seifert (2011), AM methods do not assume model parameters before creating them, but rather provide a range of potential options which are tested against using independent data. Through an AM approach, models are evaluated on the Akaike information criterion (AIC) which is an estimate of the difference between a model using training and testing data (the fit) of a model taking into account the parameters used (Katz & Zellmer, 2018; Wagenmakers & Farrell, 2004). It is worth noting, however, that AIC has been called into question with Velasco & González-Salazar (2019) finding models that performed well with regards to AIC were associated with high omission and commission errors, through simulated modelling studies.

The raw output of maxent represents the relative suitability of habitat. What is often used within the literature, however, is the default output which is a logistic scale of relative suitability, giving a value of between zero and one based on "*tau*", a user-defined parameter for the probability of presence. This is often misinterpreted as the actual probability of presence. In interpreting the output, it is essential to remember sampling design, particularly for motile organisms. In its default settings, the output also assumes that tau = 0.5%. This can be altered by the user and depends also on sampling design. The arbitrary value of 0.5% is used within many studies utilising Maxent. However, unless 0.5% is proven to be related to the probability of seeing a species at a given site at a given sampling effort, then direct comparisons between models of different species are impossible with regards to the values. It is stressed here that the logistic outputs from Maxent are relative habitat suitability and not probability of presence.

3 Methods

3.1 Study system

This thesis encompasses the coastal and continental shelf waters of Iceland. Iceland is located on the mid-Atlantic and Greenland-Scotland ridges between 63°23’ N and 66°32’ N in latitude and 13°30’ W and 24°32’ W in the Northern Atlantic (Figure 3). The closest major landmasses to the country are Greenland (~290km northwest), Scotland (~ 800km south-southeast), Norway (~970km southeast) and the Faroe Islands (~420km east-southeast) (Einarsson, 1984; European Environment Agency, 2015) (Figure 3). Most of the primary data collection in this thesis was focussed in Ísafjarðardjúp and Arnarfjörður in the Westfjord region of the country, a peninsula in the northwest of Iceland comprising numerous fjord systems.

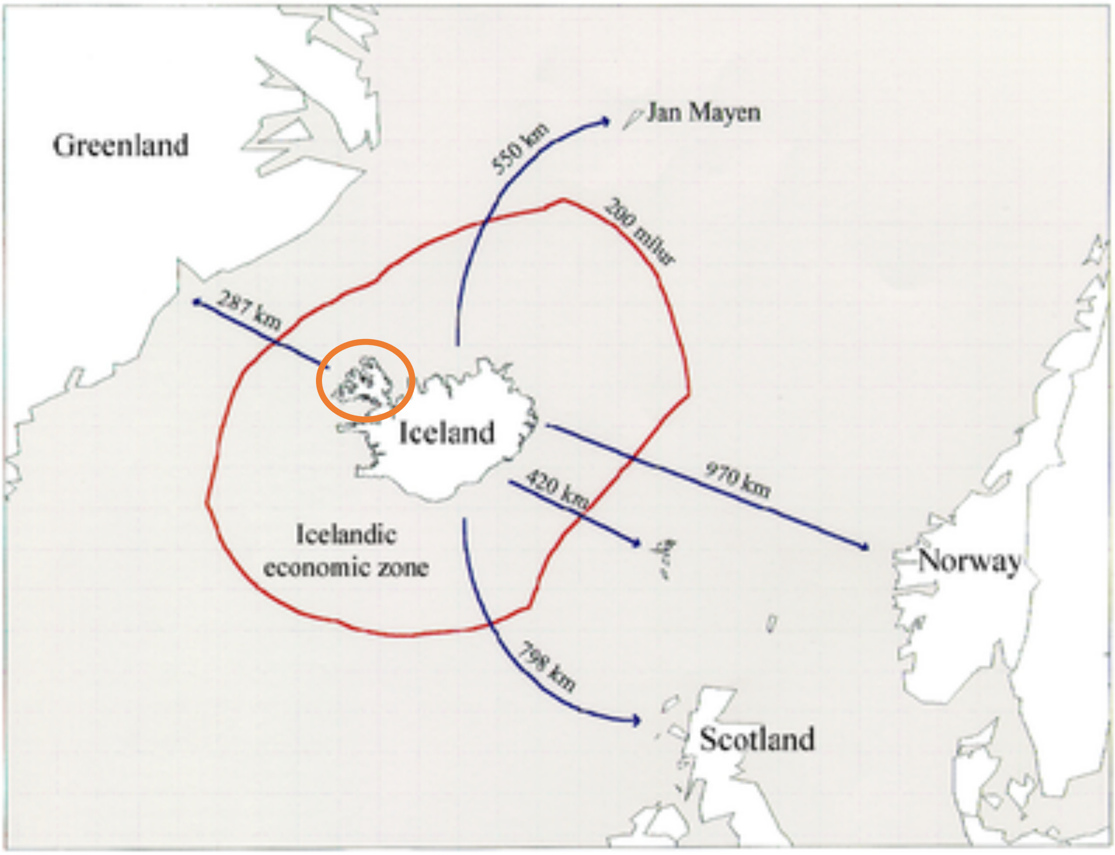


Figure 3. *Location of Iceland in relation to other major landmasses. The Exclusive Economic Zone (EEZ) is shown in red, distances to other major landmassess shown by blue arrows and the Westfjords marked by orange. Taken and adapted from the European Environment Agency (2015).*

Two major oceanic currents dominate the marine systems around Iceland, the Irminger and East Greenland currents. Originating from the Gulf Stream, the Irminger current originates in the South West before meeting the colder East Greenland Current where it splits, the western branch of which forms an eddy in the Irminger Sea and the eastern branch redirected north and north-east around Iceland (Valdimarsson & Malmberg, 1999). The Irminger Current carries warm waters (~6-8 °C) which are circulated in a clockwise direction around the country. The East Greenland Current originates in colder Arctic waters and splits south-westward and south-eastward north of Iceland (Figure 4). This cold (<0-2 °C), Arctic water dominates the surface layers around Iceland, with warmer waters found between 150-800 m in depth as far as 64° N (Valdimarsson & Malmberg, 1999). The Irminger current is responsible for the relatively warm waters considering the geographical region in which Iceland lies. Ice is generally not present in significant quantities unless it drifts inshore, usually in winter or spring.

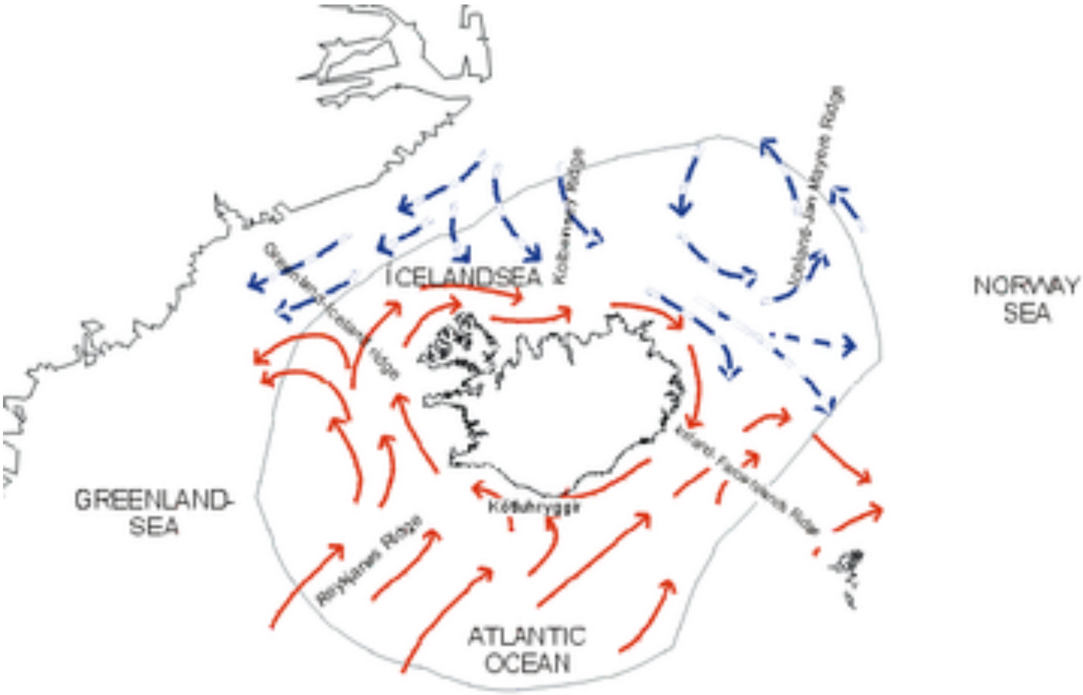


***Figure 4**. Simplified diagram of current flow around Iceland where red, unbroken lines denote warm currents and blue, broken lines denote colder currents. Taken from European Environment Agency (2015).*

3.2 Primary data collection

Data was collected from both the MFRI Autumn northern shrimp survey in 2021, from by-catch from commercial shrimp fishing vessels which have close working relationships with MFRI as well as a follow-up MFRI survey in February 2022. This theoretically allowed for a high-resolution intensive period of data collection during the survey to be supplemented with a coarser approach over a longer period through commercial by-catch. For the purposes of this thesis, primary data collection refers to the samples in which sprat were analysed in the laboratory, either from research trawls or commercial vessel catch.

3.2.1. MFRI surveys

Data collection took place in tandem with the MFRI Autumn shrimp survey (Survey ID = B11-2021) in Ísafjarðardjúp and Arnarfjörður (and connected fjords) in the Westfjords of Iceland in October 2021 (Figure 5). For survey B11-2021, a shrimp bottom-trawl net of 1010 meshes was used. The mean distance between wings was 14.9 m with a mean vertical opening of 4.6 m (± 0.35 SD). Tow length was standardised (for continuity over time and between surveys) of two nautical miles. Tows took place during the day as a bottom trawl at a speed of 2-2.2 knots. Length of tows sometimes deviated from the standard format to account for undersea hazards or high catch rates (Jónsdóttir, Bakka, & Elvarsson, 2019). Coordinates of the cast and haul were recorded for each tow in nearly all cases. For analysis, the midpoint of each tow was used where available.

For each station where clupeids were caught, these were checked and identified to species level with the numbers of sprat and herring recorded. For station 1083 where large numbers of clupeids were caught, a sub-sample of ~20.5 kg was taken and the fish were identified to species level for the purposes of extrapolating this to the entire catch. No sprat were identified at station 1083. All identified sprat or clupeids of uncertain species were bagged individually, frozen and stored on-board to be taken to the MFRI laboratory in Hafnarfjörður for re-checking and bio-metric analysis.

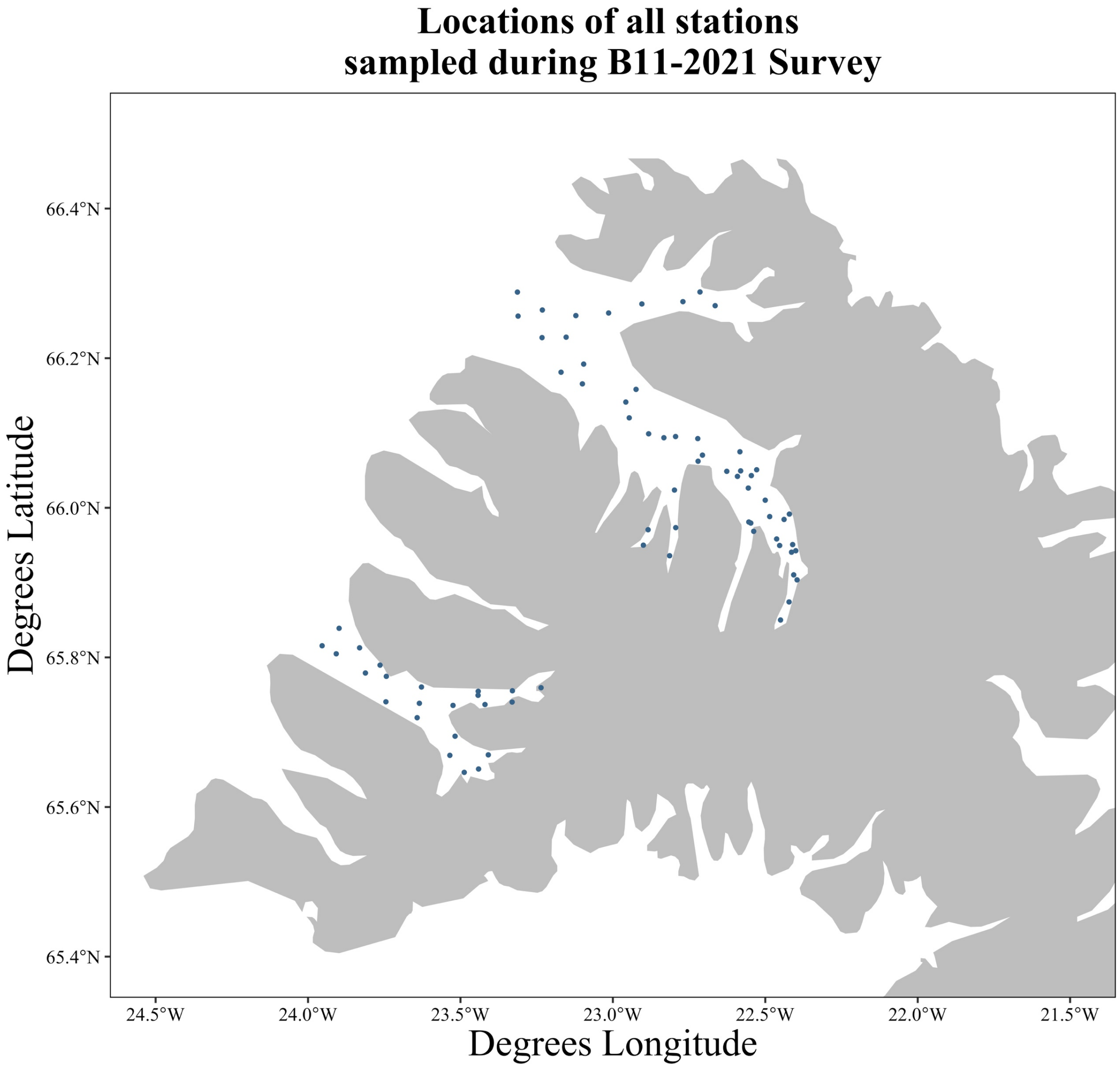


***Figure 5**. Locations of sampling stations from Survey B11-2021. Note, locations are shown to demonstrate the relative locations of data points and due to the resolution of basemap imagery are only given as a basic depiction.*

A follow-up shrimp survey (Survey ID = ISJ1-2022) was undertaken by MFRI in February 2022. Clupeid samples were collected and frozen on shore for analysis. For survey ISJ1-2022, which was carried out on commercial vessels, net and trawl specifications were kept as close to those of B11-2021 as feasible.

3.2.2. Commercial trawls

Two vessels Valur ÍS-20 and Egill ÍS-77, working closely with MFRI in Ísafjörður, sent in periodical samples of by-catch caught during their operation in the study area. These arrived at the laboratory in Ísafjörður as frozen, bagged samples of a mix of clupeids, capelin and shrimp. These were sorted and all clupeids were identified to species level. Sprat and herring numbers were recorded and sprat were retained for biometrics. Midpoints of tows were used where both cast and haul locations were supplied. Where only one location was given it was recorded as cast location and used within analysis.

3.3 Biometrics

3.3.1. Weight and length

All sprat identified in samples from surveys B11-2021, ISJ1-2022 and commercial vessels were retained in a frozen state before weights and lengths were recorded. Weights were recorded using electronic scales accurate to at least 0.1 g. The total length of each individual was measured in mm using either graph paper or in some cases a measuring board. Total length, as opposed to standard length, was recorded to maintain parity with MFRI survey records. It is known within the literature that both weight and length can be significantly impacted during the freezing process (Armstrong & Stewart, 1997; Ogle, 2009). In order to allow for a conversion factor to be created for both weight and length after freezing, 40 individuals from station 1096 were weighed and measured before freezing on the MFRI research vessel. These were then re-weighed and after defrosting within approximately four weeks of freezing.

The conversion factor was created by performing a linear regression on both the lengths (mm) and weights (g) of sprat before and after freezing, with the regression equation then used to create the factor by which to convert the lengths and weights of the sprat frozen before measuring and weighing. The length before freezing (L_f) was found by:

$$(0.988 * L_d) + 4.760$$

Where L_d is length after defrosting. Weight before freezing (W_f) was found by:

$$(0.998 * W_d) + 0.249$$

Where W_d is weight after defrosting.

All other sprat collected during the B11-2021 & ISJ1-2022 cruises, as well as the sprat received from commercial vessels, were measured after defrosting and the conversion factors were applied to estimate weight and length before freezing. Converted weight and length were log-transformed and plotted against each other to describe the relationship between the two values.

The relationship between length and weight is given as:

$$W_t = a \text{ x } {L_i}^b$$

Where W_t is total weight (g) , L_i is total length (mm), a is a scaling coefficient for weight (intercept) at length and b is the slope (Silva, Ellis, & Ayers, 2013). This is linearized using logistic regression to give the model as (Guðmundsdóttir & Steinarsson, 1997; Silva, Ellis, & Ayers, 2013):

$$W_t = a + b \text{ x } \log L_i$$

3.3.2. Maturity staging

After weights and lengths were recorded for each individual, sprat gonadal maturity for samples from B11-2021 and the commercial trawls were analysed and individuals staged accordingly. The fish were cut along the left side of the body from near the pectoral fin to approximately the end of the body cavity (Figure 6). Gonads were separated from other internal organs and staged macroscopically.

***Figure 6**. Example of sprat (*Sprattus sprattus*) maturity staging process showing male and female sprat at maturity stage VIII. Males are numbers 1, 2, 3, 4, 7, 8, 10, 11, 12 and 13. Females are numbers 2, 5, 6, 9, 14 and 15. Photo credit: Svanhildur Egilsdóttir.*

Due to the desire to record sprat staging in a comparable format to the herring staging employed by MFRI, two main sources were used to inform the staging process. These were "Manual to determine gonadal maturity of herring (*Clupea harengus L.*)" and an internal document used by the institute (Bucholtz, Tomkiewicz, & Dalskov, 2008). Sprat were recorded as either male (1), female (2) or unknown (NA) along with maturity stage, split from I-VIII (Table 2). For the purposes of comparison with studies from other regions, sprat stages are grouped into reproductively inactive (I and II), maturing and spawning in the next/current spawning season

(III-VI) or having already spawned in the current season (VII and VIII) (Brown-Peterson *et al.*, 2011; Vitale *et al.*, 2015).

***Table 2**. Summary of maturity stages used in the analysis. Modified from Bucholtz et al. (2008) and an internal document.*

Maturity Stage	Description
I	Juvenile. Has not spawned.
II	Immature. Has not spawned.
III	Maturing. Has not spawned in the current spawning season.
IV	Final maturation. Has not spawned in the current spawning season.
V	Maturing. Spawning Prepared.
VI	Mature. Spawning active.
VII	Mature. Spawning completed.
VIII	Spent. Resting after spawning period.

3.3.3. Age and genetics

In order to allow for further investigation into population dynamics, otoliths were taken from a subsample of sprat for which sex and maturity were known (*n* = 73). These samples were analysed by MFRI in order to provide an age classification for these individuals. Growth rings corresponding with one years growth were identified, defined as a light opaque section with an associated dark, translucent region (Moore *et al.*, 2019).

Genetic analysis of a sub-sample of sprat would be useful in determining, for instance, which existing population the Icelandic sprat derive from. Tissue samples, approximately 10 mm long were taken from the end of the caudal vertebrae to approximately halfway up the caudal fin. All tools were sterilised by soaking in ethanol and burning off the excess between each sampled fish. Samples were labelled and preserved before being refrigerated. While not analysed within this thesis, the samples are available for MFRI as needed.

3.4 Secondary data collection

3.4.1. Secondary sources of occurrence data

In addition to primary data collection, data from eight surveys which took place in 2021 were provided by MFRI giving location and abundance of sprat identified in trawls. Data from these surveys, including environmental data collected by survey vessels, was used as input into the SDMs alongside the primary data. Some physical and environmental data was also supplied from net-based instruments as in section 2.2.1. Sprat numbers, locations and dates from records previous to 2021 were also taken from Pálsson *et al*. (2022).

Sprat presence records from outside of the Icelandic EEZ were taken from the Ocean Biodiversity Information System (OBIS) (OBIS, 2022). Occurrence records were cleaned to remove flagged records. Within the OBIS, the flagged results represent points where, for instance, depth records were missing, the maximum recorded depth of sprat presence exceeded the bathymetry value or the locations registered as being on land. The maximum depth of the observation was also filtered, as in Schickele *et al*. (2020), to remove records inconsistent with small pelagic species depth distribution. Here, the maximum depth of the observation was limited to ≤ 200 m to encompass the understood preference of sprat (~150 m max) whilst giving some margin for flexibility but excluding depth ranges seen to be excessively deep. Dropped and absence records were already removed from the data set. Finally, coordinate uncertainty was limited to ≤ 5000 m in order to limit highly uncertain coordinates.

3.4.2. Bio-Oracle environmental raster layers

In running future projections on sprat habitat suitability under differing climate scenarios, different data sources were required in order to maintain continuity in variable metrics and coverage. Bio-Oracle supplies environmental raster layers for present-day conditions as well as projected future conditions under RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5. Present-day raster layers are formulated from a long-term average of data from 2010 to 2014. Variables were taken from both the surface and the bottom of the water column where possible. For the selection of bottom water variables, the variable at the average bottom depth per grid cell was selected as opposed to either the maximum or minimum bottom depths.

Sea temperature layers were selected due to the relevance of water temperatures to fish distribution as discussed in sections 2.1.3 and 2.2.2. Chlorophyll *a* layers were selected due to act as a proxy for primary productivity and salinity layers were selected due to the recognition that it can be a limiting factor on the distribution of the species (Keyl, 2017).

Present-day predictor raster layers for mean surface temperature, mean bottom temperature, mean surface salinity and mean chlorophyll concentration were downloaded directly from Bio-Oracle (Version 2.2) (Assis et al., 2018; Bio-Oracle, 2017a; Tyberghein et al., 2012). Corresponding future climate layers were also downloaded for RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5 for the years 2050 and 2100. Data was supplied by Bio-Oracle at a 0.83° by 0.83° spatial resolution.

3.4.3. NASA distance from coast and GEBCO bathymetric data

Both distance to the nearest coast and bathymetry layers were selected due to the fact that sprat are known to be most frequently found within 100 km from shore up to around 50 m in depth (Whitehead, 1985, Muus & Dahlstrøm, 1989 from Binohlan, n.d.).

A GeoTiff package for the distance to the nearest coast for all areas of the globe was provided from Ocean Color Web Distance to Nearest Coast page (NASA, 2022). Data was supplied at a 0.01$°^2$ spatial resolution with the distance given in kilometres.

Bathymetric data in a GeoTiff format was supplied by the GEBCO and provided at a 0.0042° by 0.0042° spatial resolution with data given in meters (GEBCO, 2022).

3.4.4. Removing collinearity

To avoid overfitting of the model through collinearity of environmental data, Pearson coefficients were run on each pair of environmental raster layers. In pairs where there was a ≥ 0.9 relationship, one was removed. This cut-off was selected based largely on anecdotal evidence of effective thresholds for correlation used by practitioners in Iceland. The removal was based chosen by estimating the most relevant of the two collinear variables. This process is subjective and largely down to the discretion of the researcher and should be done with a view to retaining the most biologically relevant predictor variables within the model and removing those which are less so, where collinearity occurs (Muhling *et al.*, 2020).

3.5 Analysis

3.5.1. Relationships with environmental data collected from trawls

The environmental variables recorded by MFRI vessels during data collection from both primary and secondary surveys (bottom temperature, surface temperature and depth) were tested against both sprat abundance and presence (where one equates to presence and zero equates to absence). A Shapiro-Wilk test for normality was used for all variables and a multiple regression used to test if the environmental variables significantly predicted sprat abundance, while binary generalized linear regression was used for presence/absence data where present was one and absence was zero.

3.5.2. Maximum Entropy (Maxent) models

For SDM modelling of sprat potential distribution across Iceland and Europe, a Maxent approach was utilised to take into account that species presence data was essentially PO. No standardised survey of an assumed distribution was undertaken. However, routine surveys have been taking place over the regions within Iceland that would be an ecologically reasonable estimate of potential distribution. As such, it is a stretch to say that absence of sprat in samples is a true absence both due to the fact that the surveys were not targeting sprat as well as the fact that the depths targeted for the trawls were focused on the near-bottom region of the ocean, rather than the pelagic region in which sprat could also be expected. The data can, therefore, be viewed as PO. Furthermore, the assumption within Maxent that sampling is undertaken over the presumed potential range of the species within the study locality also holds to some degree, due to the fact that sampling was undertaken in areas of habitat that were seen as potentially suitable habitat.

Maxent modelling was run on R-Studio 2021.09.0 Build 351 using the *ENMeval* package and followed the example in the tutorial of Feng, Walker, & Gebresenbet (2017) and Kass, Muscarella, Pinilla-Buitrago, & Galante, (2022) resulting in the methodology laid out below (Hijmans *et al.*, 2021).

Predictor variables were resampled using a bilinear method in order to allow for the creation of raster stacks which require matching resolutions. The largest resolution of the available raster layers was chosen in order to ensure that grid cells would only be enlarged and not split into smaller cells for each raster layer. This process gave each raster a $0.83^{\circ 2}$ resolution. Raster layers were then formed into stacks based on the time period and RCP. Predictor layers were reprojected to an Albers Equal-Area projection with a latitude of false origin of 61.5° and a longitude of false origin of -2°.

Sprat PO data was downloaded from OBIS supplemented by the addition of primary and secondary data for Iceland. Icelandic point data was created by finding the midpoint between cast and haul latitudes and longitudes. Duplicates, or multiple presence points within a cell in the $0.83^{\circ 2}$ raster grid, were removed to prevent spatial auto-correlation (Rhoden, Peterman, & Taylor, 2017).

The study location was defined by taking the extent of sprat PO data + 10° to the nearest whole degree in latitude and longitude North, East and West. However, due to the lack of presence points in the Mediterranean region, this area was cut out of the analysis. This gave a study region of -34° W, 32° E, 47° N and 76° N. In order to address potential sampling bias, 10046 background points were created and distributed over a background confined to the study area. These were selected using a modified version of the target-group background point method laid out in Phillips *et al*. (2009), where a selection of presence points for other small-pelagic fish were used as background points to reflect sampling bias within the dataset of the study organism. In this case, the species selected were Atlantic herring, capelin, Atlantic mackerel, European anchovy (*Engraulis encrasicolus*) and blue whiting as it was hypothesised that these species would experience a similar sampling bias over the extent of the model area. Presence points for these species were downloaded from the OBIS as well as the MFRI database and cleaned following the same process as the sprat presence points, regarding location and flagging, but not depth. Furthermore, duplicate points were removed from raster cells at the same resolution as the predictor layers as spatial autocorrelation was seen to be less apparent in the background data.

For selection of the optimum parameters of the Maxent model, ENMevaluate (*ENMeval*) was used. This package within R allows the user to input multiple parameters to test multiple

Maxent models using combinations of these parameters for omission rate and AUC. The most appropriate model can then be selected. Linear, quadratic and linear/quadratic hybrid features were tested alongside RM values of one to five. Higher RMs were included due to the lower values capability of overfitting the model. Presence points were partitioned using the "block" method, which splits presence points into four groups of (near)equal proportions based on latitude and longitude. Partitioning creates separate presence data which can be used for training and validation. The block approach is suggested by Muscarella *et al.*, (2014) to be suitable for models planning to extrapolate models geographically or temporally. As discussed, AIC is not always an optimal criterion for assessing a model (Velasco & González-Salazar, 2019). Due to this, the selection was run through *ENMeval* and the model with the lowest omission rate and highest AUC was selected for use for subsequent predictions (after Jamie M. Kass *et al.*, 2020; Radosavljevic & Anderson, 2014). Omission rate was threshold-dependent (10th percentile) after Radosavljevic & Anderson (2014). This meant that during the running of the testing models the pixels falling in the lowest 10% of predicted values were excluded, which provides a "less permissive" model. In other words, test models were created which retained the top 90% of predictions. Using these, omission rates were calculated to determine the most suitable parameters under this less permissive rule. Presence and background data are inputted into this process alongside current predictor raster layers. The prediction from the optimum model is then applied to the current predictor stack and future environmental predictor layer stacks for each RCP.

Thresholding was not applied within the analysis. Relative habitat suitability predictions were utilised within this thesis based on the advice of Merow *et al.* (2013), with binary predictions based on thresholds left unused.

3.6 Software use

Throughout this thesis, analysis was run using R Studio 2021.09.0 Build 351 "Ghost Orchid" for macOS (R Core Team, 2021). The main packages used were *ENMeval* for Maxent modelling *dismo* for some maxent outputs and *tidyverse* for map creation and figure creation (Hijmans *et al.*, 2021; Kahle & Wickham, n.d.; Kass *et al.*, 2021; Wickham, 2016; Wickham *et al.*, 2019).

4 Results

4.1 Locations and abundance of sprat

From primary and secondary data collection, 894 individual sprat, across 55 stations were recorded from the Icelandic EEZ. The numbers of sprat identified in each survey are given in Table 3 and mapped in Figure 7. Presence records from 2021 represented the highest proportion of observations in Iceland (*n* = 745), followed by 2022 (*n* = 110), 2020 (*n* = 36), 2019 (*n* = 2) and 2017 (*n* = 1). The majority of stations with positive identification were located along the South and West coasts of Iceland as well as within Ísafjarðardjúp and Arnarfjörður, in the Westfjords (Figure 8).

From primary data collection, a total of 240 sprat were found from survey B11-2021, 110 from survey ISJ1-2022 and 101 were identified in samples sent in from commercial vessels. One commercial sample (IJUL-2021-2, totalling one individual) was excluded from the analysis due to unavailable geographic coordinates for the sample location. Locations and months of each station/site in which sprat were identified during primary data collection are given in Appendix B. A further 404 had been identified previously in 2021 on MFRI and 39 from surveys prior to 2021 and these were included within the distribution analysis. This gave the oldest record used within this analysis as 26th August 2017 and the most recent record as 16th February 2022.

***Table 3**. Records of sprat (*Sprattus sprattus*) from Iceland since first identification. Data was collected from primary and secondary sources (Pálsson et al., 2022).*

Survey	Station	Number identified at station	Number identified in survey
A5-2021	97	1	**3**
A5-2021	137	2	
B11-2021	1042	1	**240**
B11-2021	1051	1	
B11-2021	1078	1	
B11-2021	1095	1	
B11-2021	1111	1	
B11-2021	1117	1	
B11-2021	1123	1	
B11-2021	1059	2	

B11-2021	1094	2	
B11-2021	1097	2	
B11-2021	1086	3	
B11-2021	1035	4	
B11-2021	1079	8	
B11-2021	1087	19	
B11-2021	1037	27	
B11-2021	1096	54	
B11-2021	1080	55	
B11-2021	1039	57	
IAPR-2021	3	9	**54**
IAPR-2021	4	4	
IAPR-2021	5	12	
IAPR-2021	6	29	
IJUL-2021	2	1	**1**
IJUN-2021	12	9	**9**
IMAI-2021	13	6	**6**
IRAE-2021	36	31	**31**
ISJ1-2022	1	9	**110**
ISJ1-2022	6	2	
ISJ1-2022	8	55	
ISJ1-2022	9	18	
ISJ1-2022	10	3	
ISJ1-2022	11	23	
TB1-2021	68	1	**373**
TB1-2021	84	1	
TB1-2021	97	1	
TB1-2021	72	2	
TB1-2021	89	2	
TB1-2021	98	2	
TB1-2021	70	4	
TB1-2021	69	15	
TB1-2021	88	52	
TB1-2021	66	68	
TB1-2021	87	225	
TM1-2021	86	1	**28**
TM1-2021	124	2	
TM1-2021	125	2	
TM1-2021	102	4	
TM1-2021	101	19	
		1	

Data taken from Pálsson *et al.*, (2022).	1	**40**
	1	
	1	
	2	
	2	
	2	
	2	
	10	
	16	
	1	

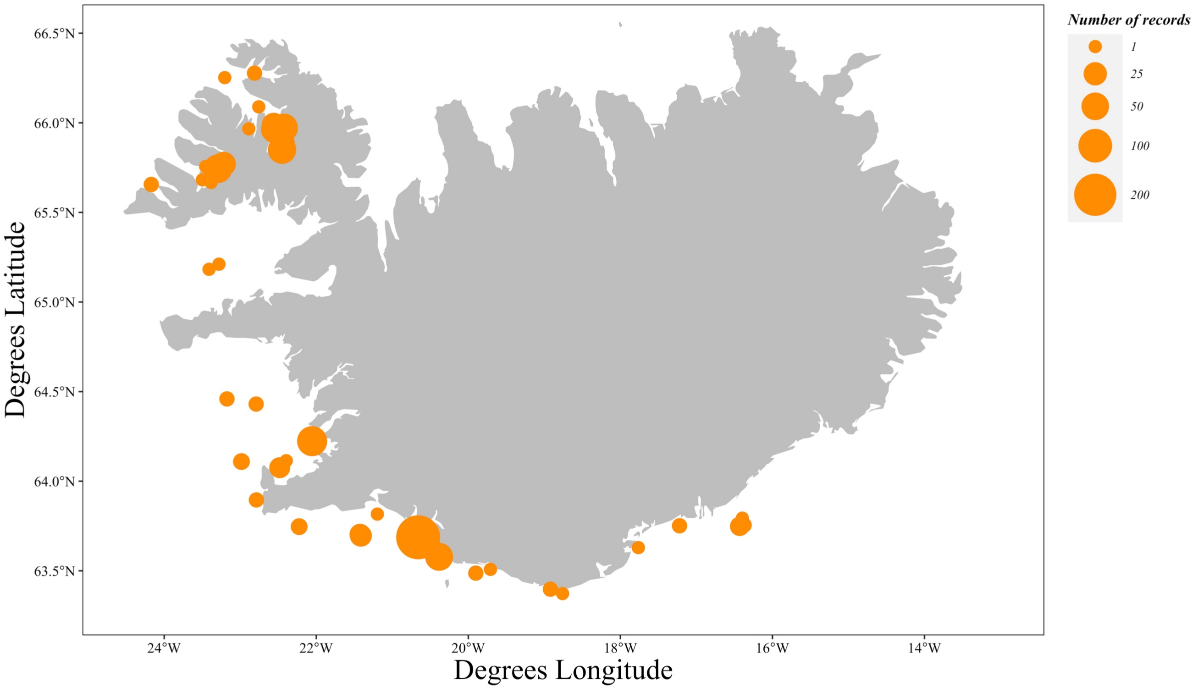


***Figure** 7. Numbers and locations of sprat (<u>Sprattus</u> <u>sprattus</u>) recorded in Icelandic waters, based on all records of the species from August 2017 to February 2022. These are records of the species identified accross multiple research cruises from 2017 distributed across the Iclelandic EEZ.*

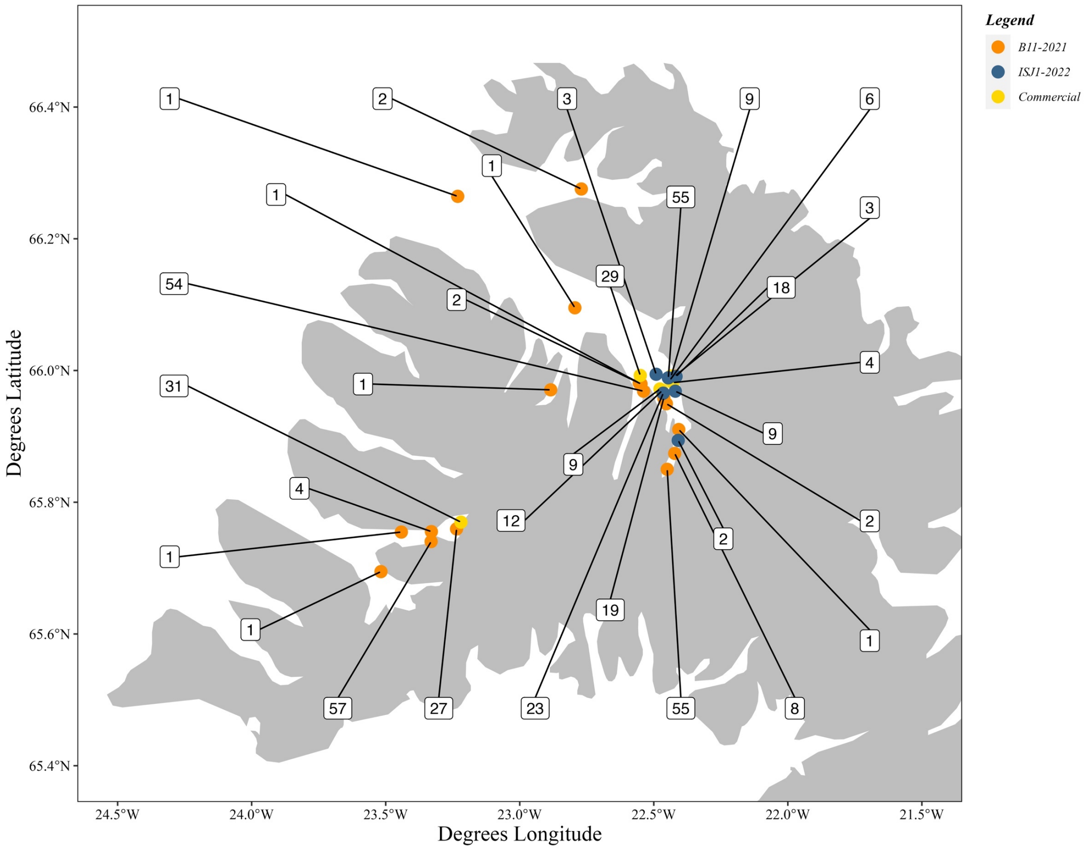


Figure 8. *Locations of positive sprat (*Sprattus sprattus*) records from the primary data collection phase. Colour key represents survey in which sprat were identified whilst number represent the number of sprat identified.*

4.2 Biological characteristics of sprat

4.2.1 Weight and length

Key statistics for sprat converted weights and lengths as well as from linear regression after log-transformation are given in Table 4.

Table 4*. Key statisics from log-transformed weight and length linear regressions for male, female and all sprat (*Sprattus sprattus*) for which weight and length were recorded..*

Value	Male	Female	Male + Female + Unknown
Number of specimens	176	149	451
Minimum Length (mm)	84.8	89.7	56.1
Maximum Length (mm)	140.1	138.1	140.1
Length Range (mm)	55.3	48.4	84
Minimum Weight (g)	3.24	4.34	1.05
Maximum Weight (g)	20.12	19.22	20.12
Weight Range (g)	16.87	14.88	19.07
exp(a)	0.000000209	0.00000281	0.00000195
b	3.7253	3.18349	3.25698

The relationship between converted weight and length for all individuals for which biometric data was obtained for both weight and length is given for all individuals (n = 451), for males (n = 176) and for females (n = 149) in Figure 9.

For all individuals grouped together, as well as males and females seperately, sprat weight to length relationship is shown to be significant ($P < 0.001$ in each case). Plots for each, along with equations, are given in Figure 9.

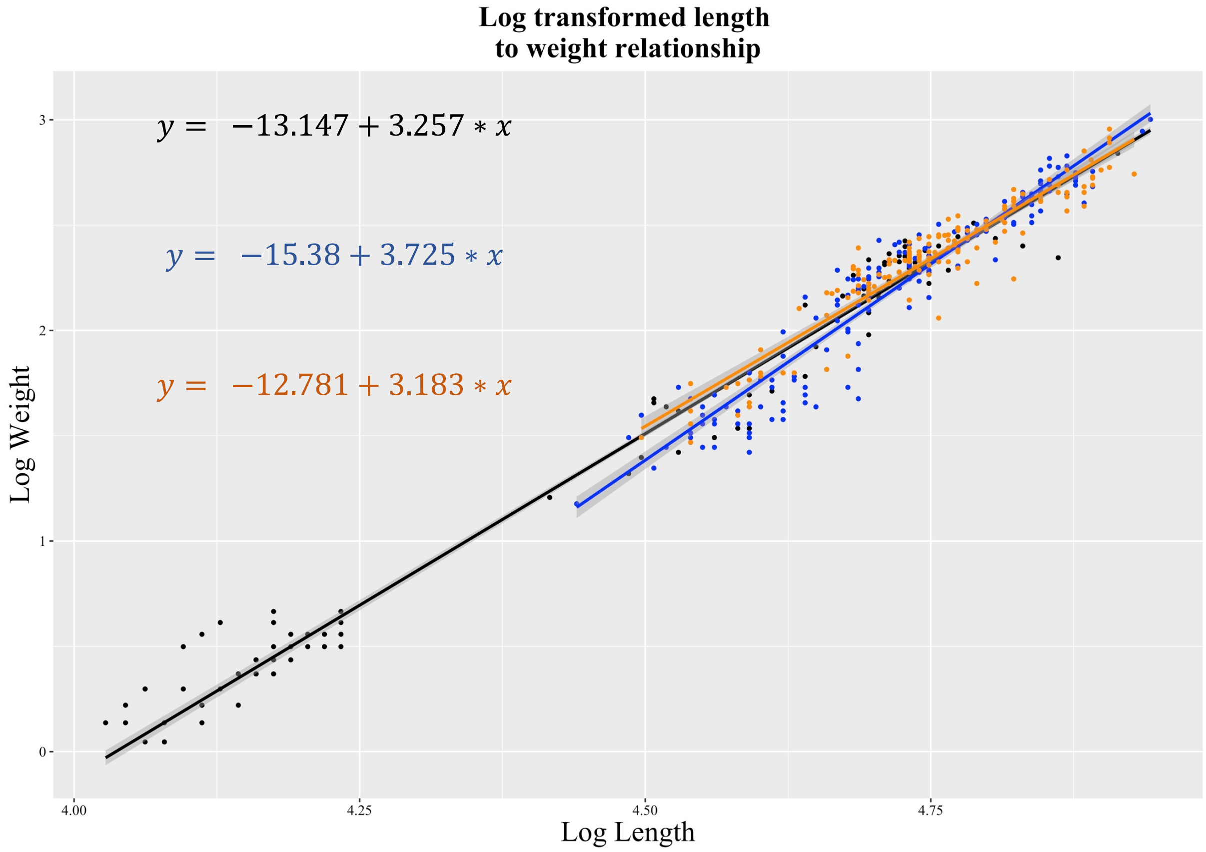


Figure 9. *Linear regression of* $_{log}$*weight to* $_{log}$*length for all (black), male (blue) and female (orange) sprat (*Sprattus sprattus*) for which weight and length were identified.*

With W_t as total weight (g), L_i as total length (mm), a as a scaling coefficient for weight (intercept) at length and b as the slope, the relationship between weight and length can be given for sprat in Iceland. For the model for all sprat sexed (Figure 9), a is -13.147 and b is 3.257. In the equation below, a is equated as the exponent of the intercept coefficient while b is found from the $\log_L$ coefficient. This gives the following relationship for estimated weight at length:

$$W_t = \exp\,(-13.147 + 3.257 \text{ x} \log L_i)$$

Following this method, the following relationship for males (mW_t) is given as:

$$mW_t = \exp\,(-15.38 + 3.725 \text{ x} \log L_i)$$

And females (fW_t) as:

$$fW_t = \exp\,(-12.781 + 3.183 \text{ x} \log L_i)$$

4.2.2 Maturity and sex

A subset of sprat samples (*n* = 451) was successfully sexed and staged for maturity (*n* = 325). Distribution of maturity stages by month and sex are given in Table 5, while the distribution of all sprat staged by month is given in Table 6. Sexual maturity of mature individuals showed development over the course of the year. Most sprat sampled in February-May were assigned maturity stage III-IV sprat sampled from June to November were nearly all at stages VI-VIII, with actively spawning fish (stage VI) found in June-August. Of the sexed individuals, 176 were male and 149 were female. Juvenile individuals at stage I were mostly found in February and October.

***Table 5**. Maturity classes for sprat (*Sprattus sprattus*) successfully staged and sexed.*

	Maturity of sprat staged by month and sex																	
	Feb		**Apr**		**May**		**Jun**		**Jul**		**Aug**		**Oct**		**Nov**		**Total**	
Sex	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	**F**	**M**
VIII												1	99	87	15	16	**114**	**104**
VII								1				4	2	3			**2**	**8**
VI							3	2		1		1					**3**	**4**
V				1														**1**
IV		5	2	25		3											**2**	**33**
III	10	12	8	6	1												**19**	**18**
II	7	3		2													**7**	**5**
I																		

***Table 6**. Maturity classes for sprat (*Sprattus sprattus*) successfully staged by month.*

	Maturity of all sprat staged by month								
	Feb	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Oct**	**Nov**	**Total**
VIII						1	186	31	218
VII				1		4	5		10
VI				5	1	1			7
V		1							1
IV	5	27	3						35
III	22	14	1						37
II	10	2							12
I	55	1	1				4		61

4.2.3 Age and genetics

A subset of sprat samples ($n = 72$) was used for otolith removal and age verification by MFRI. All sprat sampled were 1 year old or more. In total 19 individuals were aged at four years old, 17 of which were at maturity stage VIII, one at stage VII and one at stage IV. Two sprat were three years old (maturity stage VIII), two were one year old (maturity stage I and VIII) and the rest were two years old ($n = 49$, one at stage I, three at stage III, five at stage IV and 40 at stage VIII).

Due to logistical constraints, genetic analysis of tissue samples was not carried out during this thesis. Fin clip samples were retained by MFRI for analysis at a later date.

4.2.4 Recorded environmental variables

The Shapiro-Wilk test found sprat abundance, bottom temperature, surface temperature and depth to not be normally distributed ($P < 0.001$, < 0.0005, $= 0.002$ and $= 0.09$ respectively). As most of the data was non-parametric, a multiple regression was performed to test the effect of the three environmental variables on abundance.

The multiple regression model is given as:

$$Sprat\ abundance = 53.029 - 2.699 * (Bottom\ temperature) \\ + 1.76 * (Surface\ temperature) - 0.419 * (Bottom\ temperatue)$$

The model was not significant overall ($R^2 = 0.115$, $F_{(3,\ 32)} = 1.385$, $p = 0.265$). The effect of bottom temperature, surface temperature or bottom depth on sprat abundance was not significant with $p > 0.05$ for each combination (Table 7).

***Table** 7. Multiple linear regression output giving the results for the test of the effect of bottom temperature, surface temperature, and bottom depth on sprat (*Sprattus sprattus*) abundance.*

Variable or variable combination	Standard error	t-value	Pr(> | t |)
Bottom temperature	4.6407	-0.582	0.565
Surface temperature	5.4543	0.323	0.749
Bottom depth	0.2295	-1.824	0.078

Presence and absence plotted against the three environmental variables from the trawls can be seen in Figure 10. From this, there appears to be a stronger relationship between bottom temperature and bottom depth and presence than there does between surface temperature and presence. The binomial generalized linear regression for the presence/absence data demonstrated both bottom temperature and depth to be significant predictors of presence ($P < 0.05$ and $P < 0.001$, respectively). The output of the linear regression can be seen in Table 8.

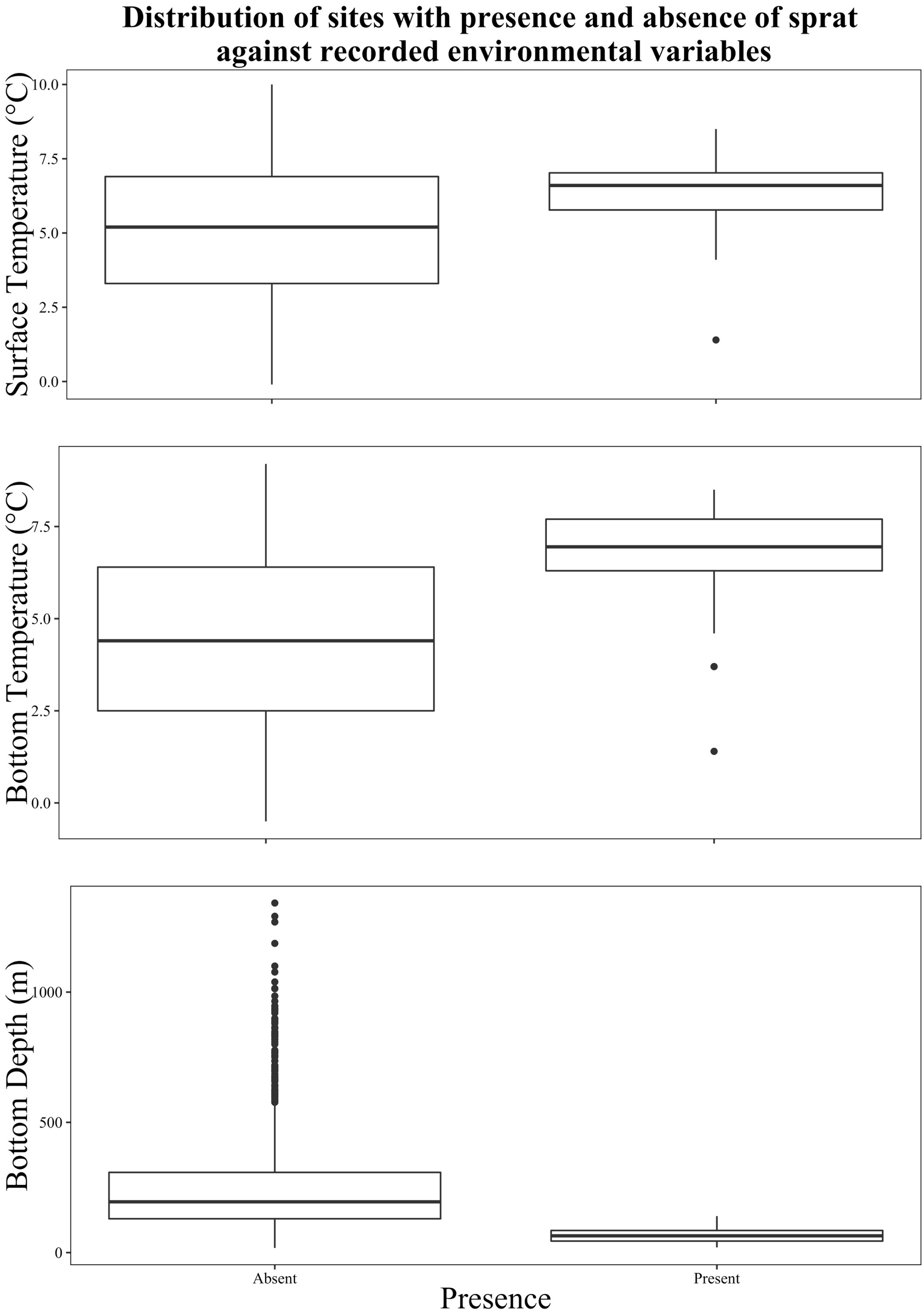


Figure 10. *Box plots showing the environmental values of three variables (surface temperature = top, bottom temperature = middle and bottom depth = bottom) collected during surveys against associated presence and absence of sprat (*Sprattus sprattus*).*

Table 8*. Output of binomial generalized linear regression for the significance of bottom temperature, surface temperature and depth on presence of sprat (*Sprattus sprattus*).*

	Estimated Coefficient	Standard Error	Z value	Pr(>|z|)
Intercept	-2.04	1.147	-1.779	0.075
Bottom temperature	0.374	0.158	2.365	0.018
Surface temperature	0.155	0.146	1.061	0.289
Bottom depth (m)	-0.04	0.007	-5.902	3.58^{-9}

4.3 Predicted current and future habitat suitability

In total, 234,199 presence records were compiled from Icelandic sprat records and data returned from the OBIS spanning the period 1770 to 2019. Following data cleaning, 97,906 records remained. After duplicates were removed from each grid cell, a total of 3,086 presence points remained for use in the Maxent model. Data from the OBIS was recorded to the species level with no distinction between subspecies.

From the OBIS records (from the years 2000 onwards), presence points were located primarily in the North and Baltic seas extending to the West coast of France to about 47° North, 4° East. The most northerly point was on the northern Baltic coast at around 66° North, 23° East. With the exception of the latter point mentioned, the presence points from the Icelandic records were considerably more northern in their distribution and all represented the most westerly data. In total, 551,406 background points were combined from data downloaded from the OBIS as well as survey trawl locations from Iceland. After cleaning, 368,493 records were deemed viable and after removing duplicates from grid cells, 10,046 points remained. Records for this target-group background occurrence were distributed more extensively than the presence points and reached the northern Scandinavian coast as well as along the coast of Greenland (Figure 11).

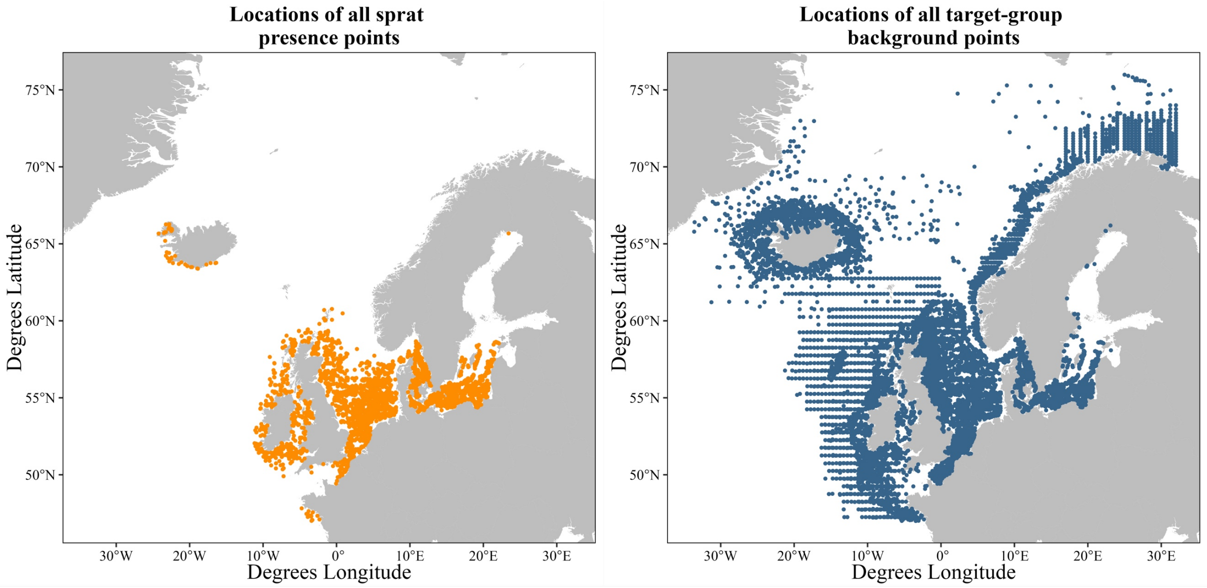


***Figure 11**. Locations of sprat (*Sprattus sprattus*) presence (lef) and background (right) data points (after cleaning the data) collected through primary and secondary data collection.*

Results from the Pearson test for collinearity are given in Table 9, with the selected variables and their corresponding future layers given in Table 10. The variables selected for the maxent model were as follows:

1. Mean sea surface temperature
2. Minimum sea surface temperature
3. Range of sea surface temperatures
4. Mean sea bottom temperature
5. Minimum sea bottom temperature
6. Mean sea surface salinity
7. Range of sea surface salinities
8. Mean sea surface chlorophyll concentration
9. Bathymetry (bottom depth)
10. Distance from the coast

Table 9*. Results of Pearsons‘ test for correlation between predictor variables tested. Blue shows predictors kept for analysis, light orange shows predictors excluded and the values on which exclusion was made based on a correlation of >0.9.*

	Surface Water Temperature (Mean)	Surface Water Temperature (Max)	Surface Water Temperature (Min)	Surface Water Temperature (Range)	Bottom Water Temperature (Mean)	Bottom Water Temperature (Max)	Bottom Water Temperature (Min)	Bottom Water Temperature (Range	Surface Water Salinity (Mean)	Surface Water Salinity (Max)	Surface Water Salinity (Min)	Surface Water Salinity (Range)	Bottom Water Salinity (Mean)	Bottom Water Salinity (Max)	Bottom Water Salinity (Min)	Bottom Water Salinity (Range)	Surface Water Chlorophyl *a* (Mean)	Bathymetry	Distance From Coast
Surface Water Temperature (Mean)	1.00	0.91	0.88	0.17	0.55	0.44	0.61	0.56	0.05	0.02	0.15	-0.47	-0.01	-0.01	-0.01	-0.01	0.00	-0.12	0.31
Surface Water Temperature (Max)		1.00	0.63	0.54	0.60	0.59	0.51	0.61	-0.31	-0.33	-0.21	-0.32	-0.35	-0.34	-0.35	-0.35	-0.02	0.02	0.19
Surface Water Temperature (Min)			1.00	-0.31	0.33	0.12	0.57	0.32	0.40	0.36	0.51	-0.60	0.32	0.32	0.33	0.33	-0.03	-0.28	0.41
Surface Water Temperature (Range)				1.00	0.38	0.59	0.01	0.40	-0.81	-0.79	-0.81	0.25	-0.77	-0.77	-0.78	-0.78	0.01	0.33	-0.21
Bottom Water Temperature (Mean)					1.00	0.94	0.88	0.99	-0.14	-0.13	-0.12	-0.02	-0.12	-0.11	-0.13	-0.13	0.33	0.57	-0.23
Bottom Water Temperature (Max)						1.00	0.67	0.94	-0.37	-0.35	-0.36	0.11	-0.34	-0.33	-0.35	-0.35	0.34	0.62	-0.32
Bottom Water Temperature (Min)							1.00	0.86	0.18	0.16	0.21	-0.21	0.17	0.17	0.17	0.17	0.23	0.39	-0.06
Bottom Water Temperature (Range								1.00	-0.17	-0.16	-0.14	-0.02	-0.15	-0.14	-0.15	-0.15	0.33	0.58	-0.24
Surface Water Salinity (Mean)									1.00	0.99	0.98	-0.18	0.98	0.97	0.98	0.98	0.14	-0.30	0.24
Surface Water Salinity (Max)										1.00	0.96	-0.08	0.99	0.99	0.99	0.99	0.17	-0.28	0.22
Surface Water Salinity (Min)											1.00	-0.36	0.93	0.93	0.94	0.94	0.11	-0.34	0.29
Surface Water Salinity (Range)												1.00	-0.03	-0.02	-0.05	-0.05	0.14	0.28	-0.29
Bottom Water Salinity (Mean)													1.00	1.00	1.00	1.00	0.17	-0.24	0.19
Bottom Water Salinity (Max)														1.00	1.00	1.00	0.18	-0.23	0.18
Bottom Water Salinity (Min)															1.00	1.00	0.17	-0.25	0.19
Bottom Water Salinity (Range)																1.00	0.17	-0.24	0.19
Surface Water Chlorophyl *a* (Mean)																	1.00	0.36	-0.30
Bathymetry																		1.00	-0.73
Distance From Coast																			1.00

Table 10. Predictor variables selected after analysis of collinearity for use within the model Present-day variable names from Bio-Oracle are given along with their corresponding future layer names alongside units.

Predictor	Bio-Oracle Layer Code	Bio-Oracle Corresponding Future Codes	Units
Mean Sea Temperature (Surface)	BO22_tempmean_ss	BO22_RCP26_2050_tempmean_ss	°C
		BO22_RCP26_2100_tempmean_ss	
		BO22_RCP45_2050_tempmean_ss	
		BO22_RCP45_2100_tempmean_ss	
		BO22_RCP60_2050_tempmean_ss	
		BO22_RCP60_2100_tempmean_ss	
		BO22_RCP85_2050_tempmean_ss	
		BO22_RCP85_2100_tempmean_ss	
Minimum Sea Water Temperature (Surface)	BO22_tempmin_ss	BO22_RCP26_2050_tempmin_ss	°C
		BO22_RCP26_2100_tempmin_ss	
		BO22_RCP45_2050_tempmin_ss	
		BO22_RCP45_2100_tempmin_ss	
		BO22_RCP60_2050_tempmin_ss	
		BO22_RCP60_2100_tempmin_ss	
		BO22_RCP85_2050_tempmin_ss	
		BO22_RCP85_2100_tempmin_ss	
Sea Water Temperature Range (Surface)	BO22_temprange_ss	BO22_RCP26_2050_temprange_ss	°C
		BO22_RCP26_2100_temprange_ss	
		BO22_RCP45_2050_temprange_ss	
		BO22_RCP45_2100_temprange_ss	
		BO22_RCP60_2050_temprange_ss	
		BO22_RCP60_2100_temprange_ss	
		BO22_RCP85_2050_temprange_ss	
		BO22_RCP85_2100_temprange_ss	

Mean Sea Temperature (Mean Bottom Depth)	BO22_tempmean_bdmax	BO22_RCP26_2050_tempmean_bdmax	°C
		BO22_RCP26_2100_tempmean_bdmax	
		BO22_RCP45_2050_tempmean_bdmax	
		BO22_RCP45_2100_tempmean_bdmax	
		BO22_RCP60_2050_tempmean_bdmax	
		BO22_RCP60_2100_tempmean_bdmax	
		BO22_RCP85_2050_tempmean_bdmax	
		BO22_RCP85_2100_tempmean_bdmax	
Minimum Sea Water Temperature (Mean Bottom Depth)	BO22_tempmin_bdmean	BO22_RCP26_2050_tempmin_bdmean	°C
		BO22_RCP26_2100_tempmin_bdmean	
		BO22_RCP45_2050_tempmin_bdmean	
		BO22_RCP45_2100_tempmin_bdmean	
		BO22_RCP60_2050_tempmin_bdmean	
		BO22_RCP60_2100_tempmin_bdmean	
		BO22_RCP85_2050_tempmin_bdmean	
		BO22_RCP85_2100_tempmin_bdmean	
Mean Sea Water Salinity (Surface)	BO22_salinitymean_ss	BO22_RCP26_2050_salinitymean_ss	PSS
		BO22_RCP26_2100_salinitymean_ss	
		BO22_RCP45_2050_salinitymean_ss	
		BO22_RCP45_2100_salinitymean_ss	
		BO22_RCP60_2050_salinitymean_ss	
		BO22_RCP60_2100_salinitymean_ss	
		BO22_RCP85_2050_salinitymean_ss	
		BO22_RCP85_2100_salinitymean_ss	
Range of Sea Water Salinity (Surface)	BO22_salinityrange_ss	BO22_RCP26_2050_salinityrange_ss	PSS
		BO22_RCP26_2100_salinityrange_ss	
		BO22_RCP45_2050_salinityrange_ss	
		BO22_RCP45_2100_salinityrange_ss	
		BO22_RCP60_2050_salinityrange_ss	
		BO22_RCP60_2100_salinityrange_ss	

		BO22_RCP85_2050_salinityrange_ss	
		BO22_RCP85_2100_salinityrange_ss	
Mean Chlorophyll Concentration (Sea Surface)	BO22_chlomean_ss	BO22_RCP26_2050_chlomean_ss	mg/m^3
		BO22_RCP26_2100_chlomean_ss	
		BO22_RCP45_2050_chlomean_ss	
		BO22_RCP45_2100_chlomean_ss	
		BO22_RCP60_2050_chlomean_ss	
		BO22_RCP60_2100_chlomean_ss	
		BO22_RCP85_2050_chlomean_ss	
		BO22_RCP85_2100_chlomean_ss	
Bathymetry	Not from Bio-Oracle	Same as present layer	m
Distance From Coast	Not from Bio-Oracle	Same as present layer	km

Graphs of the performance of multiple models tested to assess for optimum parameters show that the hybrid linear-quadratic model with an RM of two performs best in terms of lowest average omission rates (or.mtp) (Figure 12). The omission rate was prioritised, however, based on the process of Radosavljevic & Anderson (2014), which takes into account AUC score.

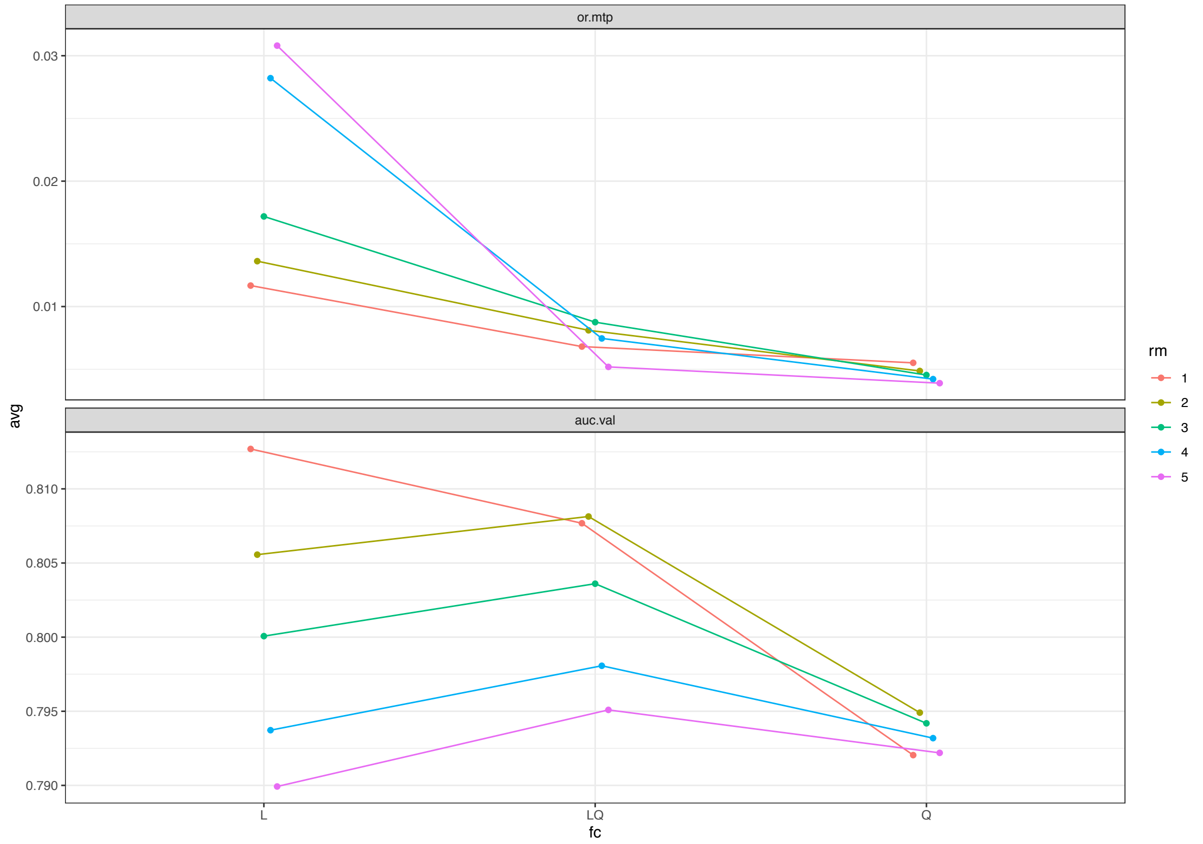


Figure 12. Performance of each model with respect to omission rate (or.mtp, above) and AUC (auc.val, below). The colour key gives the regularization multiplier (rm).

Model parameters were, therefore, set to run a linear feature class with an RM of one. Once run, this gave the statistics given in Table 11. Values are given in means and standard deviations, reflecting the fact that they are created from multiple testing data sets set aside during the partitioning process. These results indicate a good model performance with a mean AUC of 0.813. The very low or.mtp and AUC mean difference scores suggest reliability of the model with little to no difference between the runs on the partitioned data.

***Table 11**. Key outputs from the optimum Maxent model found through the testing of multiple model parameters and taken the model with the lowest omission rate.*

or.mtp (Mean)	**or.mtp (sd)**	**Training AUC**	**AUC Difference (Mean)**	**AUC Difference (sd)**	**AUC Value (Mean)**	**AUC Value (sd)**	**AIC**
0.012	0.023	0.795	0.106	0.091	0.813	0.141	65219.66

Response curves from the model, showing how each environmental variable affects the Maxent model, assuming each other variable is at its average value, are given in Figure 13 (Phillips, 2010). From the response curves, it can be seen that habitat suitability has a marked response to increases in mean and minimum surface temperatures. For mean surface temperature there is a positive relationship, with prediction values of around 0 until around -1 °C, where there is a rise to a prediction value of just around 1 at 15 °C (Figure 13, A). For minimum surface temperature, there is a slight positive negative association from around 0 °C to 0.2 °C, before a clear negative association from 0.2 °C , with prediction values dropping to just over 0 at around 10 °C. From 0 °C to < -10 °C, prediction value is around 0.7 (Figure 13, B). For the range in surface temperature, prediction values were highest (a little over 0.5) at 20 °C and over, while a range of around 5 °C and below corresponded with a predicted value of just over 0.4 (Figure 13, C). Bathymetry shows a positive relationship, with higher predictions associated with shallower depths (Figure 13, I). Mean bottom temperature showes a positive relationship with predictions of just over 0.6 for temperatures of 15 °C and above and values of around 0.25 for a temperature of about 0 °C and below (Figure 13, D). The range of surface salinity showed a negative relationship with values of around 0.5 at 0 PSS and below and values of around 0.25 at around 22 PSS and higher. Mean chlorophyll *a* showed a sharp drop in values with a prediction value of just over 0.5 at 0 mg/m^3 and below and around 0.35 at around 2 mg/m^3 and higher. Distance from the coast showed no relationship. It is worth noting that the ranges of the variables within the outputs from maxent do not suggest that these are values which may represent suitable habitat for sprat and are often just extensions of the modelled response curve. For instance, the minimum value of -10 °C for minimum surface temperature is simply an extension of the modelled response down to this value.

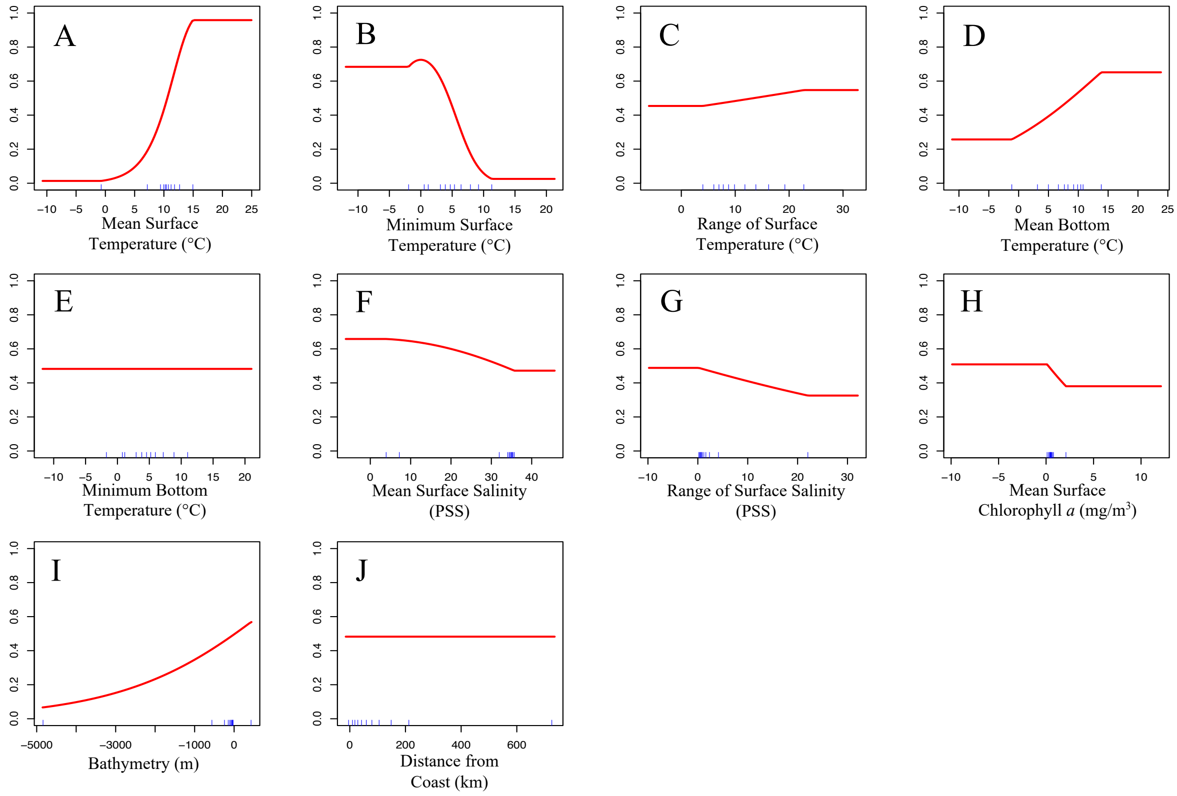


***Figure 13**. Response curves for each of the environmental predictor layers used in the model. The x-axis represents the value of the environmental variable and the y-axis represents the (log)Maxent prediction. Response curves demonstrate the effect of each variable whilst assuming the average value for all other variables. A = mean surface temperature, B = minimum surface temperature, C = range of surface temperature, D = mean bottom temperature, E = minimum bottom temperature, F = mean surface salinity, G = range of surface salinity, H = mean surface chlorophyll* a, *I = bathymetry and J = distance from coast. Blue tick marks represent observed values of sprat (*Sprattus sprattus*) at corresponding values within the model.*

Log-transformed predictions of relative habitat suitability created from the selected model are shown below. The relative habitat suitability values outputs from the Maxent model are given for the model area as well as for the Icelandic EEZ in Figures 14 and 15 respectively. Figures 16 to 19 show the continuous predictions of the model when applied to RCP2.6, RCP4.5, RCP6.0 and RCP8.5 for the years 2050 and 2100.

Predictions for European waters also show a relatively constant spatial distribution of suitable habitat, although the relative suitability within those areas does vary slightly. In particular, in the Baltic Sea, there is a slight northward expansion of higher habitat suitability, particularly under RCP6.0 and RCP8.5 for the year 2100. Under RCP 8.5 for the year 2100, there also appears to be a decline in predicted habitat suitability in the southernmost mapped area (off the coast of Cornwall), which may be due to average or minimum surface temperatures becoming a limiting factor.

Focussing on Iceland, the model gives results which are useful in terms of understanding the current distribution and potential future distributions of sprat. The model suggested relative habitat suitability to be more extensive on the west coast of the country, which is supported by the distribution of observations of the species to date. Low suitability can be seen around the rest of the country, with some small areas of higher suitability in the Westfjords region. Predicted habitat suitability reaches a maximum of about 0.5 to 0.6 in highly coastal areas, with the most frequent higher predicted habitat suitability of about 0.4 slightly more extensive areas in the west. Values of around 0.2 to 0.3 are extensively spread around the majority of the coast to varying degrees. Northward expansion of more highly suitable habitat areas (values of 0.4 to 0.5) occurs under RCP8.5 with the distribution of these values more extensive over the north coast. The geographic distribution of lower values of around 0.2 to 0.3 remains fairly consistent throughout each RCP for both the years 2050 and 2100 although increases slightly for the later year modelled.

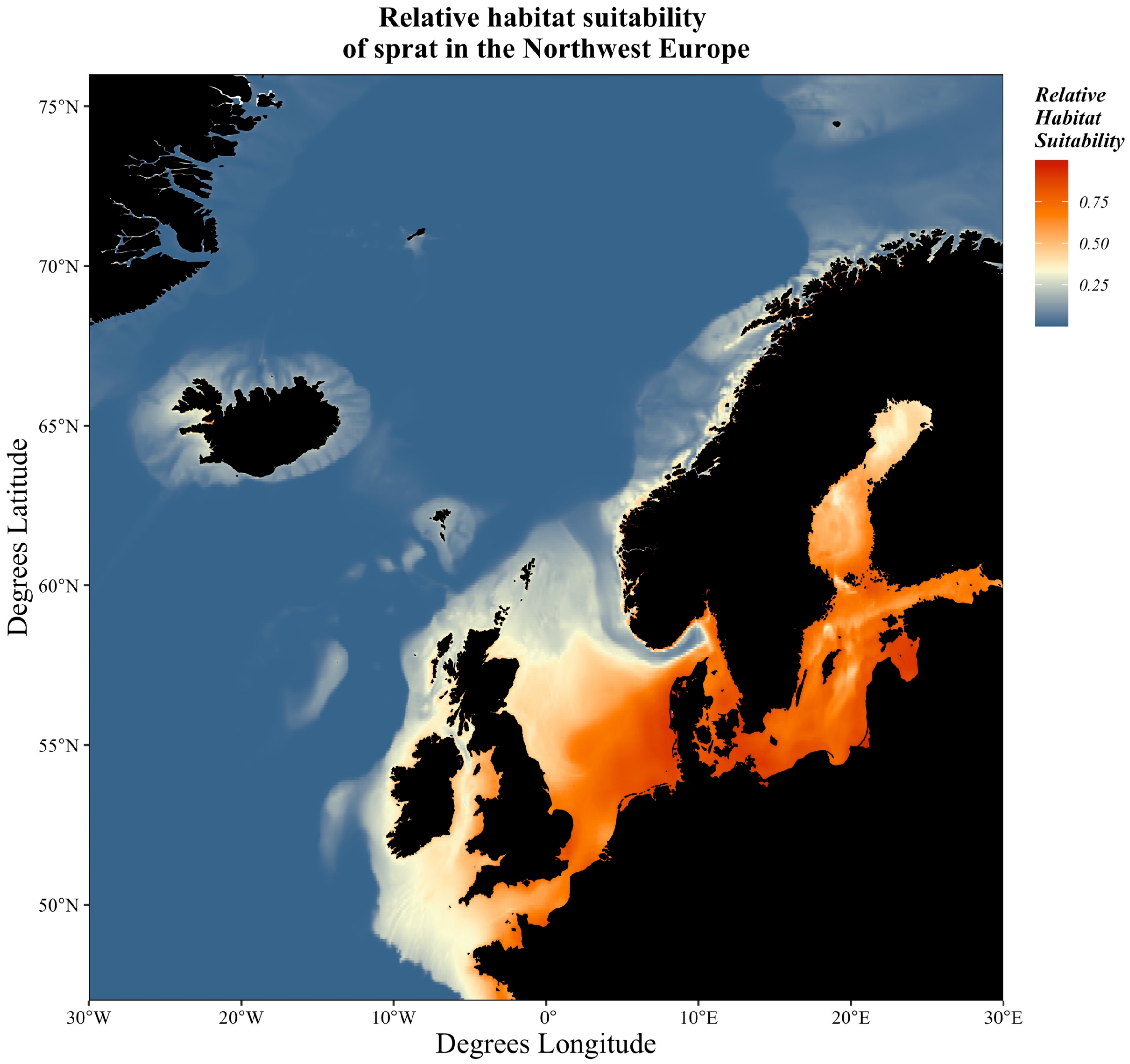


***Figure 14**. Modelled prediction of presence for sprat (*Sprattus sprattus*) in Western Europe under present oceanographic conditions (2000-2014 data). Darker yellow through red shading represents progressively higher relative habitat suitability.*

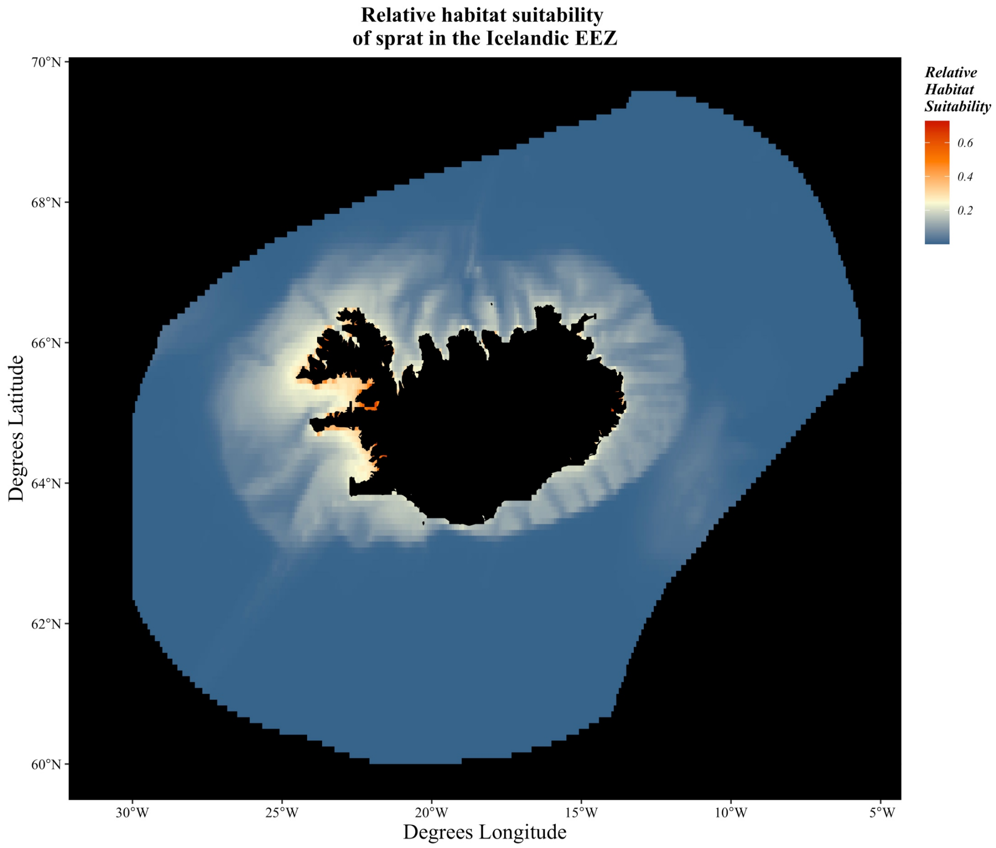


Figure 15*. Modelled prediction of presence for sprat (*Sprattus sprattus*) within the Icelandic EEZ under present oceanographic conditions (2000-2014 data). Darker yellow through red shading represents progressively higher relative habitat suitability.*

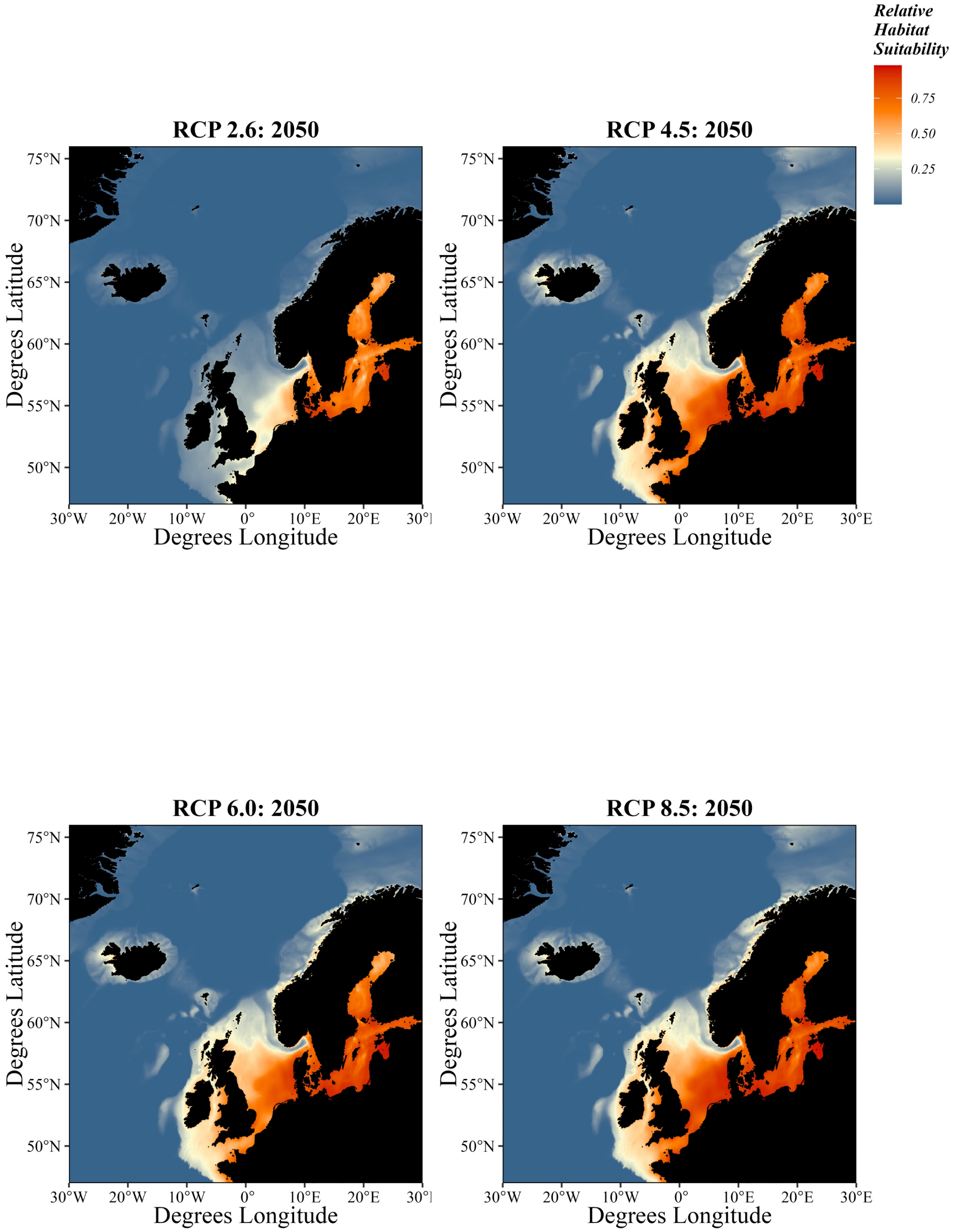


Figure 16. *Modelled prediction of presence for sprat (*Sprattus sprattus*) within Europe under projected oceanographic conditions for the year 2050 under RCP 2.6, 4.5, 6.0 and 8.5. Darker yellow through red shading represents progressively higher relative habitat suitability.*

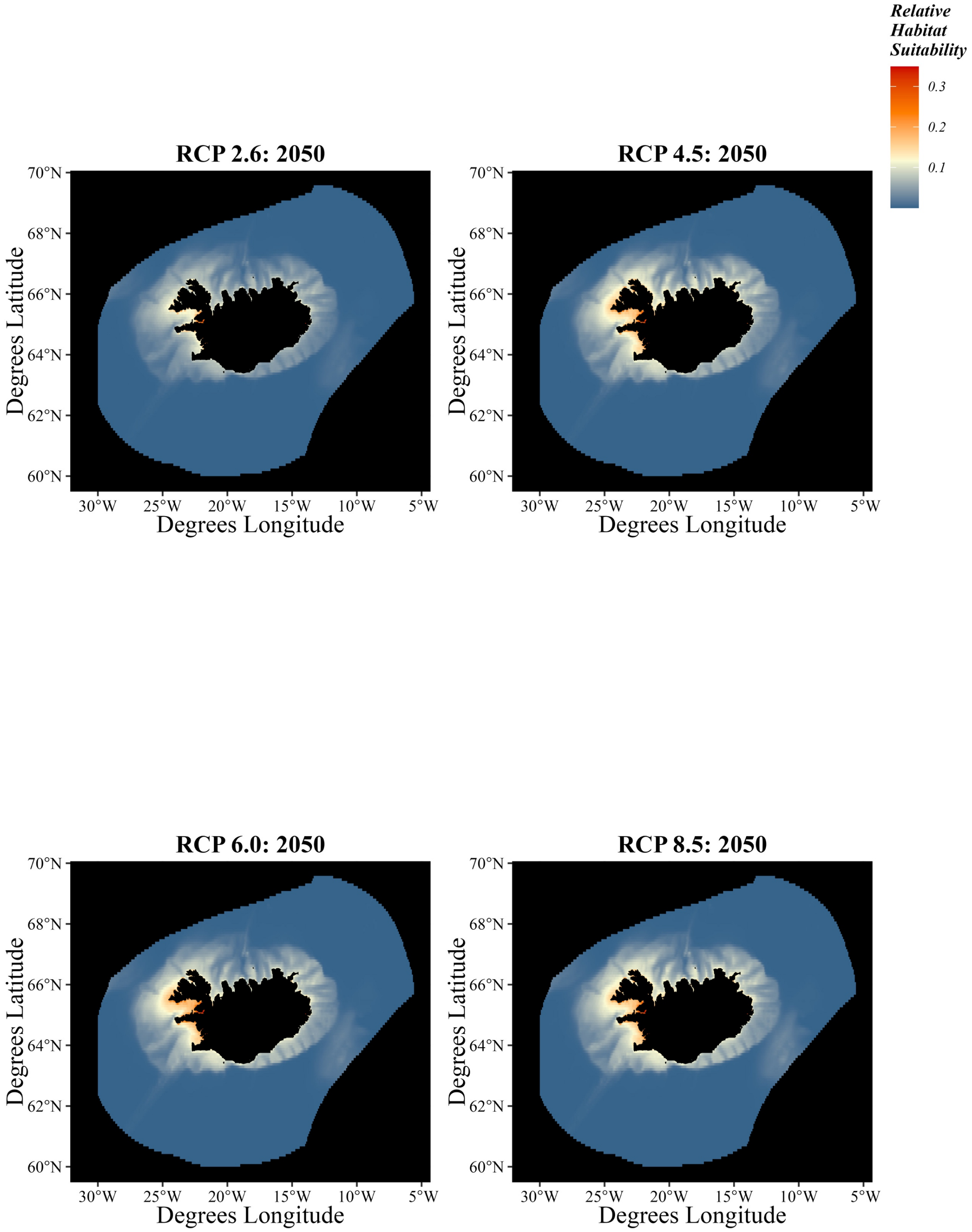


***Figure 17**. Modelled prediction of presence for sprat (*Sprattus sprattus*) within the Icelandic EEZ under projected oceanographic conditions for the year 2050 under RCP 2.6, 4.5, 6.0 and 8.5. Darker yellow through red shading represents progressively higher relative habitat suitability.*

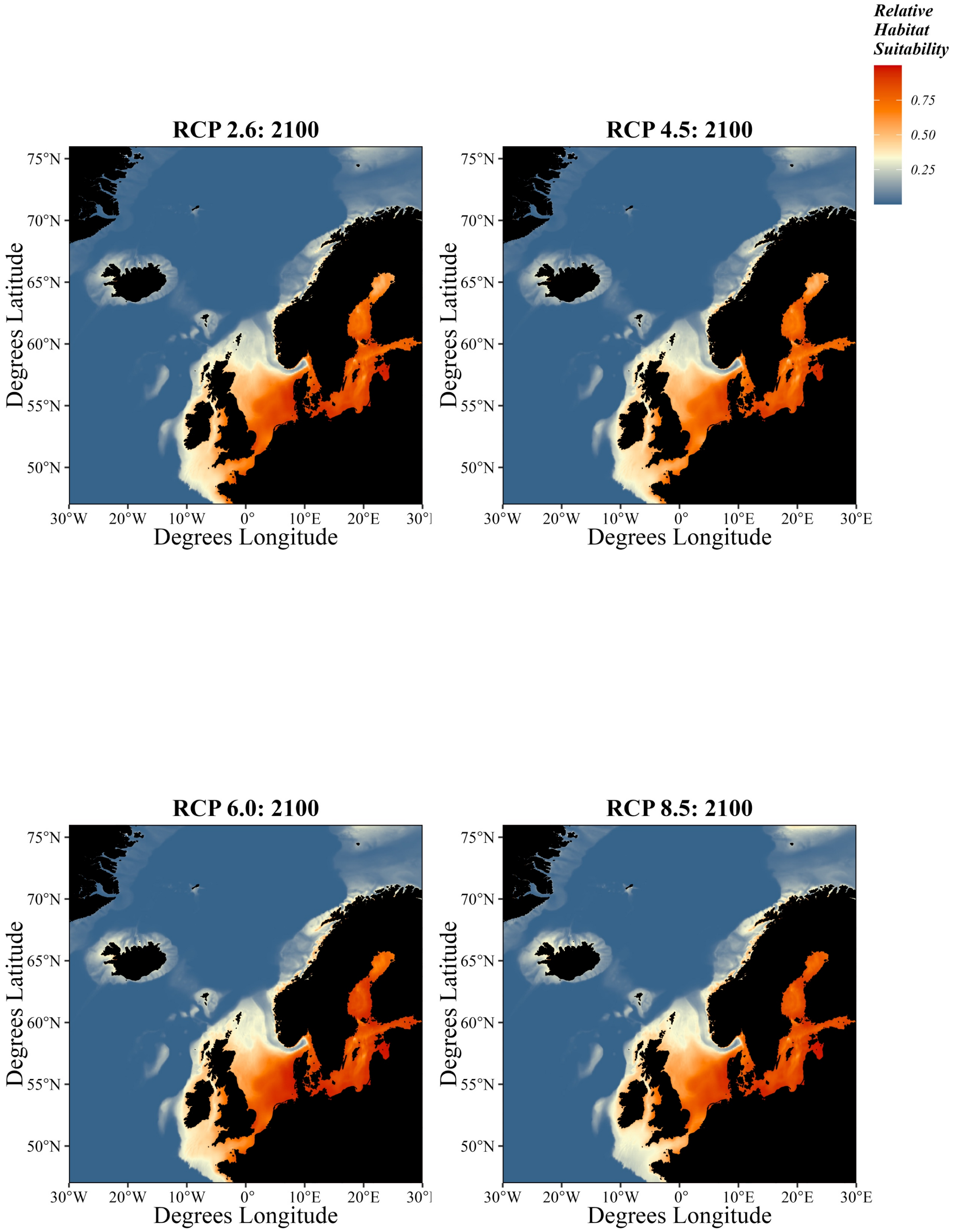


***Figure 18**. Modelled prediction of presence for sprat (*Sprattus sprattus*) within Europe under projected oceanographic conditions for the year 2100 under RCP 2.6, 4.5, 6.0 and 8.5. Darker yellow through red shading represents progressively higher relative habitat suitability.*

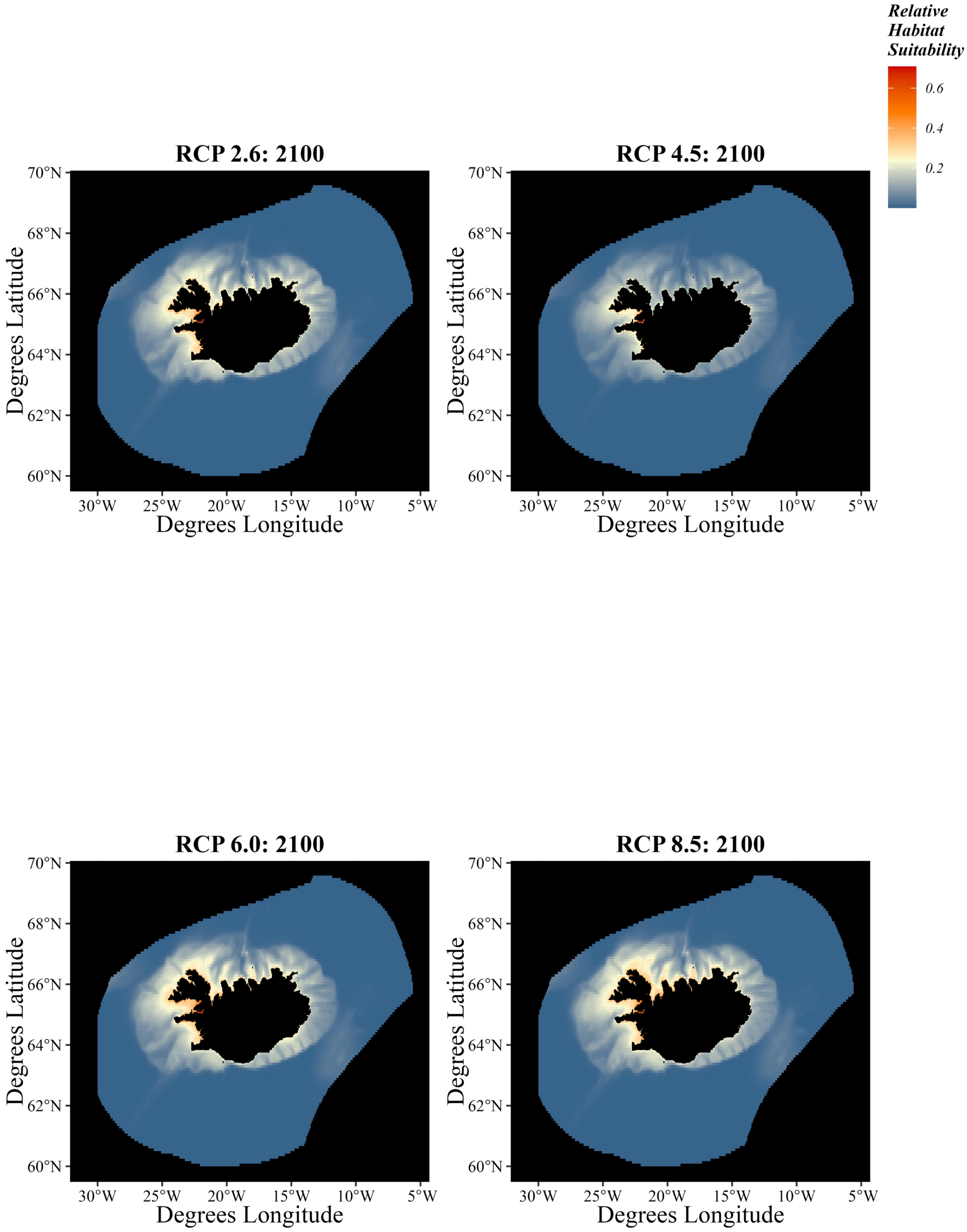


***Figure 19**. Modelled prediction of presence for sprat (*Sprattus sprattus*) within the Icelandic EEZ under projected oceanographic conditions for the year 2100 under RCP 2.6, 4.5, 6.0 and 8.5. Darker yellow through red shading represents progressively higher relative habitat suitability.*

5 Discussion

5.1 Overview

This thesis has brought together much of the current knowledge on sprat distribution and status in Icelandic waters up until February 2022. Data on sprat presence and abundance in Icelandic waters was compiled and analysed in combination with data from the OBIS. The distribution of presence points, maturity stage, sex and age of a subset of the data and a Maxent model of potential distribution under current and future climatic scenarios is presented. This discussion goes into further detail on the results of the locations and abundance of sprat, as well as the biological characteristics. Following this, the predicted current and future habitat suitability for the species around Iceland is discussed. This section then discusses the introduction of sprat into Icelandic waters in the context of the changes to and pressures on ecosystems set out in the theoretical background in sections 2.1 and 2.2. Finally, implications of the findings of this thesis to management are suggested.

5.2 Locations and abundance

From the records analysed within this thesis, all sprat records to date have occurred in the South, Southwest, West and Westfjords of Iceland. Primary data collection from the Westfjords showed both small (n<10) and large (n >50) numbers being recorded in both Ísafjarðardjúp and Arnarfjörður. No records were found of sprat in other areas of the Icelandic EEZ. This might be expected given the difference in oceanographic conditions in Iceland, with warmer waters generally being found in the south and west. As shown by the modelling carried out in this thesis and discussed later, modelled habitat suitability in the regions in which sprat have been observed to date all fall within the areas of relatively high suitability.

5.3 Biological characteristics

5.3.1. Weight and length

In this study, length-weight relationships for males, females and both sexes were created. Sample size was adequate according to Froese, Tsikliras, & Stergiou (2011).

These relationships were created from length (mm) and weight (g) from sprat collected during surveying. From these values, sprat seem to be exhibiting hyperallometric growth, where weight is put on at a greater rate than the rate at which it grows in length. This is demonstrated by *b*, where < 3 relates to hypoallometric growth (where length is put on at a greater rate than weight), = 3 relates to allometric growth where weight and length are proportional and > 3 relates to hyperallometric growth, as described (Froese, Tsikliras, & Stergiou, 2011). The *b* values given in this study fall within the range of many studies of sprat from multiple subspecies found in the literature (Satilmis *et al.*, 2014; Silva, Ellis, & Ayers, 2013).

5.3.2. Sex, maturity and age

The maturity staging of sprat demonstrated that many individuals are reaching sexual maturity and spawning. Seven individuals were recorded at stage VI between June and August. Stage VI individuals are active spawners demonstrating that spawning is occurring in Icelandic waters in at least this period. Sprat reaching stage VII shows that individuals are completing spawning in the current spawning season. This possibly means multiple spawning events have taken place, which in other regions represents up to 10 unique spawning events for females (Alheit, 1988 in Wahl & Alheit, 1988). This is in keeping with the state of knowledge of spawning periods in other regions. In sprat populations in the Kattegat and Skagerrak region in the eastern North Sea show an extended spawning period from the early spring through summer with a peak proportion of spawning individuals observed in April / May (Skagerrak) through to July (Kattegat) (Vitale *et al.*, 2015). Furthermore, individuals have been observed to reach the age of four years, with approximately 80 % of individuals reaching maturity at two years old according to ICES and approximately 90 % according to Kaljuste & Raid (2002) in their study in the Baltic, this suggests the survivability of sprat through multiple spawning seasons in Iceland (ICES, n.d.; Kaljuste & Raid, 2002). From the maturity stages of sprat, spawning appears to be taking place around early summer, finishing around October. Further sampling would need to be done to confirm this, but this is in line with what might be expected given the spawning periods of North Sea sprat (ICES, n.d.; Vitale *et al.*, 2015). Future research could utilise the data from this thesis alongside further records in Iceland to construct Icelandic ogives through binomal generalised linear regressions, for example (ICES, 2008).

Knowing that sprat are spawning in Icelandic waters demonstrates that this is likely to be a species which has the potential to establish. The extent to which this happens, if it does, will be dependent on multiple environmental and ecological factors. Through the modelling element of this study, key environmental variables which may influence the distribution of the species were used to try to further understand potential habitat suitability now and in the future.

5.3.3. Recorded environmental variables

The environmental variables collected during research trawls showed no significant effect on predicting the abundance of sprat in each sample although it should be noted that stations were only used in which sprat were observed. When looking at sprat presence/absence, however, bottom temperature and depth showed to be significant predictors of presence, with sprat more likely to be found in warmer bottom waters of around 6.5 to 7.5 °C and shallower waters of around 50 to 100 m. This is also in keeping with the literature on the species in other areas, with regard to depth distribution and temperature preferences, at least regarding spawning (Morawa, 1954 in Wahl & Alheit, 1988, Whitehead, 1985, Muus & Dahlstrøm, 1989 from Binohlan, n.d.). Serpetti *et al.* (2017), gave the the optimum temperature for sprat at around 10 °C, with a minimum temperature tolerance of 4 °C. The minimum required temperature for spawning is also given as 6 °C (Morawa, 1954 in Wahl & Alheit, 1988). It appears from these results that sprat in Iceland are utilising waters that reach the minimum requirements for the species and that temperature is a limiting factor for the distribution of the species.

5.4. Predicted current and future habitat suitability

From binomial generalized linear regression analysis, it was found that both bottom temperature and depth were significant predictors of presence ($P < 0.05$ and $P < 0.001$, respectively). These factors were selected for use within the Maxent model alongside surface chlorophyll to act as a proxy for primary productivity as well as distance from coast due to the observed coastal nature of sprat. Surface temperature was retained in the model due to fact that the impact of surface temperature may be seen to be more influential over a larger sample size and over a larger geographic range. The results of the binomial generalized linear regression can be seen to be echoed in the response curves of the Maxent model to some degree, with bathymetry showing a more pronounced response curves than many of the other predictor variables. However, the minimum and range of surface temperatures along with, to a lesser degree, mean bottom temperature, were also demonstrated as being strong predictors of habitat suitability, not picked up in the prior analysis.

The difference in predicted suitability between the west coast and shelf area and the rest of the Icelandic coastal waters likely has an oceanographic basis, due to the average sea temperature differences around the country due to the influence of both the warmer Irminger and colder East Greenland currents, creating relatively more suitable habitat in the west. The model has relatively high predicted habitat suitability scattered around the Westfjords, but surprisingly not within Ísafjarðardjúp and Arnarfjörður, where sprat were primarily identified during this thesis. For present day predictions, the variation between areas of higher predicted suitability (in the south and west) and the areas of lower predicted suitability (in the north and east) is likely forced by surface temperatures. As seen in the response curves for the model, surface and bottom temperatures appear to be some of the most influential predictors on predicted habitat suitability and the importance of water temperatures (both surface and bottom) to the distribution of species' is in keeping with the literature (e.g. Campana, *et al.*, 2020b). Bathymetry was also an influential predictor, which is logical given the species' recognised preference for waters of 150 m depth and shallower (Muus & Dahlstrøm, 1989 from Binohlan, n.d.). However, the model did not include oceanographic variables such as current velocity which has been shown to be of utility in modelling other small pelagic species (Lima *et al.*, 2022). This was deliberate. With relatively few presence points in the Icelandic EEZ compared with the North and Baltic Seas, the latter potentially exhibiting very different conditions regarding current velocity and bearing, these variables were excluded from the model. However, oceanic and coastal currents may have the potential to significantly predict sprat presence or suitable habitat. Currents have the potential to be a major dispersal mechanism for the larval stages of a range of species (up to 400 km for shrimp, for instance), with eddies, fronts and other features being critical to how and where larvae are transported (Pedersen, Storm, & Simonsen, 2002). The ability to build in these oceanographic variables into the modelling approach could, therefore, be valuable in further development of this research.

The continuous prediction shows similar patterns between the present-day model and future scenarios. Under present-day predictions, there is generally a higher value associated to the west of Iceland and the predictions for the future show very similar patterns, with some near-shore higher values distributed mostly on the west coast with lower values widely distributed over the shelf area. For RCP 2.6 in 2050, an interesting output is given, with lower predicted habitat suitability's than the more extreme scenarios. The mechanics of this is beyond the scope of this thesis, but similar findings have been recognised by modelers for the earlier years of predictions for the year 2050 (Bio-Oracle, 2017b). As such, the 2100 predictions can be seen as more indicative of the future predicted distribution of suitable habitat. The relatively consistent results of predicted habitat suitability for sprat between RCPs could be due to an effect of the methodology on the model. Sprat data points were used from a diverse geographic region, including two subspecies. Average surface temperatures across this distribution may clearly vary from the average surface temperatures around Iceland, even under each RCP. This may be forcing the prediction down in areas of lower average surface temperature, such as around Iceland. With increasing records of sprat in Iceland, it may be possible to adapt the model and use only Icelandic data to fine-tune the outputs for the Icelandic context and potentially build a model which utilises presence and absence points within the approach. Presence points in Iceland are few in comparison to the rest of Western Europe, in part due to its recent identification in Icelandic waters. Relative habitat suitability reaches a maximum of around 0.5 to 0.6 in locations close to shore, predominantly in the west but also in one location on the east coast for the present-day model when focused on the Icelandic EEZ. This is clearly lower than the maximum prediction value across the rest of Northwest Europe, which is around one. It is worth re-iterating that the results of the Maxent model should be viewed as indicative of relative habitat suitability, rather than as a prediction of presence (Merow, Smith, & Silander, 2013). As such, it would be reasonable to view the results, focussing on Iceland, as relative suitability within that region. While a predicted habitat suitability value of 0.3 or 0.4 may be low in the European context, it is known that sprat are utilising habitats with a predicted value close to 0.2 to 0.3 in Iceland. Sprat appear able to utilise these environments and retain a viable population in Icelandic waters. The limitations of the log-output, as mentioned earlier, should also be remembered. In this model, the default assumption for *tau* was left at 0.5% which, as discussed is an arbitrary number unless backed by some evidence that sampling had a 50% chance of observing the species at every sample site in which habitat was suitable. This is a value which can be defined, based on sampling effort, temporal scale of sampling effort and the likelihood of observing the study species given these. However, this is often hard to do, particularly with datasets obtained from multiple sources over different temporal scales. Within this thesis, sprat presence points were taken from multiple surveys, for multiple aims, from multiple countries, using multiple gear types making defining tau impossible. While efforts were made to attempt to reduce sample bias for the presence locations, this is still likely to be impacting the model, with the relative sampling effort in Iceland clearly much lower than across the rest of Northwest Europe. It may, therefore, be valuable for future development of this approach may consider multiple runs of the model under different values for *tau* in order to assess how consistent the results are. For the purposes of this thesis, however, it is known that sprat are present and spawning in Icelandic waters, so it can be judged to be a fair assumption that the values of regions in which sprat have been identified are a meaningful representation of suitable habitat. Here, sprat have been recorded across most of the region of a relative habitat suitability prediction of around 0.3. Values of around 0.3 to 0.4 in the future predictions are therefore viewed as very likely being representative of potential suitable habitat for sprat under these scenarios.

The model used in this thesis has certain other limitations which should be taken into account. Firstly, the finer-scale temporal variability in distribution is not considered, with presence and background points taken from 2000 to present, with no delineation between seasonality. There is a strong case for including this within SDMs in some cases. Keyl (2017), found sprat to show a varied inter-annual distribution pattern in the North Sea between winter and summer and understanding this temporal variation in habitat preference could be important for understanding how sprat behave within the ecosystem. That said, it was noted that in most cases the areas of high abundance agreed with areas of high abundance from other sources which do not take seasonality into account (e.g. Engelhard, Peck, *et al*., (2014)). This can be seen to a degree within other species distribution models. For instance, the predicted habitat suitability for sprat from Schickele *et al*. (2020) shows a similar, if slightly more widespread, distribution to the area of high abundance given by Keyl (2017) although it should be noted that these were modelling different dynamics (habitat suitability and abundance, respectively). Another limitation for the model in this thesis is the lack of incorporation of vertical distribution. In Iceland, surveys in which sprat have been found have, to date, been exclusively targeted at the benthic region. This may have had an impact on the model outputs, although the incorporation of data from the rest of Europe would alleviate this to some degree. However, it would be expected that the lack of data on how sprat are utilising surface waters in Iceland may impact outputs. Bottom trawls are those utilised by ICES during stock assessment (ICES, 2018). However, in the Baltic Sea for example, sprat school during the day lower in the water column but spend the night dispersed nearer the surface (Nilsson *et al*., 2003). For the purposes of identifying further grid cells of sprat presence, night time pelagic trawls may be of benefit. Furthermore, no data from plankton surveys was available for inclusion in this thesis, however, if molecular methods could be utilised from plankton samples in the future, the distribution of records from early life history stages may be able to further supplement this model. There may be value in future studies exploring the scaled-down temporal and spatial distribution. This may give insights into seasonal or diurnal utilisation of habitats as well as identifying spawning and nursery areas. The Maxent model did identify a small number of samples in conditions which do not fit with expectations. Most notably, one sample was identified within the model as being at around 5000 m depth. This is clearly incorrect and raw data was cleaned specifically to data no deeper than 200 m depth. Why this is occurring is unclear and may be due to errors in the raster layers provided or other reasons. Despite this, the outliers are few and are thought to not be impacting the model extensively, although in the future modelling this could be robustly tested using methods such as Cook's distance (for example, Virgili *et al*., 2017). Furthermore, it is worth reiterating that the removal of correlating predictor layers was achieved through a subjective approach. In development of this model, it may be prudent to utilise a more precise methodology, such as variance inflation factor (VIF), which describes how strongly a predictor is explained by other predictors (Naimi & Araújo, 2016).

Despite the limitations discussed, there is still value in attempting to model the habitat suitability of sprat both now and in the future. It is known sprat are in Icelandic waters, that they are spawning and that survivability is at least four years. It is demonstrated by the model that there is a degree of habitat suitability throughout most of the coastal waters of Iceland, predominantly in the south and west. The model has also described the relationship between the species (both in Iceland and throughout much of the rest of its range), regarding a number of environmental properties. It is thought that this model does give an overall impression of relative habitat suitability for sprat. Using data from the rest of Europe allowed for many more presence points and modelling sprat predicted habitat suitability over this wider region gave a visual assessment of model performance based on the known distribution of the species. Furthermore, use of background points from other small pelagic species removed some sampling bias from this dataset as recommended by *Phillips et al*. (2009). While the model does not look at seasonality or variation in-depth, it gives an overview of average habitat suitability for the species in Icelandic waters and can be used to infer areas in which the species may establish readily.

Using data from both western Europe and Iceland has given advantages to the process. Not only has it allowed for more data points to be utilised, but it means model predictions can be compared with known distribution and modelled distribution of the species. It could be inferred that if the model is performing well for Northwest Europe then there is some predictive power to the model which helps to validate the predictions around Iceland. This seems to be the case. Known and modelled distribution inferred from the literature appears to match well with the model created in this paper. Further tests could be carried out to test this; however, this would be beyond the scope of this thesis.

With reference to Robinson *et al*. (2017), the modelling element of this thesis meets many of the recommendations for effective utilisation of SDMs in research. This thesis has laid out the features which should be explicitly reported, including species name, goals of the study and geographic location and the methodological approach. Lack of absence data was addressed through the use of Maxent with background points. Sample size was high (*n* = 3086, after cleaning), however, there was still an issue of sampling bias within the presence dataset which was addressed to some degree by the portioning of data. In response to this a form of target-group background data, adapted by Phillips *et al*. (2009), using a selection of other small pelagic fish from the same data source and cleaned to the same standard, as well as data partitioning of the presence dataset after Radosavljevic & Anderson (2014) was employed. Multiple models were tested and the parameters for these were given, as well as a summary of the comparative evaluations. Training and testing models were discussed with respect to their relative AUCs. And the model has been applied over different time periods through the modelling of predicted future climate scenarios. Lastly, the model results have been compared to other available models (Keyl, 2017; Schickele *et al*., 2021). However, some aspects were not reported, partly due to the scope of this thesis. In particular, the testing of the model with truly independent data was not undertaken here. For future steps, testing the model with updated research cruise data from Iceland, assuming further sprat samples are caught, as well as with European data from other sources would be a useful test of the validity of the model. Further to this, potential other functional predictor layers were not explored beyond those available through Bio-Oracle. This was not an oversight, as such, but chosen to simplify the modelling process due to parity in coverage between layers both geographically and temporally. Something which would have been complicated by trying to incorporate layers from other freely available sources.

5.5. Changes in Icelandic waters historically and into the future

As discussed in the theoretical background, various pressures can be put on marine systems. Here, these are put into context of the potential entry of sprat into marine ecosystems in the Icelandic marine zone.

Icelandic fisheries are sometimes regarded as some of the most sustainable in the world. Since the early 1980s, the number of stocks which are allocated TACs has grown from six to around 25 and for the majority of these, annual catch is the same as, or lower than, the TAC and overfishing of important species is almost non-existent (Gunnlaugsson & Valtysson, 2022). However, while this may be true, the utilisation of marine species has an ongoing impact on the marine environment. While overfishing as described in section 2.1.1 may not be occurring, humans are still exploiting certain stocks of species to a level that does not mimic natural patterns of mortality. The sprat has entered a system that is exploited on an industrial scale and with that it may have a more, or less, likely chance of establishing permanently than it would in a theoretically pristine environment. The relevance of this is that with potential future changes in fishing pressure, may vary and as a result, the competition which sprat may encounter in terms of predation or competition for food, may fluctuate. In the case of cod, the competition with sprat at different stages of its lifecycle, already discussed, has been seen to have had an impact on dominance of one or other of the species under different fishing pressures (e.g. Parmanne *et al*., 1994 in Köster *et al*., 2003).

Alongside competition with other species which may or may not be affected by fishing pressure, climate change may well have had an impact on the establishment of sprat. While this cannot be proven here, if sprat larvae or eggs drifted to Icelandic waters prior to the recent identification of the species, then it seems likely that this has happened before. Whether a variety of factors outside of water temperatures, for instance, were responsible for unsuccessful establishment before now we cannot know. However, although warming of ocean waters has been less pronounced than the warming of air temperatures over past decades, it has occurred, with a 0.33 °C increase of bottom waters on average from 1996 to 2010 (Campana, *et al*., 2020b). Water temperatures have been seen to impact the distribution of species in historic warming events, giving both clues as to species' responses in the future as well as supporting the findings of models such as the one presented here. For instance, during a period of dramatic warming around Iceland in the 1920s to the 1930s, an influx of warmer Atlantic water into flowing eastwards along the north coast saw changes in species distributions, with colder water species such as capelin tending to stay further north and boreal species such as cod gaining a greater overall abundance as well as spawning in greater numbers in the north (Drinkwater, 2006). In their analysis, Serpetti (2017), while focussing on the west coast of Scotland and therefore a more temperate environment, predicted a reduction in certain key species shared by Iceland. Notably, cod, herring and haddock, each with low optimum temperatures, showed decreases in biomass under most predicted climate scenarios modelled. Whiting, which shared a similar thermal tolerance to sprat, showed an increase in biomass under each climate scenario, partly due to its higher thermal tolerance as well as from the decline in biomass of its predators, grey seals and cod (Serpetti *et al.*, 2017). While this study may not be directly transferable to the Icelandic ecosystem, it is worth highlighting as it demonstrates the multiple modes by which changes in water temperatures may impact sprat in this environment. The model presented in this thesis supports the idea that water temperatures are going to be a driving force in future presence of sprat in Iceland in so far as response plots demonstrate mean surface temperature as one of the most influential predictor variables. That said, changes in the distribution of predicted habitat suitability are limited and not highly apparent. Under predicted climatic changes, it seems that sprat will continue to have access to suitable habitat in Icelandic coastal waters. It is worth highlighting here that effects of temperature on species distribution may be indirect and a proxy for other inter-specific interactions. The examples of the Icelandic scallop and northern shrimp collapses due to increasing disease pressure and enhanced predation by cod (respectively) were both facilitated by warmer temperatures rather than directly due to them (Jonasson *et al.*, 2007; Jónsdóttir, Björnsson, & Skúladóttir, 2012; Valtýsson & Jonsson, 2018). However, this isn't taken into account within this model and future development of this work may find value in attempting to address this, although this may add considerable complexity.

5.6. Management implications

Taking the above into account, the implications for management of the sprat presence in Icelandic waters can be discussed. It is not possible to draw any firm conclusions with regard to this, there have been no stock assessments or attempts to estimate abundance of the species as a whole in Iceland. However, below are laid out some key considerations.

With sprat successfully spawning in Icelandic waters, a clear question is what the impacts will be, if any, on the current marine ecosystem. There is limited scope for making any definitive statements on this based on the results of this thesis, however, potential impacts can be inferred from the literature which may require further investigation in the future. Firstly, how the sprat will interact with other species is a clear route for further investigation. Sprat have been seen to be more generalist than herring with regard to diet in both the North and Baltic Seas (Ojaveer *et al.*, 2018; Raab *et al.*, 2012). In the Baltic, it has also been seen that sprat have the potential to outcompete herring, with a broader diet and higher success in feeding (Ojaveer *et al.*, 2018). As mentioned previously, the recovery of herring in Iceland has been stock-dependent, with the Icelandic and Norwegian summer-spawning herring showing recovery and Icelandic spring-spawning herring showing a routinely low spawning stock biomass since collapse in the late 1960s (Óskarsson, 2018; Sigurdsson, 2006). It was seen in the Firth of Clyde that recovery of both herring and sprat reversed dominance between the two species (Thurstan & Roberts, 2010). While the context is clearly different, questions could be asked about whether sprat in Iceland, which also appear to be spawning in spring/early summer, may be able to utilise a niche, at least in part, which was formally occupied by spring-spawning herring.

The observations of sprat competition with other key fishery species including herring, in the Baltic Sea, are also important (Parmanne *et al.*, 1994 in Köster *et al.*, 2003; Casini *et al.*, 2010). While no claim about the Icelandic ecosystem being currently susceptible to ecosystem hysteresis is being made, the capability of sprat to “exploit” opportunities created by reductions in predator/competitor abundance or become an influential predator of larval stages of other fish in their own right, has been demonstrated in other ecosystems. Fishing is an economic cornerstone of the Icelandic economy and understanding more about how sprat will compete with or predate on currently valuable species may become important if the population remains or increases. Such studies could incorporate dietary analysis to identify overlaps between sprat and other species, similar to the study performed by Raab *et al.* (2012) in their analysis of the same question with regards to anchovy, herring and sprat in the North Sea.

Sprat are able to tolerate warmer waters than a range of species native to Iceland and at least one previous model has suggested a northwards shift in the species under future climate scenarios (Schickele *et al.*, 2021; Serpetti *et al.*, 2017). The modelling aspect of this thesis supports the prediction that habitat suitability will increase around Iceland and in northern

Europe extending to mid/northern Norway and the northern Baltic. This thesis was not able to predict stock levels at present or predict change under different climate scenarios. However, the fact that sprat are seen to be spawning in Iceland, as well as surviving to four years old in some cases, suggests survivability and fitness are, at least, at the minimum required for the species. With this in mind, the fact that suitable habitat range is expected to expand under most climate scenarios, or in the most extreme case, shift northwards, suggests that the sprat is a species that may well be present in Icelandic waters for a significant period of time. This change to the community structure of Icelandic marine fishes will probably not happen in isolation, however. As discussed, other species have entered the marine zone over the course of history and it could be expected that more are to follow. Further to this, northwards shifts of species historically present, or geographical changes in suitable habitat, may well take place in Iceland. In the wider Arctic region, this has been highlighted by Conservation of Arctic Flora and Fauna (CAFF) as a key finding in their State of Marine Biodiversity, with important consequences for the wider ecosystem (CAFF, 2021). For example, capelin has been observed to have shifted northwards in the Hudson Bay area, altering the diet of local seabird populations. In Iceland, 72% of species are expected to re-distribute as a response to warming waters (Campana *et al.*, 2020b). Cold water species are expected to lose areas of suitable habitat, while warmer water species are expected to gain (Mason *et al.*, 2021). For instance, species' such as cod are expected to lose suitable habitat in the south and west, up to the Westfjords of Iceland, while gaining suitable habitat in the north and east (Mason *et al.*, 2021). Considering the potential interactions between cod and sprat, as observed in the Baltic, interactions between the species under a theoretical 'squeeze' to the northern areas of Iceland could be of interest in future studies under continued climate change (Parmanne *et al.*, 1994 in Köster *et al.*, 2003, Köster & Möllmann, 2000). It is too early to tell if sprat biomass will reach a level to support a viable fishery. However, should this occur, decisions on catch may be based on observed interactions with other as well as with predicted changes in multi-species distribution and biomass resulting from climate change. Modelling approaches can help managers choose the best management plan for species allowing for predicted climate change as well as identify risks on food web structure through the relative exploitation rates of multiple species (Serpetti *et al.*, 2017). However, further information on sprat functioning within the ecosystem, as discussed, will be needed to inform these models.

Monitoring of the sprat in Icelandic waters is clearly necessary in order to develop an understanding of potential impacts of the species with regards to inter-specific interactions, as already discussed, but also other dynamics. In particular, efforts could be put in to understanding parasite and diseases within the species, with regards to the potential for sprat to act as a host for pathogens which may be influential on other fish species in Iceland.

Continued monitoring would allow for a longer time-series to be built which could be used to update an updated model such as the one presented in this thesis. In theory, a citizen science approach could be of some utility in the case of the Icelandic sprat. As shown in a number of studies and projects around the world, commercial fishers have been willing in other instances to become involved in the monitoring of a range of aspects relating to their respective fisheries (Fulton *et al*., 2019; Kinver, 2015; Liboiron *et al*., 2016; SIARC, 2022). The involvement of a small number of fishing vessels working in targeted fisheries, such as shrimp, could provide data at a higher spatial and temporal resolution than annual surveys. Judging from the experience in this thesis, it seems likely that some vessels would be willing to support data collection to some degree. Vessels were willing to put aside clupeid samples to be identified in the laboratory and may be willing to learn to identify sprat at sea. While this may be less rigorous and would likely be dictated by the capability of fishers to do this alongside higher priority duties on the vessel, the continued updates in records may aid in helping to map the spread of the species over time. The caveat to this approach, however, is that this may become untenable under a situation where sprat becomes a commercially exploited species. Therefore, a citizen science approach should only be used to supplement routine monitoring of the species and not be used as the primary survey methodology.

5.7. Closing statements

The results from this thesis demonstrate for the first time that sprat are spawning in Icelandic waters. Sprat caught in April/May show a high proportion of sexually maturing individuals whilst samples from August to November showed high proportions of post-spawning sprat, with actively spawning individuals in June to August. Sprat are living up to four years of age in Icelandic waters suggesting the ability to spawn over multiple years. Furthermore, suitable habitat has been modelled to be consistently available in Iceland, to varying degrees, over the next 100 years and under all scenarios modelled. Potential next steps for management of the species will be ongoing monitoring of the species to gain further insight into aspects such as feeding ecology, habitat utilisation and biomass as well as citizen science initiatives in order to gain a continuous update on the spread of the species in Icelandic waters. It may also be important to establish early on if this species can be seen just as an immigrant/non-native or an invasive species. Through further understanding the biology and ecology of the species (particularly the interactions with other species) a greater understanding of the impact of the sprat in Iceland, whether ecological or commercial can be gained.

References

Alofs, K. M., Jackson, D. A., & Lester, N. P. (2014). Ontario freshwater fishes demonstrate differing range-boundary shifts in a warming climate. *Diversity and Distributions*, *20*(2), 123–136. https://doi.org/10.1111/ddi.12130

Alsos, I. G., Lammers, Y., Kjellman, S. E., Merkel, M. K. F., Bender, E. M., Rouillard, A., Erlendsson, E., Guðmundsdóttir, E. R., Benediktsson, Í. Ö., Farnsworth, W. R., Brynjólfsson, S., Gísladóttir, G., Eddudóttir, S. D., & Schomacker, A. (2021). Ancient sedimentary DNA shows rapid post-glacial colonisation of Iceland followed by relatively stable vegetation until the Norse settlement (Landnám) AD 870. *Quaternary Science Reviews*, *259*. https://doi.org/10.1016/j.quascirev.2021.106903

Arias, P. A., Bellouin, N., Coppola, E., Jones, R. G., Krinner, G., Marotzke, J., Naik, V., Palmer, M. D., Plattner, G.-K., Rogelj, J., Rojas, M., Sillmann, J., Storelvmo, T., Thorne, P. W., Trewin, B., Rao, K. A., Adhikary, B., Allan, R. P., Armour, K., … Zickfeld, K. (2021). Technical Summary. In Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*. Cambridge University Press. https://doi.org/:10.1017/9781009157896.002

Armstrong, J. D., & Stewart, D. C. (1997). The effects of initial length and body curvature on shrinkage of juvenile Atlantic salmon during freezing. *Journal of Fish Biology*, *50*(4), 903–905. https://doi.org/10.1006/jfbi.1996.0349

Arnason, R. (2008). Iceland ' s ITQ system creates new wealth. *The Electronic Journal of Sustainable Development*, *1*(2), 35–41.

Aro, E. (1989). A review of fish migration patterns in the Baltic. *Rapports et Procès-Verbaux Des Réunions / Conseil Permanent International Pour l'Exploration de La Mer*, *190*, 72–96. http://en.scientificcommons.org/26047672

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & De Clerck, O. (2018). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, *27*(3), 277–284. https://doi.org/10.1111/geb.12693

Astthorsson, O. S., Valdimarsson, H., Gudmundsdottir, A., & Óskarsson, G. J. (2012). Climate-related variations in the occurrence and distribution of mackerel (Scomber scombrus) in Icelandic waters. *Journal of Marine Science*, *69*(7), 1289–1297. https://doi.org/10.1038/278097a0

Bailey, R. S. (1980). Problems in the Management of short-lived pelagic fish as exemplified by North Sea sprat. *Rapports et Procès-Verbaux Des Réunions*, *177*, 477–488.

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, *3*(2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Bax, N., Williamson, A., Aguero, M., Gonzalez, E., & Geeves, W. (2003). Marine invasive alien species: A threat to global biodiversity. *Marine Policy*, *27*(4), 313–323. https://doi.org/10.1016/S0308-597X(03)00041-1

Binohlan, C. B. (n.d.). *Sprattus sprattus (Linnaeus, 1758)*. Fishbase.Se. Retrieved April 19, 2022, from https://www.fishbase.se/Summary/SpeciesSummary.php?ID=1357&AT=sprat

Bio-Oracle. (2017a). *Download Manager*. Bio-Oracle.Org.

Bio-Oracle. (2017b). *Frequently Asked Questions*. Bio-Oracle.Org. https://www.bio-oracle.org/faq.php

Bond, N., Thomson, J., Reich, P., & Stein, J. (2011). Using species distribution models to infer potential climate change-induced range shifts of freshwater fish in south-eastern Australia. *Marine and Freshwater Research*, *62*(9), 1043–1061. https://doi.org/10.1071/MF10286

Brown-Peterson, N. J., Wyanski, D. M., Saborido-Rey, F., Macewicz, B. J., & Lowerre-Barbieri, S. K. (2011). A standardized terminology for describing reproductive development in fishes. *Marine and Coastal Fisheries*, *3*(1), 52–70. https://doi.org/10.1080/19425120.2011.555724

Bucholtz, R. H., Krüger-Johnsen, M., & Tomkiewicz, J. (2011). *Report of the Workshop on Sexual Maturity Staging of Herring and Sprat (WKMSHS), 20-23 June 2011, Charlottenlund, Denmark.* (Issue June). www.ices.dk

Bucholtz, R. H., Tomkiewicz, J., & Dalskov, J. (2008). Manual to determine gonadal maturity of herring (Clupea harengus L.). In *DTU Aqua-report*. http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Manual+to+determine+gonadal+maturity+of+herring+(Clupea+harengus+L.)#0

Byström, P., Karlsson, J., Nilsson, P., Van Kooten, T., Ask, J., & Olofsson, F. (2007). Substitution of top predators: Effects of pike invasion in a subarctic lake. *Freshwater Biology*, *52*(7), 1271–1280. https://doi.org/10.1111/j.1365-2427.2007.01763.x

CAFF. (2021). *State of the Arctic Marine Biodiversity Report Update: Seabirds*.

Campana, S. E., Casselman, J. M., Jones, C. M., Black, G., Barker, O., Evans, M., Guzzo, M. M., Kilada, R., Muir, A. M., & Perry, R. (2020). Arctic freshwater fish productivity and colonization increase with climate warming. *Nature Climate Change*, *10*(5), 428–433. https://doi.org/10.1038/s41558-020-0744-x

Campana, S. E., Stefánsdóttir, R. B., Jakobsdóttir, K., & Sólmundsson, J. (2020). Shifting fish distributions in warming sub-Arctic oceans. *Scientific Reports*, *10*(1), 1–14. https://doi.org/10.1038/s41598-020-73444-y

Casini, M., Bartolino, V., Molinero, J. C., & Kornilovs, G. (2010). Linking fisheries, trophic interactions and climate: Threshold dynamics drive herring clupea harengus growth in the central Baltic Sea. *Marine Ecology Progress Series*, *413*(Ec 2008), 241–252. https://doi.org/10.3354/meps08592

Casini, M., Rouyer, T., Bartolino, V., Larson, N., & Grygiel, W. (2014). Density-dependence in space and time: Opposite synchronous variations in population distribution and body condition in the baltic sea sprat (Sprattus sprattus) over three decades. *PLoS ONE*, *9*(4), 1–9. https://doi.org/10.1371/journal.pone.0092278

Cigliano, J. A., Meyer, R., Ballard, H. L., Freitag, A., Phillips, T. B., & Wasser, A. (2015). Making marine and coastal citizen science matter. *Ocean and Coastal Management*, *115*, 77–87. https://doi.org/10.1016/j.ocecoaman.2015.06.012

Comte, L., & Olden, J. D. (2017). Climatic vulnerability of the world's freshwater and marine fishes. *Nature Climate Change*, *7*(10), 718–722. https://doi.org/10.1038/nclimate3382

Coyer, J. A., Hoarau, G., Skage, M., Stam, W. T., & Olsen, J. L. (2006). Origin of Fucus serratus (Heterokontophyta; Fucaceae) populations in Iceland and the Faroes: A microsatellite-based assessment. *European Journal of Phycology*, *41*(2), 235–246. https://doi.org/10.1080/09670260600652820

Croll, D. A., Maron, J. L., Estes, J. A., Danner, E. M., & Byrd, G. V. (2005). Introduced predators transform subarctic islands from grassland to tundra. *Science*, *307*(5717), 1959–1961. https://doi.org/10.1126/science.1108485

Dänhardt, A., & Becker, P. H. (2011). Herring and Sprat Abundance Indices Predict Chick Growth and Reproductive Performance of Common Terns Breeding in the Wadden Sea. *Ecosystems*, *14*(5), 791–803. https://doi.org/10.1007/s10021-011-9445-7

Danielsen, F., Burgess, N. D., Balmford, A., Donald, P. F., Funder, M., Jones, J. P. G., Alviola, P., Balete, D. S., Blomley, T., Brashares, J., Child, B., Enghoff, M., Fjeldså, J., Holt, S., Hübertz, H., Jensen, A. E., Jensen, P. M., Massao, J., Mendoza, M. M., … Yonten, D. (2009). Local participation in natural resource monitoring: A characterization of approaches. *Conservation Biology*, *23*(1), 31–42. https://doi.org/10.1111/j.1523-1739.2008.01063.x

Drinkwater, K. F. (2006). The regime shift of the 1920s and 1930s in the North Atlantic. *Progress in Oceanography*, *68*(2–4), 134–151. https://doi.org/10.1016/j.pocean.2006.02.011

Dugmore, A. J., Church, M. J., Buckland, P. C., Edwards, K. J., Lawson, I., McGovern, T. H., Panagiotakopulu, E., Simpson, I. A., Skidmore, P., & Sveinbjarnardóttir, G. (2005). The Norse landnám on the North Atlantic islands: An environmental impact assessment. *Polar Record*, *41*(216), 21–37. https://doi.org/10.1017/S0032247404003985

Dunstan, P. K., & Bax, N. J. (2007). How far can marine species go? Influence of population biology and larval movement on future range limits. *Marine Ecology Progress Series*, *344*, 15–28. https://doi.org/10.3354/meps06940

Einarsson, M. Á. (1984). Climate of Iceland. In *World survey of climatology* (Vol. 15, pp. 673–697). Elsevier. https://doi.org/10.1002/qj.49702511010

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A. Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M. Overton, J., Townsend Peterson, A., … E. Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, *29*(2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, *17*(1), 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Elliot, A. (2022, May 20). Pink salmon are breeding in Iceland. *RUV*.

Emblemsvåg, M., Núñez-Riboni, I., Christensen, H. T., Nogueira, A., Gundersen, A., & Primicerio, R. (2020). Increasing temperatures, diversity loss and reorganization of deep-sea fish communities east of Greenland. *Marine Ecology Progress Series*, *654*, 127–141. https://doi.org/10.3354/meps13495

Enders, E. C., & Boisclair, D. (2016). Effects of environmental fluctuations on fish metabolism: Atlantic salmon Salmo salar as a case study. *Journal of Fish Biology*, *88*(1), 344–358. https://doi.org/10.1111/jfb.12786

Engelhard, G. H., Peck, M. A., Rindorf, A., Smout, S. C., Deurs, M. Van, Raab, K., Andersen, K. H., Garthe, S., Lauerburg, R. A. M., Scott, F., Brunel, T., Aarts, G., Kooten, T. Van, & Dickey-collas, M. (2014). Forage fish, their fisheries, and their predators: who drives whom? *ICES Journal of Marine Science*, *71*(1), 90–104.

Engelhard, G. H., Righton, D. A., & Pinnegar, J. K. (2014). Climate change and fishing: A century of shifting distribution in North Sea cod. *Global Change Biology*, *20*(8), 2473–2483. https://doi.org/10.1111/gcb.12513

Eriksson, B. K., Rubach, A., & Hillebrand, H. (2006). Community dominance by a canopy species controls the relationship between macroalgal production and species richness. *Limnology and Oceanography*, *51*(4), 1813–1818.

https://doi.org/10.4319/lo.2006.51.4.1813

European Environment Agency. (2015). *Country profile - Distinguishing factors (Iceland)*. The European Environment — State and Outlook. https://www.eea.europa.eu/soer/2010/countries/is/country-introduction-iceland

Falk-Petersen, J., Bøhn, T., & Sandlund, O. T. (2006). On the numerous concepts in invasion biology. *Biological Invasions*, *8*(6), 1409–1424. https://doi.org/10.1007/s10530-005-0710-6

FAO. (1995). *Code of Conduct for Responsible Fisheries*. https://doi.org/10.5040/9781509955572.0062

FAO. (2020). The State of World Fisheries and Aquaculture. In *Sustainability in action*. https://doi.org/10.4060/ca9229en

FAO. (2022). *Sprattus sprattus Linnaeus,1758*. Fisheries and Aquaculture Division.

Farrell, D. P. O. (2012). *Range expansion of European Flounder Platichthys flesus to Icelandic waters . A threat to native salmonids ? May*.

Feng, X., Walker, C., & Gebresenbet, F. (2017). Shifting from closed-source graphical-interface to open-source programming environment: 2 a brief tutorial on running Maxent in R. *PeerJPreprints*. https://peerj.com/preprints/3346/

Frainer, A., Primicerio, R., Kortsch, S., Aune, M., Dolgov, A. V., Fossheim, M., & Aschan, M. M. (2017). Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(46), 12202–12207. https://doi.org/10.1073/pnas.1706080114

Frank, K. T., Petrie, B., Choi, J. S., & Leggett, W. C. (2005). Ecology: Trophic cascades in a formerly cod-dominated ecosystem. *Science*, *308*(5728), 1621–1623. https://doi.org/10.1126/science.1113075

Franklin, J. (2013). Species distribution models in conservation biogeography: Developments and challenges. *Diversity and Distributions*, *19*(10), 1217–1223. https://doi.org/10.1111/ddi.12125

Froese, R., Tsikliras, A. C., & Stergiou, K. I. (2011). Editorial note on weight-length relations of fishes. *Acta Ichthyologica et Piscatoria*, *41*(4), 261–263. https://doi.org/10.3750/AIP2011.41.4.01

Fulton, S., López-Sagástegui, C., Weaver, A. H., Fitzmaurice-Cahluni, F., Galindo, C., Melo, F. F. R., Yee, S., Ojeda-Villegas, M. B., Fuentes, D. A., & Torres-Bahena, E. (2019). Untapped potential of citizen science in Mexican small-scale fisheries. *Frontiers in Marine Science*, *6*(AUG). https://doi.org/10.3389/fmars.2019.00517

GEBCO. (2022). *GEBCO*. Homepage. https://www.gebco.net

Guðjónsson, Þ. (1961). *Occurrence of Pink Salmon (Oncorhvnchus porbuscha) in Iceland in 1960 and 1961* (Issue September).

Guðmundsdóttir, Á., & Steinarsson, B. Æ. (1997). An attempt to model the length-weight relationship for saithe in Icelandic waters. *ICES Annual Science Conference Biology and Behaviour (II)*.

Gunnlaugsson, S. B., & Valtysson, H. (2022). Sustainability and wealth creation, but no consensus: Recent decades in Iceland's ITQ-managed fisheries. *Marine Policy*, *135*(October 2021), 104836. https://doi.org/10.1016/j.marpol.2021.104836

Hafrannsóknastofnun. (2022). LOÐNA – CAPELIN Mallotus villosus. In *Ástand nytjastofna sjávar og ráðgjöf 2022*. https://doi.org/10.31857/s0042875220010166

Hannesson, R. (2013). Sharing the Northeast Atlantic mackerel. *ICES Journal of Marine Science*, *70*(2), 259–269. https://doi.org/10.1038/278097a0

Haslob, H. (2011). *Reproductive ecology of Baltic sprat and its application in stock assessment* [Christian-Albrechts-Universität zu Kiel]. http://oceanrep.geomar.de/12150/

Heath, M. R., & Speirs, D. C. (2012). Changes in species diversity and size composition in the Firth of Clyde demersal fish community (1927-2009). *Proceedings of the Royal Society B: Biological Sciences*, *279*(1728), 543–552. https://doi.org/10.1098/rspb.2011.1015

Henke, T. (2018). *Ecological impact of the invasive European flounder (Platichthys flesus) on the native European plaice (Pleuronectes platessa) on nursery grounds in Iceland. May*.

Henke, T., Patterson, W. P., & Ólafsdóttir, G. Á. (2020). First record of niche overlap of native european plaice (Pleuronectes platessa) and non-indigenous european flounder (platichthys flesus) on nursery grounds in iceland. *Aquatic Invasions*, *15*(4), 671–682. https://doi.org/10.3391/ai.2020.15.4.08

Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2021). *dismo: Species Distribution Modeling. R package version 1.3-5.*

Hindar, K., Hole, L. R., Kausrud, K., Malmstrøm, M., Rimstad, E., Robertson, L., Sandlund, O. T., Thorstad, E. B., Vollset, K. W., Boer, H. de, Eldegard, K., Järnegren, J., Kirkendall, L., Måren, I., Nielsen, A., Nilsen, E. B., Rueness, E., & Velle, G. (2020). *Assessment of the risk to Norwegian biodiversity and aquaculture from pink salmon (Oncorhynchus gorbuscha). Scientific Opinion of the Panel on Alien Organisms and Trade in Endangered Species (CITES).* https://vetinst.brage.unit.no/vetinst-xmlui/bitstream/handle/11250/2828612/HindarAssessmentVKMrapport01_2020.pdf?sequence=2

Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(SUPPL. 2), 19659–19665. https://doi.org/10.1073/pnas.0905137106

Hyder, K., Townhill, B., Anderson, L. G., Delany, J., & Pinnegar, J. K. (2015). Can citizen science contribute to the evidence-base that underpins marine policy? *Marine Policy*, *59*, 112–120. https://doi.org/10.1016/j.marpol.2015.04.022

ICES. (n.d.). Sprat. In *ICES FishMap Species Factsheet*. ICES. https://doi.org/10.1109/igarss.1998.703812

ICES. (2008). Report of the Workshop on Maturity Ogive Estimation for Stock Assessment (WKMOG). *ICES CM2008/ACOM*, *33*, 72.

ICES. (2013). *ICES WKSPRAT REPORT 2013 Report of the Benchmark Workshop on Sprat Stocks (WKSPRAT) International Council for the Exploration of the Sea* (Issue ACOM:48).

ICES. (2018). Benchmark Workshop on Sprat (WKSPRAT 2018). *ICES CM 2018/ACOM*, *35*, 60.

ICES. (2021). Icelandic Waters ecoregion – Ecosystem overview. *ICES Ecosystem Overviews*, *December*.

Ingólfsson, A. (2008). The invasion of the intertidal canopy-forming alga Fucus serratus L. to southwestern Iceland: Possible community effects. *Estuarine, Coastal and Shelf Science*, *77*(3), 484–490.

IPCC. (2014a). *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (eds.)). Cambridge University Press. https://doi.org/10.2307/1881805

IPCC. (2014b). *Synthesis Report. Contribution of Working Groups, I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)].*

Jakobsson, J., & Stefánsson, G. (1999). Management of summer-spawning herring off Iceland. *ICES Journal of Marine Science*, *56*(6), 827–833. https://doi.org/10.1006/jmsc.1999.0542

Jenkins, S. R., Norton, T. A., & Hawkins, S. J. (1999). Settlement and post-settlement interactions between Semibalanus balanoides (L.) (Crustacea: Cirripedia) and three species of fucoid canopy algae. *Journal of Experimental Marine Biology and Ecology*, *236*(1), 49–67. https://doi.org/10.1016/S0022-0981(98)00189-0

Jenkins, S. R., Norton, T. A., & Hawkins, S. J. (2004). Long term effects of Ascophyllum nodosum canopy removal on mid shore community structure. *Journal of the Marine Biological Association of the United Kingdom*, *84*(2), 327–329. https://doi.org/10.1017/S0025315404009221h

Jeppesen, E., Meerhoff, M., Holmgren, K., González-Bergonzoni, I., Teixeira-de Mello, F., Declerck, S. A. J., De Meester, L., Søndergaard, M., Lauridsen, T. L., Bjerring, R., Conde-Porcuna, J. M., Mazzeo, N., Iglesias, C., Reizenstein, M., Malmquist, H. J., Liu, Z., Balayla, D., & Lazzaro, X. (2010). Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. *Hydrobiologia*, *646*(1), 73–90. https://doi.org/10.1007/s10750-010-0171-5

Jochumsen, K., Schnurr, S. M., & Quadfasel, D. (2016). Bottom temperature and salinity distribution and its variability around Iceland. *Deep-Sea Research Part I: Oceanographic Research Papers*, *111*, 79–90. https://doi.org/10.1016/j.dsr.2016.02.009

Jonasson, J. P., Thorarinsdottir, G., Eiriksson, H., Solmundsson, J., & Marteinsdottir, G. (2007). Collapse of the fishery for Iceland scallop (Chlamys islandica) in Breidafjordur, West Iceland. *ICES Journal of Marine Science*, *64*(2), 298–308. https://doi.org/10.1093/icesjms/fsl028

Jónsdóttir, I. G., Bakka, H., & Elvarsson, B. T. (2019). Groundfish and invertebrate community shift in coastal areas off Iceland. *Estuarine, Coastal and Shelf Science*, *219*, 45–55.

Jónsdóttir, I. G., Björnsson, H., & Skúladóttir, U. (2012). Predation by Atlantic cod Gadus morhua on northern shrimp Pandalus borealis in inshore and offshore areas of Iceland. *Marine Ecology Progress Series*, *469*(November 2012), 223–232. https://doi.org/10.3354/meps09977

Jónsdóttir, I. G., Magnússon, Á., & Skúladóttir, U. (2013). Influence of increased cod abundance and temperature on recruitment of northern shrimp (Pandalus borealis). *Marine Biology*, *160*(5), 1203–1211. https://doi.org/10.1007/s00227-013-2172-1

Kaartvedt, S., Røtad, A., & Klevjer, T. A. (2009). Sprat sprattus sprattus can exploit low oxygen waters for overwintering. *Marine Ecology Progress Series*, *390*(2003), 237–249. https://doi.org/10.3354/meps08196

Kahle, D., & Wickham, H. (n.d.). ggmap: Spatial Visualization with ggplot2. *The R Journal*, *5*(1), 144–161.

Kaljuste, O., & Raid, T. (2002). Recent observations of the sex ratio and maturity ogive of Baltic sprat in the north-eastern Baltic Sea. *Bulletin of the Sea Fisheries Institute*, *3*(157), 47–54.

Kasapoğlu, N. (2018). Age, Growth, and Mortality of Exploited Stocks: Anchovy, Sprat, Mediterranean Horse Mackerel, Whiting, and Red Mullet in the Southeastern Black Sea. *Aquatic Sciences and Engineering*, *33*(2), 39–49. https://doi.org/10.18864/ase201807

Kass, J. M., Anderson, R. P., Espinosa-Lucas, A., Juárez-Jaimes, V., Martínez-Salas, E., Botello, F., Tavera, G., Flores-Martínez, J. J., & Sánchez-Cordero, V. (2020). Biotic predictors with phenological information improve range estimates for migrating monarch butterflies in Mexico. *Ecography*, *43*(3), 341–352. https://doi.org/10.1111/ecog.04886

Kass, J. M., Muscarella, R., Galante, P. J., Bohl, C. L., Pinilla-Buitrago, G. E., Boria, R. A., Soley-Guardia, M., & Anderson, R. P. (2021). ENMeval 2.0: Redesigned for customizable andvreproducible modeling of species' niches and distributions. *Methods in Ecology and Evolution*. https://doi.org/https://doi.org/10.1111/2041-210X.13628

Kass, J. M., Muscarella, R., Pinilla-Buitrago, G. E., & Galante, P. J. (2022). *ENMeval 2.0 Vignette*. Jamiemkass.Github.Io.

Katz, T. S., & Zellmer, A. J. (2018). Comparison of model selection technique performance in predicting the spread of newly invasive species: a case study with Batrachochytrium salamandrivorans. *Biological Invasions*, *20*(8), 2107–2119. https://doi.org/10.1007/s10530-018-1690-7

Kearney, M. R., Wintle, B. A., & Porter, W. P. (2010). Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. *Conservation Letters*, *3*(3), 203–213. https://doi.org/10.1111/j.1755-263X.2010.00097.x

Keller, R. P., Geist, J., Jeschke, J. M., & Kühn, L. (2011). Invasive species in Europe: Ecology, status, and policy. *Environmental Sciences Europe*, *23*(1), 8–11. https://doi.org/10.1186/2190-4715-23-23

Keyl, F. (2017). Inter-annual variability in distribution and spatial abundance of sprat, Norway pout and small herring in the North Sea. *Hydrobiologia*, *795*(1), 239–256. https://doi.org/10.1007/s10750-017-3132-4

Kinver, M. (2015, July 20). *Fishing boats become citizen science data platforms*. BBC News. https://www.bbc.com/news/science-environment-33434517

Knútsson, Ö., Kristófersson, D. M., & Gestsson, H. (2016). The effects of fisheries management on the Icelandic demersal fish value chain. *Marine Policy*, *63*, 172–179. https://doi.org/10.1016/j.marpol.2015.03.015

Kokorsch, M., & Benediktsson, K. (2018). Prosper or perish? The development of Icelandic fishing villages after the privatisation of fishing rights. *Maritime Studies*, *17*(1), 69–83. https://doi.org/10.1007/s40152-018-0089-5

Köster, F. W., Hinrichsen, H., Schnack, D., John, M. A. S. T., Mackenzie, B. R., Tomkiewicz, J., Möllmann, C., Kraus, G., Plikshs, M., Makarchouk, A., & Aro, E. (2003). Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock-recruitment relationships. *Scientia Marina*, *67*(S1), 129–154.

Köster, F. W., & Möllmann, C. (2000). Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES Journal of Marine Science*, *57*(2), 310–323. https://doi.org/10.1006/jmsc.1999.0528

Kourantidou, M., Kaiser, B. A., & Fernandez, L. M. (2015). Towards Arctic Resource Governance of Marine Invasive Species. In L. Heininen, H. Exner-pirot, & J. Plouffe (Eds.), *Arctic Yearbook 2015: Arctic Governance and Governing* (pp. 68–85). Northern Research Forum. http://library.arcticportal.org/1903/1/arctic-yearbook-2015.pdf

Laidre, K. L., Born, E. W., Atkinson, S. N., Wiig, Ø., Andersen, L. W., Lunn, N. J., Dyck, M., Regehr, E. V., McGovern, R., & Heagerty, P. (2018). Range contraction and increasing isolation of a polar bear subpopulation in an era of sea-ice loss. *Ecology and Evolution*, *8*(4), 2062–2075. https://doi.org/10.1002/ece3.3809

Laidre, K. L., Stirling, I., Lowry, L. F., Wiig, Ø., Heide-Jørgensen, M. P., & Ferguson, S. H. (2008). Quantifying the sensitivity of arctic marine mammals to climate-induced habitat change. *Ecological Applications*, *18*(SUPPL.2), 97–125. https://doi.org/10.1890/06-

0546.1

Lawrence, J. M., & Fernandes, P. G. (2021). A switch in species dominance of a recovering pelagic ecosystem. *Current Biology*, *31*(19), 4354-4360.e3. https://doi.org/10.1016/j.cub.2021.07.020

Lefevre, S., Wang, T., & McKenzie, D. J. (2021). The role of mechanistic physiology in investigating impacts of global warming on fishes. *Journal of Experimental Biology*, *224*. https://doi.org/10.1242/jeb.238840

Lehodey, P., Alheit, J., Barange, M., Baumgartner, T., Beaugrand, G., Drinkwater, K., Fromentin, J. M., Hare, S. R., Ottersen, G., Perry, R. I., Roy, C., van der Lingen, C. D., & Werner, F. (2006). Climate variability, fish, and fisheries. *Journal of Climate*, *19*(20), 5009–5030. https://doi.org/10.1175/JCLI3898.1

Lema, S. C., Bock, S. L., Malley, M. M., & Elkins, E. A. (2019). Warming waters beget smaller fish: Evidence for reduced size and altered morphology in a desert fish following anthropogenic temperature change. *Biology Letters*, *15*(10). https://doi.org/10.1098/rsbl.2019.0518

Liboiron, M., Liboiron, F., Wells, E., Richárd, N., Zahara, A., Mather, C., Bradshaw, H., & Murichi, J. (2016). Low plastic ingestion rate in Atlantic cod (Gadus morhua) from Newfoundland destined for human consumption collected through citizen science methods. *Marine Pollution Bulletin*, *113*(1–2), 428–437. https://doi.org/10.1016/j.marpolbul.2016.10.043

Lima, A. R. A., Baltazar-soares, M., Garrido, S., Riveiro, I., Carrera, P., Piecho-santos, A. M., Peck, M. A., & Silva, G. (2022). Forecasting shifts in habitat suitability across the distribution range of a temperate small pelagic fish under different scenarios of climate change. *Science of the Total Environment*, *804*. https://doi.org/10.1016/j.scitotenv.2021.150167

Lindegren, M., Diekmann, R., & Möllmann, C. (2010). Regime shifts, resilience and recovery of a cod stock. *Marine Ecology Progress Series*, *402*, 239–253. https://doi.org/10.3354/meps08454

Linnæus, C. (1758). *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (1st ed.).

Liu, C., Berry, P. M., Dawson, T. P., & Pearson, R. G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, *28*(3), 385–393. https://doi.org/10.1111/j.0906-7590.2005.03957.x

Lobo, J. M., Jiménez-valverde, A., & Real, R. (2008). AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, *17*(2), 145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x

Lundström, K., Hjerne, O., Lunneryd, S. G., & Karlsson, O. (2010). Understanding the diet composition of marine mammals: Grey seals (Halichoerus grypus) in the Baltic Sea. *ICES Journal of Marine Science*, *67*(6), 1230–1239. https://doi.org/10.1093/icesjms/fsq022

Mackenzie, B. R., Payne, M. R., Boje, J., Høyer, J. L., & Siegstad, H. (2014). A cascade of warming impacts brings bluefin tuna to Greenland waters. *Global Change Biology*, *20*(8), 2484–2491. https://doi.org/10.1111/gcb.12597

Mason, J. G., Woods, P. J., Thorlacius, M., Guðnason, K., Saba, V. S., Sullivan, P. J., & Kleisner, K. M. (2021). Projecting climate-driven shifts in demersal fish thermal habitat in Iceland's waters. *ICES Journal of Marine Science*, *78*(10), 3793–3804. https://doi.org/10.1093/icesjms/fsab230

Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography*, *36*(10), 1058–1069. https://doi.org/10.1111/j.1600-0587.2013.07872.x

MFRI. (2022). *A new species of red algae discovered in Iceland*. Marine and Freshwater Research Institute. https://www.hafogvatn.is/en/about/news-announcements/a-new-species-of-red-algae-discovered-in-iceland

Molnar, J. L., Gamboa, R. L., Revenga, C., & Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, *6*(9), 485–492. https://doi.org/10.1890/070064

Moore, C., Lynch, D., Clarke, M., Officer, R., Mills, J., Defour, J. L., & Brophy, D. (2019). Age verification of north Atlantic sprat. *Fisheries Research*, *213*(May), 144–150.

Morais, P., & Teodósio, M. A. (2016). The transatlantic introduction of weakfish Cynoscion regalis (Bloch & Schneider, 1801) (Sciaenidae, Pisces) into Europe. *BioInvasions Records*, *5*(4), 259–265. https://doi.org/10.3391/bir.2016.5.4.11

Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., Van Vuuren, D. P., Carter, T. R., Emori, S., Kainuma, M., Kram, T., Meehl, G. A., Mitchell, J. F. B., Nakicenovic, N., Riahi, K., Smith, S. J., Stouffer, R. J., Thomson, A. M., Weyant, J. P., & Wilbanks, T. J. (2010). The next generation of scenarios for climate change research and assessment. *Nature*, *463*(7282), 747–756. https://doi.org/10.1038/nature08823

Muhling, B. A., Brodie, S., Smith, J. A., Tommasi, D., Gaitan, C. F., Hazen, E. L., Jacox, M. G., Auth, T. D., & Brodeur, R. D. (2020). Predictability of Species Distributions Deteriorates Under Novel Environmental Conditions in the California Current System. *Frontiers in Marine Science*, *7*(July), 1–22. https://doi.org/10.3389/fmars.2020.00589

Muscarella, R., Galante, P. J., Soley-Guardia, M., Boria, R. A., Kass, J. M., Uriarte, M., & Anderson, R. P. (2014). ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models . *Methods in Ecology and Evolution*, *5*(11), 1198–1205. https://doi.org/10.1111/2041-210x.12261

Muus, B. J., & Dahlstrøm, P. (1989). *Havfisk og Fiskeri i Nordvesteuropa*. GEC Gads Forlag.

Nabout, J. C., Caetano, J. M., Ferreira, R. B., Teixeira, I. R., & Alves, S. M. de F. (2012). Using correlative, mechanistic and hybrid niche models to predict the productivity and impact of global climate change on maize crop in Brazil. *Natureza a Conservacao*, *10*(2), 177–183. https://doi.org/10.4322/natcon.2012.034

Naimi, B., & Araújo, M. B. (2016). sdm : a reproducible and extensible R platform for species distribution modelling. *Ecography*, *39*, 368–375. https://doi.org/10.1111/ecog.01881

NASA. (2022). *Distance to the Nearest Coast*. Ocean Colour Web. https://oceancolor.gsfc.nasa.gov/docs/distfromcoast/

Nati, J. J. H., Svendsen, M. B. S., Marras, S., Killen, S. S., Steffensen, J. F., McKenzie, D. J., & Domenici, P. (2021). Intraspecific variation in thermal tolerance differs between tropical and temperate fishes. *Scientific Reports*, *11*(1), 1–8. https://doi.org/10.1038/s41598-021-00695-8

Nilsson, F., Thygesen, U. H., Lundgren, B., Nielsen, B. F., Nielsen, J. R., & Beyer, J. E. (2003). Vertical migration and dispersion of sprat (Sprattus sprattus) and herring (Clupea harengus) schools at dusk in the Baltic Sea. *Aquatic Living Resources*, *16*(3), 317–324. https://www.sciencedirect.com/science/article/abs/pii/S0990744003000391

O'Neill, B. C., Tebaldi, C., Van Vuuren, D. P., Eyring, V., Friedlingstein, P., Hurtt, G., Knutti, R., Kriegler, E., Lamarque, J. F., Lowe, J., Meehl, G. A., Moss, R., Riahi, K., & Sanderson, B. M. (2016). The Scenario Model Intercomparison Project (ScenarioMIP) for CMIP6. *Geoscientific Model Development*, *9*(9), 3461–3482. https://doi.org/10.5194/gmd-9-3461-2016

OBIS. (2022). *Sprattus sprattus (Linnaeus, 1758)*. Ocean Biodiversity Information System.

OECD. (2021). *Fisheries and Aquaculture in Iceland* (Issue January).

Ogle, D. H. (2009). The effect of freezing on the length and weight measurements of ruffe (Gymnocephalus cernuus). *Fisheries Research*, *99*, 244–247. https://doi.org/10.1016/j.fishres.2009.06.009

Oguz, T., Fach, B., & Salihoglu, B. (2008). Invasion dynamics of the alien ctenophore Mnemiopsis leidyi and its impact on anchovy collapse in the Black Sea. *Journal of Plankton Research*, *30*(12), 1385–1397. https://doi.org/10.1093/plankt/fbn094

Ojaveer, H., Lankov, A., Raid, T., Põllumäe, A., & Klais, R. (2018). Selecting for three copepods—feeding of sprat and herring in the Baltic Sea. *ICES Journal of Marine Science*, *75*(7), 2439–2449. https://doi.org/10.1093/icesjms/fsx249

Óskarsson, G. J. (2018). The existence and population connectivity of Icelandic spring-spawning herring over a 50-year collapse period. *ICES Journal of Marine Science*, *75*(6), 2025–2032. https://doi.org/10.1093/icesjms/fsy120

Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., & Folke, C. (2007). Human-induced trophic cascades and ecological regime shifts in the baltic sea. *Ecosystems*, *10*(6), 877–889. https://doi.org/10.1007/s10021-007-9069-0

Pálsson, J., Sigurðsson, G. M., Jónsdóttir, I. G., Jakobsdóttir, K., Hoad, N., Bogason, V., & Sólmundsson, J. (2022). Brislingur, Sprattus sprattus (Linnaeus, 1758), ný fisktegund við Íslandsstrendur. *Tímarit Hins Íslenska Náttúrufræðifélags*.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. (1998). Fishing down marine food webs. *Science*, *279*(5352), 860–863. https://doi.org/10.1126/science.279.5352.860

Peck, M. A., Baumann, H., Bernreuther, M., Jens-Peter, H., Haslob, Holger Huwer, B., Kanstinger, P., Köster, F. W., Petereit, C., Temming, A., & Voss, R. (2012). Reprint of: The ecophysiology of Sprattus sprattus in the Baltic and North Seas. *Progress in Oceanography*, *107*(31–46).

Pedersen, S. A., Storm, L., & Simonsen, C. S. (2002). Northern Shrimp (Pandalus borealis) Recruitment in West Greenland Waters Part I. Distribution of Pandalus Shrimp Larvae in Relation to Hydrography and Plankton. *Journal of Northwest Atlantic Fishery Science*, *30*, 19–46.

Perrette, M., Yool, A., Quartly, G. D., & Popova, E. E. (2011). Near-ubiquity of ice-edge blooms in the Arctic. *Biogeosciences*, *8*(2), 515–524. https://doi.org/10.5194/bg-8-515-2011

Perry, A. L., Low, P. J., Ellis, J. R., & Reynolds, J. D. (2005). Ecology: Climate change and distribution shifts in marine fishes. *Science*, *308*(5730), 1912–1915. https://doi.org/10.1126/science.1111322

Phillips, S. (2010). “A Brief Tutorial on Maxent” in Species Distribution Modeling for Educators and Practitioners. *Lessons in Conservation*, *3*, 107–135. http://ncep.amnh.org/linc

Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: an open-source release of Maxent. *Ecography*, *40*(7), 887–893. https://doi.org/10.1111/ecog.03049

Phillips, S. J., & Dudík, M. (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography*, *31*(2), 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, *19*(1), 181–197. https://doi.org/10.1890/07-2153.1

Phillips, S. J., Dudík, M., & Schapire., R. E. (n.d.). *Maxent software for modeling species niches and distributions (Version 3.4.1)*. American Museum of Natural History. Retrieved May 17, 2022, from http://biodiversityinformatics.amnh.org/open_source/maxent/

Phillips, S. J., Dudík, M., & Schapire, R. E. (2004). A maximum entropy approach to species distribution modeling. *Proceedings, Twenty-First International Conference on Machine Learning, ICML 2004*, 655–662. https://doi.org/10.1145/1015330.1015412

Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*(3 SPEC. ISS.), 273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

Plirú, A., Kooij, J. Van Der, Engelhard, G. H., Fox, C. J., Milligan, S. P., & Hunter, E. (2012). Sprat feeding behaviour, selective predation, and impact on plaice egg mortality. *ICES Journal of Marine Science*, *69*(6), 1019–1029.

Pörtner, H. O., Bock, C., & Mark, F. C. (2017). Oxygen- & capacity-limited thermal tolerance: Bridging ecology & physiology. *Journal of Experimental Biology*, *220*(15), 2685–2696. https://doi.org/10.1242/jeb.134585

Quintela, M., Kvamme, C., Bekkevold, D., Nash, R. D. M., Jansson, E., Sørvik, A. G., Taggart, J. B., Skaala, Ø., Dahle, G., & Glover, K. A. (2020). Genetic analysis redraws the management boundaries for the European sprat. *Evolutionary Applications*, *13*(8), 1906–1922. https://doi.org/10.1111/eva.12942

R Core Team. (2021). *A language and environment for statistical computing.* R Foundation for Statistical Computing.

Raab, K., Nagelkerke, L. A. J., Boerée, C., Rijnsdorp, A. D., Temming, A., & Dickey-Collas, M. (2012). Dietary overlap between the potential competitors herring, sprat and anchovy in the North Sea. *Marine Ecology Progress Series*, *470*(December), 101–111. https://doi.org/10.3354/meps09919

Radosavljevic, A., & Anderson, R. P. (2014). Making better Maxent models of species distributions: Complexity, overfitting and evaluation. *Journal of Biogeography*, *41*(4), 629–643. https://doi.org/10.1111/jbi.12227

Rantanen, M., Karpechko, A., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2021). The Arctic has warmed four times faster than the globe since 1980. *Nature Portfolio*, 0–29. https://www.researchsquare.com/article/rs-654081/latest.pdf%0Ahttps://doi.org/10.21203/rs.3.rs-654081/v1

Rhoden, C. M., Peterman, W. E., & Taylor, C. A. (2017). Maxent-directed field surveys identify new populations of narrowly endemic habitat specialists. *PeerJ*, *2017*(7), 1–21. https://doi.org/10.7717/peerj.3632

Robinson, N. M., Nelson, W. A., Costello, M. J., Sutherland, J. E., & Lundquist, C. J. (2017). A systematic review of marine-based Species Distribution Models (SDMs) with recommendations for best practice. *Frontiers in Marine Science*, *4*(DEC), 1–11. https://doi.org/10.3389/fmars.2017.00421

Rolls, R. J., Hayden, B., & Kahilainen, K. K. (2017). Conceptualising the interactive effects of climate change and biological invasions on subarctic freshwater fish. *Ecology and Evolution*, *7*(12), 4109–4128. https://doi.org/10.1002/ece3.2982

Saevaldsson, H., & Gunnlaugsson, S. B. (2015). The Icelandic pelagic sector and its development under an ITQ management system. *Marine Policy*, *61*, 207–215. https://doi.org/10.1016/j.marpol.2015.08.016

Sahri, A., Putra, M. I. H., Mustika, P. L. K., & Murk, A. J. (2020). A treasure from the past: Former sperm whale distribution in Indonesian waters unveiled using distribution models and historical whaling data. *Journal of Biogeography*, *47*(10), 2102–2116.

https://doi.org/10.1111/jbi.13931

Satilmis, H. H., Sumer, C., Ozdemir, S., & Bayrakli, B. (2014). Length-weight relationships of the three most abundant pelagic fish species caught by mid-water trawls and purse seine in the Black Sea. *Cahiers de Biologie Marine*, *55*(2), 259–265.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*(6856), 591–596. https://doi.org/10.1038/35098000

Schickele, A., Goberville, E., Leroy, B., Beaugrand, G., Hattab, T., Francour, P., & Raybaud, V. (2021). European small pelagic fish distribution under global change scenarios. *Fish and Fisheries*, *22*(1), 212–225. https://doi.org/10.1111/faf.12515

Schickele, A., Leroy, B., Beaugrand, G., Goberville, E., Hattab, T., Francour, P., & Raybaud, V. (2020). Modelling European small pelagic fish distribution: Methodological insights. *Ecological Modelling*, *416*(November 2019), 108902. https://doi.org/10.1016/j.ecolmodel.2019.108902

Serpetti, N., Baudron, A. R., Burrows, M. T., Payne, B. L., Helaouët, P., Fernandes, P. G., & Heymans, J. J. (2017). Impact of ocean warming on sustainable fisheries management informs the Ecosystem Approach to Fisheries. *Scientific Reports*, *7*(1), 1–15. https://doi.org/10.1038/s41598-017-13220-7

Shcheglovitova, M., & Anderson, R. P. (2013). Estimating optimal complexity for ecological niche models: A jackknife approach for species with small sample sizes. *Ecological Modelling*, *269*, 9–17. https://doi.org/10.1016/j.ecolmodel.2013.08.011

SIARC. (2022). *The Importance of Fishers*. Project SIARC. https://www.projectsiarc.com/working-with-fishers/

Sicre, M. A., Jacob, J., Ezat, U., Rousse, S., Kissel, C., Yiou, P., Eiríksson, J., Knudsen, K. L., Jansen, E., & Turon, J. L. (2008). Decadal variability of sea surface temperatures off North Iceland over the last 2000 years. *Earth and Planetary Science Letters*, *268*(1–2), 137–142. https://doi.org/10.1016/j.epsl.2008.01.011

Sigurdsson, T. . (2006). The Collapse of the Atlanto-Scandian Herring Fishery: Effects on the Icelandic Economy. *Portsmouth Proceedings*, *November*, 1–9. https://ir.library.oregonstate.edu/concern/conference_proceedings_or_journals/hm50ts95q

Silva, J. F., Ellis, J. R., & Ayers, R. A. (2013). *Length-weight relationships of marine fish collected from around the British Isles. Sci. Ser. Tech. Rep* (Issue January).

Solberg, I., Røstad, A., & Kaartvedt, S. (2015). Ecology of overwintering sprat (Sprattus sprattus). *Progress in Oceanography*, *138*, 116–135. https://doi.org/10.1016/j.pocean.2015.08.003

Soudijn, F. H., Daniël van Denderen, P., Heino, M., Dieckmann, U., & de Roos, A. M. (2021). Harvesting forage fish can prevent fishing-induced population collapses of large piscivorous fish. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(6), 1–8. https://doi.org/10.1073/pnas.1917079118

Streeter, R., Dugmore, A. J., Lawson, I. T., Erlendsson, E., & Edwards, K. J. (2015). The onset of the palaeoanthropocene in Iceland: Changes in complex natural systems. *Holocene*, *25*(10), 1662–1675. https://doi.org/10.1177/0959683615594468

Sveinbjörnsdóttir, A. E., Heinemeier, J., & Gudmundsson, G. (2004). 14C DATING OF THE SETTLEMENT OF ICELAND. *RADIOCARBON*, *46*(1), 387–394.

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, *93*(4), 485–498. https://doi.org/10.1175/BAMS-D-11-00094.1

Thorarinsdottir, G., Gunnarsson, K., & Gíslason, Ó. S. (2014). 6. Invasive Species. Case studies from Iceland. In *Marine invasive species in the Arctic* (Issue 547, pp. 83–109).

Thresher, R. E., & Kuris, A. M. (2004). Options for managing invasive marine species. *Biological Invasions*, *6*(3), 295–300. https://doi.org/10.1023/B:BINV.0000034598.28718.2e

Thurstan, R. H., Brockington, S., & Roberts, C. M. (2010). The effects of 118 years of industrial fishing on UK bottom trawl fisheries. *Nature Communications*, *1*(2), 1–6. https://doi.org/10.1038/ncomms1013

Thurstan, R. H., & Roberts, C. M. (2010). Ecological meltdown in the firth of clyde, Scotland: Two centuries of change in a coastal marine ecosystem. *PLoS ONE*, *5*(7). https://doi.org/10.1371/journal.pone.0011767

Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, *21*(2), 272–281. https://doi.org/10.1111/j.1466-8238.2011.00656.x

Valdimarsson, H., Astthorsson, O. S., & Palsson, J. (2012). Hydrographic variability in Icelandic waters during recent decades and related changes in distribution of some fish species. *ICES Journal of Marine Science*, *69*(5), 816–825. https://doi.org/10.1038/278097a0

Valdimarsson, H., & Malmberg, S.-A. (1999). Near-surface circulation in Icelandic waters derived from satellite tracked drifters Near-surface circulation in Icelandic waters derived from satellite tracked drifters. *Rit Fiskideildar*, *16*, 23–39.

Valtýsson, H., & Jonsson, S. (2018). Impacts of a Changing Climate on Icelandic Marine Stocks. In *Impacts of a Changing Environment on the Dynamics of High-latitude Fish and Fisheries* (Issue June). https://doi.org/10.4027/icedhlff.2018.01

Valtýsson, H. Þ. (2020). Fishing history of the world. In *Fisheries sciences – Value from the sea* (Issue December).

Velasco, J. A., & González-Salazar, C. (2019). Akaike information criterion should not be a "test" of geographical prediction accuracy in ecological niche modelling. *Ecological Informatics*, *51*(January), 25–32. https://doi.org/10.1016/j.ecoinf.2019.02.005

Veloz, S. D. (2009). Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography*, *36*(12), 2290–2299. https://doi.org/10.1111/j.1365-2699.2009.02174.x

Virgili, A., Racine, M., Authier, M., Monestiez, P., & Ridoux, V. (2017). Comparison of habitat models for scarcely detected species. *Ecological Modelling*, *346*, 88–98. https://doi.org/10.1016/j.ecolmodel.2016.12.013

Vitale, F., Mittermayer, F., Krischansson, B., Johansson, M., & Casini, M. (2015). Growth and maturity of sprat (Sprattus sprattus) in the Kattegat and Skagerrak, eastern North Sea. *Aquatic Living Resources*, *28*(2–4), 127–137. https://doi.org/10.1051/alr/2016007

Wagenmakers, E. J., & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin and Review*, *11*(1), 192–196. https://doi.org/10.3758/BF03206482

Wahl, E., & Alheit, J. (1988). Changes in Distribution and Abundance of Sprat Eggs During Spawning Season. *Journal of Chemical Information and Modeling*, *53*(9), 1689–1699.

Wanner, H., Brönnimann, S., Casty, C., Gyalistras, D., Luterbacher, J., Schmutz, C., Stephenson, D. B., & and Xoplaki, E. (2001). NORTH ATLANTIC OSCILLATION – CONCEPTS AND STUDIES Everyone living in Europe knows that different winters have different characterist- ics . For example , the winters between 1975 and 1995 were generally mild and there was little snow in Central Europe , w. *Surveys in Geophysics*, *22*(4), 321–382.

Warren, D. L., & Seifert, S. N. (2011). Ecological niche modeling in Maxent: The importance of model complexity and the performance of model selection criteria. *Ecological*

Applications, *21*(2), 335–342. https://doi.org/10.1890/10-1171.1

Wassmann, P., Duarte, C. M., Agustí, S., & Sejr, M. K. (2011). Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology*, *17*(2), 1235–1249. https://doi.org/10.1111/j.1365-2486.2010.02311.x

Watkins, H. V., Yan, H. F., Dunic, J. C., & Côté, I. M. (2021). Research biases create overrepresented "poster children" of marine invasion ecology. *Conservation Letters*, *March*, 1–12. https://doi.org/10.1111/conl.12802

Weydmann, A., Walczowski, W., Carstensen, J., & Kwaśniewski, S. (2018). Warming of Subarctic waters accelerates development of a key marine zooplankton Calanus finmarchicus. *Global Change Biology*, *24*(1), 172–183. https://doi.org/10.1111/gcb.13864

Whitehead, J. P. (1985). FAO species catalog vol.7 Clupeoid fishes of the world (Suborder Clupeoidei) Part 1 - Chirocentridae, Clupeidae and Pristigasteridae. *FAO Fisheries Synopsis No.125*, *7*(Part 1), 303 pp.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L. D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T. L., Miller, E., Bache, S. M., Müller, K., Ooms, J., Robinson, D., Seidel, D. P., Spinu, V., … Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, *4*(43), 1686.

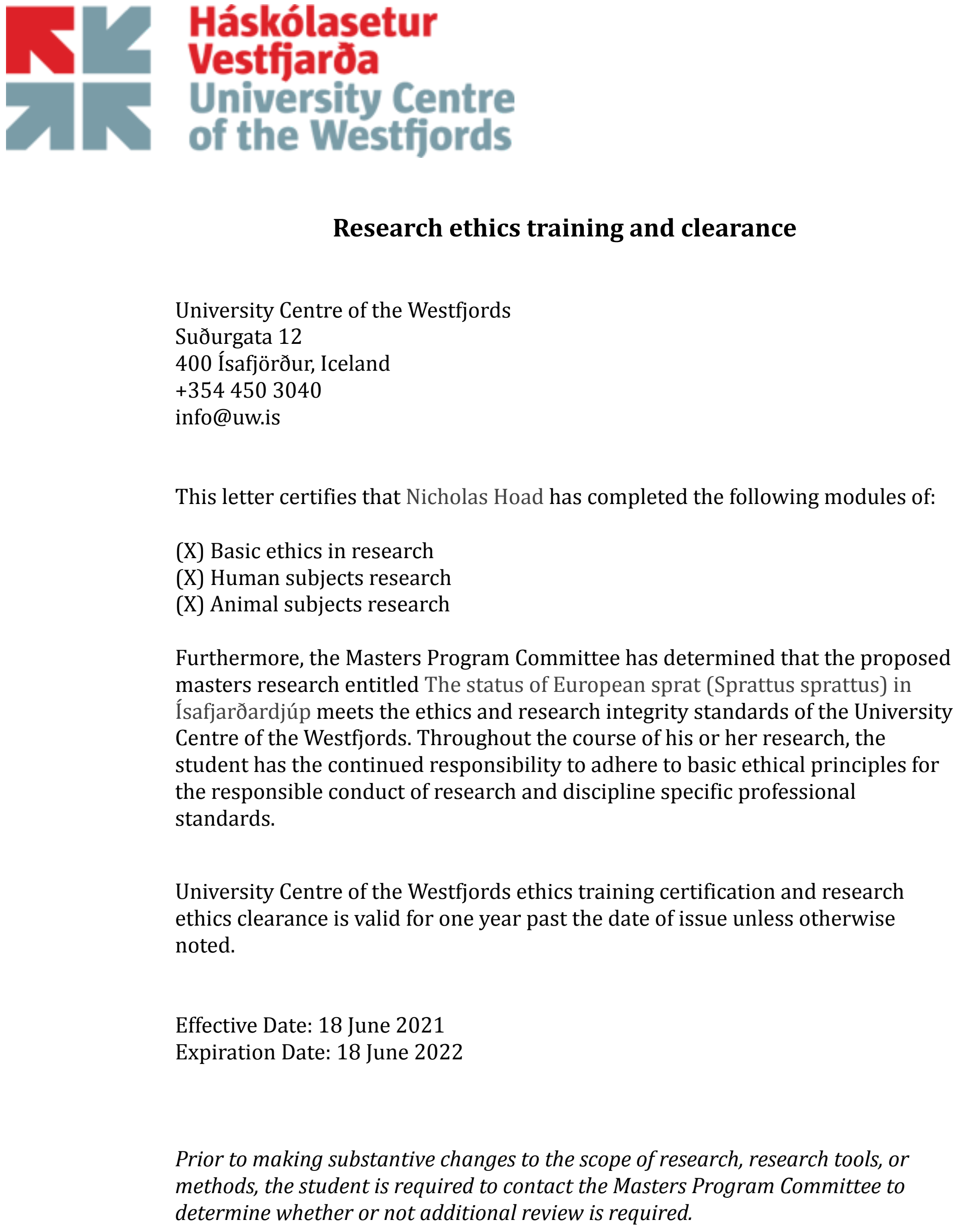
Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., Elith, J., Dudík, M., Ferrier, S., Huettmann, F., Leathwick, J. R., Lehmann, A., Lohmann, L., Loiselle, B. A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M. C., … Zimmermann, N. E. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions*, *14*(5), 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x

Wonham, M. J., Carlton, J. T., Ruiz, G. M., & Smith, L. D. (2000). Fish and ships: Relating dispersal frequency to success in biological invasions. *Marine Biology*, *136*(6), 1111–1121. https://doi.org/10.1007/s002270000303

World Climate Research Programme. (2021). *WCRP Coupled Model Intercomparison Project (CMIP)*. Www.Wcrp-Climate.Org. https://www.wcrp-climate.org/wgcm-cmip

Appendix A

Research and Ethics Training and Clearance Letter



Háskólasetur Vestfjarða
University Centre of the Westfjords

Research ethics training and clearance

University Centre of the Westfjords
Suðurgata 12
400 Ísafjörður, Iceland
+354 450 3040
info@uw.is

This letter certifies that Nicholas Hoad has completed the following modules of:

(X) Basic ethics in research
(X) Human subjects research
(X) Animal subjects research

Furthermore, the Masters Program Committee has determined that the proposed masters research entitled The status of European sprat (Sprattus sprattus) in Ísafjarðardjúp meets the ethics and research integrity standards of the University Centre of the Westfjords. Throughout the course of his or her research, the student has the continued responsibility to adhere to basic ethical principles for the responsible conduct of research and discipline specific professional standards.

University Centre of the Westfjords ethics training certification and research ethics clearance is valid for one year past the date of issue unless otherwise noted.

Effective Date: 18 June 2021
Expiration Date: 18 June 2022

Prior to making substantive changes to the scope of research, research tools, or methods, the student is required to contact the Masters Program Committee to determine whether or not additional review is required.

Appendix B

Sites in which sprat were identified from primary data collection along with month in which the site was surveyed.

Survey	Site	Number of sprat	Month	Cast latitude	Cast longitude	Haul latitude	Haul longitutde	Mipoint latitude	Midpoint longitude
B11-2021	1035	4	October	65.75	-23.37	65.76	-23.29	65.76	-23.33
B11-2021	1037	27	October	65.77	-23.23	65.75	-23.25	65.76	-23.24
B11-2021	1039	57	October	65.74	-23.30	65.74	-23.37	65.74	-23.33
B11-2021	1042	1	October	65.76	-23.46	65.75	-23.43	65.75	-23.44
B11-2021	1051	1	October	65.68	-23.50	65.71	-23.54	65.69	-23.52
B11-2021	1059	2	October	66.28	-22.81	66.27	-22.73	66.28	-22.77
B11-2021	1078	1	October	65.92	-22.41	65.90	-22.41	65.91	-22.41
B11-2021	1079	8	October	65.89	-22.41	65.86	-22.44	65.87	-22.42
B11-2021	1080	55	October	65.85	-22.45	65.82	-22.48	65.84	-22.47
B11-2021	1086	3	October	65.98	-22.41	66.00	-22.43	65.99	-22.42
B11-2021	1087	19	October	65.96	-22.47	65.96	-22.46	65.96	-22.46
B11-2021	1094	2	October	66.00	-22.54	65.96	-22.56	65.98	-22.55
B11-2021	1095	1	October	65.98	-22.56	65.98	-22.55	65.98	-22.55
B11-2021	1096	54	October	65.96	-22.54	65.97	-22.54	65.97	-22.54
B11-2021	1097	2	October	65.95	-22.46	65.95	-22.45	65.95	-22.45
B11-2021	1111	1	October	65.97	-22.89	65.97	-22.88	65.97	-22.88
B11-2021	1117	1	October	66.09	-22.76	66.10	-22.83	66.10	-22.79
B11-2021	1123	1	October	66.25	-23.20	66.28	-23.26	66.26	-23.23
IAPR-2021	3	9	April	65.97	-22.48	N/A	N/A	65.97	-22.48
IAPR-2021	4	4	April	65.99	-22.37	65.98	-22.49	65.98	-22.43
IAPR-2021	5	12	April	65.97	-22.47	65.97	-22.46	65.97	-22.47
IAPR-2021	6	29	April	65.99	-22.56	66.00	-22.54	65.99	-22.55
IJUL-2021	2	1	July	N/A	N/A	N/A	N/A	N/A	N/A
IJUN-2021	1	9	June	65.99	-22.44	N/A	N/A	65.99	-22.44
IMAI-2021	1	6	May	65.99	-22.44	N/A	N/A	65.99	-22.44
IRAE-2021	3	31	May	65.77	-23.22	N/A	N/A	65.77	-23.22
ISJ1-2022	1	9	Novembe	65.97	-22.42	N/A	N/A	65.97	-22.42
ISJ1-2022	6	2	February	65.89	-22.41	N/A	N/A	65.89	-22.41
ISJ1-2022	8	55	February	65.97	-22.43	66.01	-22.46	65.99	-22.45
ISJ1-2022	9	18	February	65.98	-22.41	66.00	-22.43	65.99	-22.42
ISJ1-2022	10	3	February	66.00	-22.48	65.99	-22.50	65.99	-22.49
ISJ1-2022	11	23	February	65.97	-22.48	65.96	-22.45	65.97	-22.46

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