Carl von Ossietzky

Universität Oldenburg

Masterstudiengang Biologie

MASTERARBEIT

Fin whale (*Balaenoptera physalus*) distribution modelling in the Nordic Seas & adjacent waters

Vorgelegt von Diandra Düngen

Externer Betreuer: Dr. Ahmed El-Gabbas

Betreuender Gutachter: Prof. Dr. Helmut Hillebrand

Zweiter Gutachter: Elke Burkhardt

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SUMMARY

Understanding the dynamics of cetacean distribution in ecologically vulnerable regions is essential to interpret the impact of environmental changes on species ecology and ecosystem functioning. Species distribution models (SDMs) are helpful tools linking species occurrences to environmental variables in order to predict a species' potential distribution. Studies on baleen whale distribution are comparably rare in polar regions, mainly due to financial or logistic constraints and habitat suitability models are scarce. Using SDMs, this master thesis aims at identifying areas of suitable habitats for fin whales (*Balaenoptera physalus*) in the Nordic Seas during summer. A further aim is to identify important environmental variables that potentially drive the species' distribution. Opportunistic data were collected during ten RV Polarstern cruises from 2007 to 2018 during summer months (May to September) along with complementary opportunistic data from open source databases. Environmental covariates were chosen based on ecological relevance to the species, comprising both static and dynamic variables. MaxEnt software was used to model fin whale distribution, with presence-only data as a function of carefully chosen environmental covariates. This master thesis is one of the first studies to use SDMs to model suitable habitats of fin whales in the Arctic Ocean and revealed a link of the occurrence of fin whales to specific environmental variables. Most contributing variables were distance to shore and distance to sea ice edge, suggesting both static and dynamic variables to have an impact on habitat suitability in the Arctic Ocean. Four other environmental variables, namely bathymetry, slope, variability of sea surface temperature and mean salinity at 100 m depth were shown to also have an impact. Areas of high suitability were pronounced around the southwestern and -eastern side of Svalbard, as well as on the northern tip of Norway and southern East Greenland. These results generally demonstrate the effective use of SDMs to predict species distribution in highly remote areas, constituting a cost-effective method for targeting future surveys and prioritizing the limited conservation resources. Results can be applied in a variety of purposes, such as designing marine protected areas, guiding seismic surveys and support the further use of opportunistic data in research.

ZUSAMMENFASSUNG

Die Dynamik der Verteilung von Walen, insbesondere innerhalb ökologisch sensibler Regionen, ist essentiell um Einfluss von Umweltveränderungen auf die Ökologie der Spezies zu verstehen. Artenverteilungsmodelle, im Folgenden Species Distribution Models (SDMs) genannt, sind hilfreiche um Umweltparameter und Artenaufkommen verknüpfen zu können. Dies geschieht um räumliche (oder zeitliche) Verteilungen einer Art darzustellen. Es gibt vergleichsweise wenige Studien, die sich mit Bartenwalen in den Polarregionen befassen. Dies ist haupstächlich auf finanzielle und/oder logistische Restriktionen zurückzuführen. Auch durch die SDMs produzierten, sogenannten Habitateignungs-Modelle (Habitat Suitability Models), sind in diesen Gebieten vergleichsweise selten. Diese Masterarbeit zielt darauf ab, unter Verwendung von SDMs, geeignete Habitate für Finnwale (*Balaenoptera physalus*) im arktischen Sommer zu erkennen. Ein weiteres Ziel ist es, wichtige Umweltparameter, die der Verteilung der Wale zugrunde liegen, zu identifizieren. Opportunistische Daten wurden während zehn wissenschaftlichen Expeditionen der RV Polarstern, von 2007 bis 2018, innerhalb der Sommermonate (Mai bis September) erhoben. Ergänzend dazu wurden opportunistische Daten von Open Source Datenbanken verwendet. Die Umweltparameter wurden bezüglich der ökologischen Relevanz der Art ausgewählt. Sie umfassen sowohl statische, als auch dynamische Variablen. Zur Modellierung der Finnwalverteilung wurde die Software MaxEnt gewählt, wobei aussschließlich Präsenzen als Funktion der ausgewählten Umweltparameter dienten. Diese Masterarbeit ist eine der ersten Studien, welche SDMs verwendet, um geeignete Habitate in der Arktis zu modellieren. Im Verlauf dieser Studie konnte ein Zusammenhang zwischen der Verteilung von Finnwalen und spezifischen Umweltparamentern hergestellt werden. Den größten Beitrag zur Verteilung der Finnwale steuerten hierbei die Distanz zur Küste, sowie die Distanz zur Eisgrenze bei. Vier weitere Umweltparameter, Bathymetrie, Hang, Abweichung der Wasseroberflächentemperatur, sowie die Salinität in einer Tiefe von 100 Metern, hatten ebenfalls Einfluss auf die Habitateignung. Besonders geeignete Gebiete fanden sich südwestlich bis -östlich vor Spitzbergen, an der nördlichen Spitze von Norwegen und dem südlichen Ost-Grönland. Die Ergebnisse demonstrieren den effektiven Gebrauch von SDMs, um Artenverteilung in abgelegenen Gebieten voraussagen zu können und stellen somit eine erschwingliche Methode für zukünftige Untersuchungen dar. Desweiteren können sie z.B. auf die Gestaltung von Meeresschutzgebieten, die Anleitung seismischer Untersuchungen oder der Förderung des weiteren Gebrauchs opportunistischer Daten in der Wissenschaft angewendet werden.

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1. INTRODUCTION

Many whales, including fin whales *(Balaenoptera physalus*), are known to occur in high numbers in the North Atlantic Arctic throughout summer months (Heide-Jørgensen et al. 2003, Heide-Jørgensen et al. 2007, Mikkelsen et al. 2007, Heide-Jørgensen et al. 2008, Heide-Jørgensen et al. 2010, Laidre et al. 2010, Storrie et al. 2018). Unfortunately, several centuries of commercial whaling have reduced many cetacean populations to a critical level (Clapham et al. 1999, Roman and Palumbi 2003). By now, some are still endangered, while others are close to extinction (Clapham et al. 1999, Kraus et al. 2005, Schipper et al. 2008). Immense changes in abundance and distribution of large whales due to extensive hunting had significant impacts on the environment as well (Hacquebord 1999, Kruse 2016). Many of the species are recovering, though this is happening during a time of rapid environmental change so that an establishment of new distributional patterns is possible (see Storrie et al. 2018 and references therein). Furthermore, ship strikes, and alterations of prey availability are potential drivers of an observed decline in fin whale abundance in some parts of the North Atlantic (Schleimer et al. 2019). The investigation of cetacean habitat use and underlying oceanographic factors therefore is of particular importance. Especially due to baleen whales specialized diets (e.g. blue whales (*Balaenoptera musculus*)) and foraging strategies (such as in minke (*Balaenoptera acutorostrata*) or humpback whales (*Megaptera novaeangliae*)), rorqual whales may have a lower capacity for adaptation (Hain et al. 1982, Lynas and Sylvestre 1988, Hoelzel et al. 1989, Weinrich et al. 1992). They could, therefore, be more vulnerable to anthropogenic change*s* in the marine environment than other species (Kovacs and Lydersen 2008). In that sense, it is important to understand the relationship between whales and their environment at various temporal and spatial scales to assess potential ecosystem-level effects in response to changing environmental conditions (Hátún et al. 2009).

1.1. The Nordic Seas Ecosystem

The Arctic is a Mediterranean Ocean, consisting mainly of the Arctic Ocean and the Nordic Seas. It covers the main parts of the Barents-, Greenland- and Norwegian Sea (Fig. 1).

1.1.1 The Nordic Seas

The Arctic Ocean is the northernmost part of the Arctic, while the Nordic Seas comprise the southward connecting Greenland-, Norwegian- and Iceland Seas (Loeng and Drinkwater 2007, Campos and Horn 2018). The Arctic Ocean and Nordic Seas are connected via Fram Strait and the Barents Sea (Fig. 1) (Ingvaldsen and Leong 2009, Campos and Horn 2018). The Barents Sea, covering most of the study area, is a shelf sea with high productivity, low biological diversity and strong species interactions (Wassmann et al. 2006). As largely enclosed ocean, only two water masses enter from other oceans, the cooler, low-salinity Pacific Water and the warmer, high-salinity Atlantic Water. The Arctic Front separates Arctic from Atlantic Water, while the more northwestward Polar Front separates Polar and Arctic Waters, being a mixture of Atlantic and Arctic Water (Loeng and Drinkwater 2007, Ingvaldsen and Loeng 2009).

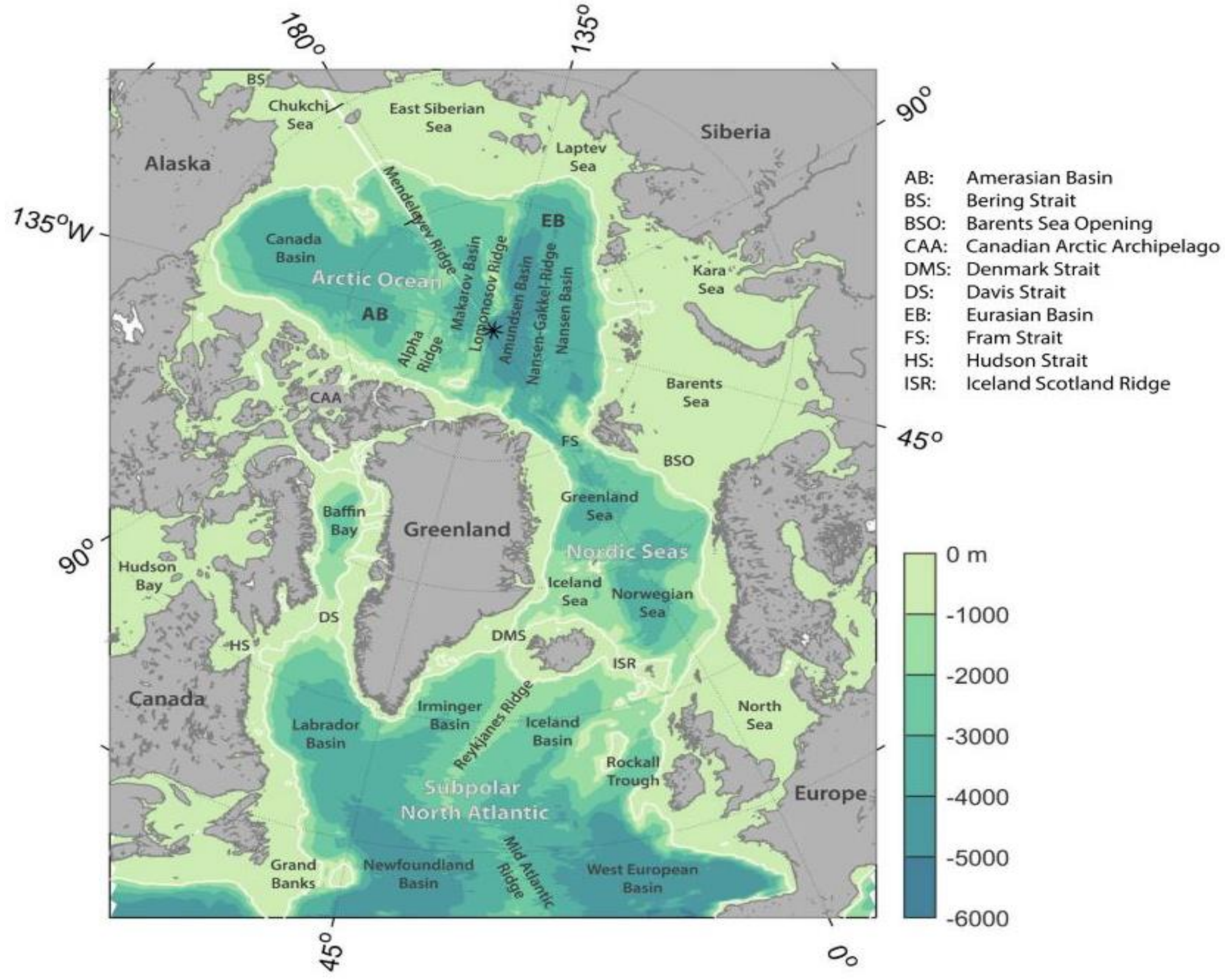

Fig. 1: Bathymetry of the Arctic Ocean and subpolar North Atlantic derived from the ETOPO2 database in 2-minute resolution. The white contour indicates the 500 m isobaths (Source: Horn 2018).

The Arctic has several unique physical characteristics amongst which are strong seasonality in light (large variations in light levels, with up to 24 hours of sunlight in summer and darkness in winter), cold overall temperatures with winter extremes, and the presence of extensive shelf seas around a deep central ocean basin (Loeng and Drinkwater 2007, Kovacs et al. 2011). Of particular importance is the accumulation of large biomass – total mean annual primary production rate is 80 to 90 g C / m^2 – either through seasonally restricted and intense blooms or by local accumulation of biomass through advection at the Arctic continental shelves (Loeng and Drinkwater 2007, Laidre et al. 2010). With the annual retreat of winter sea ice, an enormous phytoplankton bloom is triggered based on drastic increases in sunlight, which by retreat of the ice sheet reaches the sea surface. This results in high densities of zooplankton and lower trophic level foraging fish, which again attracts large numbers of top marine predators (Heide-Jørgensen et al. 2007). Seasonal sea ice in the Barents Sea typically forms in March / April (max. coverage) (Loeng and Drinkwater 2007). Main currents in the Arctic run eastwards across the southern part of the Barents Sea, while in the northern parts, they run westwards (Ingvaldsen and Leong 2009, Wekerle et al. 2017). The North Atlantic Current splits into two branches, one entering the Arctic Ocean through the Barents Sea (North Cape Current), the other through Fram Strait (West Spitsbergen Current) (Wekerle et al. 2017, Campus and Horn 2018).

1.1.2 Climate Change

Climate in the Arctic is highly dynamic, affecting many aspects of this ecosystem. The warming atmosphere supports an early sea ice melt during summer and inhibits sea ice formation during winter, which leads to an overall reduced sea ice coverage and thus a reduced albedo (Pistone et al. 2014). This consequently leads to an increase in absorption of solar radiation, which again provides extra heat to the ocean that can initiate sea ice melt from below (Horn 2018). Besides this positive feedback loop, sea ice retreating earlier in spring and advancing later in fall leads to longer summers (Laidre et al. 2015). In the Greenland- and Barents Sea (and many other parts of the Arctic), the time of fall sea ice is negatively correlated with the time of spring ice retreat (Laidre et al. 2015). The recent loss rate of Arctic sea ice is even faster than predicted by climate models (Stroeve et al. 2012), where summer sea ice extent has decreased by more than 40 % in recent decades (Overland and Wang 2013). Beyond that, sea ice loss is most likely to continue for several decades, even if emissions of greenhouse gases were limited immediately (Overland and Wang 2013).

Changes in temperature and decreasing sea ice coverage are expected to cause changes in productivity and energy cascades throughout the ecosystem (Parkinson et al. 1999, Heide-Jørgensen et al. 2007), eventually affecting cetaceans depending on this region (Derville et al. 2019). The decrease in sea ice coverage will most likely further increase anthropogenic activities in polar regions, as sea ice has previously been one of the limiting factors for accessing high latitudes (Gjosaeter et al. 2009). Already, anthropogenic activities have increased in West Greenland, including oil-, gas- and mineral exploration as well as tourism and whaling (Gjosaeter et al. 2009, Simon et al. 2010). This can affect fin whales, as they are the most commonly reported species to be involved in vessel collisions (Schleimer et al. 2019 and references therein).

1.1.3 Arctic Ecosystem

The Nordic Seas are home to a variety of species. Fish composition in the Norwegian Sea is dominated by pelagic species such as herring (*Clupea harengus*) and blue whiting (*Micromesistius poutassou*), whereas in the Barents Sea pelagic species (e.g. capelin, herring and Arctic cod (*Boreogadus saida*) and demersal species (like Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*)) occur (Loeng and Drinkwater, 2007). Zooplankton community is dominated by copepods, mainly *Calanus* spp., but other important zooplankters also exist, including amphipods (especially *Themisto* spp.) and euphausiids (e.g. *Thysanoessa spp.* in the Barents Sea and *Meganyctiphanes* spp. in the Norwegian Sea) (Melle et al. 2004). In the Norwegian Sea, Rey (2004) has provided a detailed description of the seasonal cycle of phytoplankton with low primary production in winter and early spring, and a homogeneous distribution of nutrients (Rey and Loeng 1985): Within this period, phytoplankton communities are mainly composed of small flagellates. When sea ice retreats in spring (March / April) and light levels and concentrations of nitrate increase, primary production is initiated. With the increase in stratification in May, diatom blooms develop. Chlorophyll levels tend to stay low due to zooplankton grazers and production decreases by summer. Due to wind mixing, small blooms still occur until autumn, though by October declining light levels finally limit primary production (Rey 2004). For the Barents Sea, processes seem to be similar, though time-lagged (Rey and Loeng 1985, Loeng and Drinkwater 2007). It is a home for a variety of resident marine mammal species, including polar bear (*Ursus maritimus*), seven pinniped- and five cetacean species (Kovacs et al. 2009). Additional to these residents, eight cetacean species migrate regularly to the Barents Sea (Kovacs et al. 2009).

Marine mammals in the Barents Sea display high diversity in distributional patterns: while some are associated with sea ice most of the year, others prefer pelagic, open waters (Kovacs et al. 2009). Then again, others are confined to the more temperate and shallow coastal waters (Kovacs et al. 2009). Arctic shelf regions are important to top marine predators, which are (seasonally) seeking abundant food resources in this region. Some marine mammals, such as ringed seals (*Phoca hispida*), Atlantic walrus (*Odobenus rosmarus rosmarus*) and polar bears rely on sea ice for several reasons and are, therefore, directly related to sea ice conditions (Weslawski et al. 1988, Jay and Fischbach 2008, Freitas et al. 2009). As a result, there is potential for dramatic ecosystem shifts given the observed reduction in sea ice coverage, ice thickness, extent, and duration, as well as changes in current patterns and temperature due to climate change (Carmack and Wassmann 2006). These physical changes alter biota in Arctic regions such as Svalbard, e.g. with boreal invertebrate and fish species displacing native Arctic species (Loeng and Drinkwater 2007, Fossheim et al. 2015, Dalpadado 2016, Gluchowska et al. 2016). Furthermore, the Arctic marine food web structure is altered by a general poleward shift of boreal generalists (Kortsch et al. 2015). The distribution of several fish species that are of importance for cetaceans such as the fin whale, is influenced by climate variability: e.g. cod, herring and blue whiting distribution shifts northward during extended warm periods and southward during cooler periods (Gjosaeter et al. 2009). The increase in primary (and secondary) production that goes hand in hand with climate change leads to an increased fish production through higher abundance and improved growing rates (Overholtz and Nicolas 1979, Payne et al. 1990, Loeng and Drinkwater 2007). During the past 30 years, substantial changes regarding prey sources have occurred in the Barents Sea, amongst others tremendous rises and falls of capelin and herring, the predominant pelagic shoaling fish in the area (Gjosaeter et al. 2009, Kovacs et al. 2009).

1.2. Mysticetes

The Mysticetes comprise three families: Balaenidae (the right whales), Eschrichtiidae (gray whales) and Balaenopteridae (rorqual whales). Each family employs a distinct feeding method of the type of suspension feeding and are specifically categorized as filter-, suction- or raptorial feeders (Werth 2000). Fin whales belong to the family Balaenopteridae. Compared to their body size, balaenopterids are rather shallow divers (Gaskin 1982, Hamilton et al. 1997, Panigada et al. 1999).

They grow up to 30 meters in length, with the up to 24 m fin whale being the second largest and fastest cetacean (Katona et al. 1993). In order to feed effectively, rorqual whales engulf large quantities of dense food patches - a method that is called gulping or ram filter-feeding (Bowen and Siniff 1999, Werth 2000, Kimura 2004). They filter prey out of the water using baleen, which are attached to the upper jaw (Wells et al. 1999). These vary in length, thickness and narrowness according to species. The anatomy features a fusiform body, with parallel running ventral throat grooves and a muscular, specialized tongue that enables gulping large quantities of prey (Lambertsen 1983, Orton and Brodie 1987, Hoelzel et al. 1989, Bowen and Siniff 1999). Prey abundant water masses are engulfed through rapid gulps and lunges after which the water is expelled while prey is held back by the baleen (Bowen and Siniff 1999, Werth 2000). Seasonal and annual variations in prey densities seem to play an important role in the aggregation of baleen whales and their foraging profitability (Piatt and Methven, 1992), as feeding is thought to be restricted to seasons and usually latitude-dependent (Clapham 2000, Stern 2009). Despite this, recent observations suggest that Mysticetes also forage during migration (Geijer et al. 2016 and references therein, Owen et al. 2017). Silva et al. (2019) provide strong hints that North Atlantic fin whales, migrating through central Atlantic waters, feed during winter or early spring in tropical and subtropical waters and that this strategy is more prevalent among migratory whales than is currently acknowledged. Further, feeding in winter appears common among the North Atlantic fin whales and may play a crucial role in determining their winter distribution (Silva et al. 2019). Mysticetes feed on comparatively small prey, hence they need to address high densities of prey: It has been estimated that 1–2 tons of zooplankton per day has to be ingested in order to meet energetic requirements (Kenney et al. 1986). Prey densities above a certain threshold are thought to be required to facilitate efficient foraging (Piatt and Methven 1992). Within feeding grounds, their high mobility allows the active search for the most food abundant areas and/or the highest prey patch densities (Wells et al. 1999).

1.2.1 Fin whales

Fin whales are the fastest swimmers among all whales and are believed to be the deepest diving species of all Mysticetes (Bérubé and Aguilar 1998, Panigada et al. 1999). Morphologically striking features include the asymmetric coloration of the head, dark coloration on the left anterior third of the body and baleen, and white coloration on the right lower jaw.

The right anterior part of the body is less heavily pigmented than the left part (Tershy and Wiley 1992, Aguilar 2009). Group sizes can vary, though usually fin whales occur singly or in pairs (Edds and Macfarlane 1987). Fin whales are considered opportunistic feeders, foraging on krill and pelagic fish, potentially varying preferences according to prey availability (see Table 1 for details). However, considerable variations in feeding activity were found~~,~~ depending on locality, time of the season, and prey species (Nemoto 1957, 1959).

Table 1: Prey sources of fin whales in different parts of the Nordic Seas

Region	Prey Items	Source
North Atlantic	Sand lance (*Ammodytes americanus*), capelin and krill	Overholtz and Nicolas 1979
Iceland and adjacent waters	Krill (*Meganyctiphanes norvegica*), capelin, sand eel (*Ammodytes* spp.), blue whiting	Rörvik et al. 1986, Sigurjónsson and Víkingsson 1997
Antarctic	Mature krill (*Euphausia superba*)	Santora et al. 2010
Barents Sea	Krill, amphipods (*Themisto* spp.), Arctic cod, blue whiting	Skern-Mauritzen et al. 2011
Norwegian Sea	Krill, amphipods, herring, blue whiting, capelin	Nottestad et al. 2014 (and references therein)

Fin whales utilize an energetically expensive strategy of lunge feeding at depth upon encounters with suitable densities of prey (Croll et al. 2001, Acevedo-Gutierrez et al. 2002, Simard et al. 2002, Croll et al. 2005, Goldbogen et al. 2006, 2007). There might be two scale-dependent foraging strategies of fin whales in summer: the large-scale site fidelity for the persistent area of krill habitat or, at the mesoscale, the search for the most concentrated food areas characterized by high dynamics of oceanographic processes (Cotté et al. 2009). Fin whales are thought to feed in depths of 100 to 200 meters (Katona et al. 1993) and are known to regularly return to traditional feeding grounds over many years, though winter breeding grounds have not been identified yet (Aguilar 2009). Observations of fin whales together with high prey densities support conclusions from previous satellite tracking studies that fin whales move into high latitudes to feed (Heide Jørgensen et al. 2003), which is consistent with prior findings (Stevick et al. 2008). There has been evidence that some individuals stay throughout December (Heide-Jørgensen et al. 2003, Simon 2010) rather than only visiting in summer.

In the Barents Sea, fin whales were shown to inhabit southern areas in early summer but not later in the season, clearly demonstrating a seasonal shift in their distribution (Haug et al. 2002, Skern-Mauritzen et al. 2011). Further findings suggest changes in body fattening in Icelandic waters, potentially related to food availability (Lockyer 1986). Several environmental factors have been put into context with the occurrence of fin whales, including primary productivity, bathymetry, sea surface temperature and sea surface height (Forcada et al. 1996, Littaye 2004, Sirovic et al. 2004, Laran and Gannier 2008, Panigada et al. 2008, Sirovic et al. 2009, Stafford et al. 2009, Azzellino et al. 2012, Druon et al. 2012, Breen et al. 2016, Zerbini et al. 2016, Prieto et al. 2017). Recently, Iceland established a new, increased catch quota for fin whales, which has been set to 209 individuals and may pose a risk to these stocks[1]. Despite the initial recovery from historical whaling, models predict considerable declines in Atlantic fin whale stocks, as well as local extinctions by 2100 (Tulloch et al. 2018, 2019). Stocks of fin whales in Arctic waters are not comprehensively calculated, though a considerable amount of studies exists on stocks of different parts of the study area, amongst which there are Iceland, Norway and Jan Mayen, as well as Greenland and the Faroes (Pike et al. 2005, Vikingsson et al. 2009, Vikingsson et al. 2015). There seem to be at least 25,000 to 30,000 fin whales in the North Atlantic (Kovacs et al. 2009). It has been reported that the number of fin whales in the North Atlantic has steadily increased in the past years and potentially has already recovered by 2000, though it is unclear if this is due to recovery from past whaling or favorable environmental changes (Víkingsson et al. 2015). Fin whales, like many other cetaceans, cover a wide range on foraging grounds, as their distribution is predominantly governed by prey availability (Kovacs et al. 2009). As the impact of climate change on fin whales will likely occur via changes to their prey, it is important to monitor and model their distribution in the study area to guide appropriate conservational measures. It has been hypothesized that, as marine productivity increases with the progressing loss of seasonal sea ice cover, a northward spread of cetacean species from more temperate waters to Svalbard and the northern Barents Sea can be expected, as has been shown for grey whales (Moore et al. 2003, Kovacs et al. 2009). Changes in fish, benthos and primary production in the study area have already been detected and described (Moore et al. 2003, Overland et al. 2004, Qu et al. 2006, Arrigo et al. 2008).

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[1] www.phys.org/news/2019-02-iceland-whaling-quotas-falling-profits.html

1.3. Species Distribution Modelling

One major challenge to predict patterns of species occurrence is to identify mechanisms leading to the presence of a species in a specific spatial and temporal dimension (Verity et al. 2002). Species distribution modelling (SDM), also known as environmental niche modelling (ENM), can be a helpful tool that links the occurrence of certain species to environmental variables and then provides insight into potential species' distribution. SDMs are statistical tools that estimate the relationship between species occurrences at field sites and the environmental characteristics of those sites (Franklin 2010). This is especially helpful in remote and limited-access areas, such as the polar oceans. One of the approaches commonly used to describe habitat requirements of a species, is by fitting niche- or distribution models and to use these to identify the potential distribution of the respective species by projecting onto geographical space (Robinson et al. 2011, Tyberghein et al. 2012). There are different approaches to model species distribution, including correlative (Pearson and Dawson 2003), coupled correlative and process-based models (Smolik et al. 2010), as well as mechanistic approaches (Kearney and Porter 2009). Correlative SDMs relate species occurrence data (presence-only or presence-absence) with environmental data of a specific area to explain and predict the species' distribution. In contrast, mechanistic approaches use the physiological characteristic of a species to determine the range of environmental conditions within which the species can persist (Kearney and Porter 2009). Both approaches comprise the Grinnellian understanding of "environmental niche", assuming the observed distribution of a species to be governed by its abiotic preferences, food requirements and/or microhabitat characteristics (Grinnell 1904). These approaches also vary in the kind of required data. In surveys, where sites are systematically researched and presence-absence or abundance of species is recorded, regression methods and their extensions, such as generalized linear models (GLMs), generalized additive models (GAMs) or regression trees may be used (Elith et al. 2011). For many regions though, such systematic surveys are not applicable, and accurate absence or abundance data cannot be obtained. Depending on the species, absences are not easily determined (Wintle et al. 2015). In such cases, species occurrence data are often available in the form of opportunistic presence-only records in museum databases and online repositories (e.g. GBIF or PANGAEA)[2] (Elith et al. 2011). Advantages of presence-only (or presence-background) records are the relatively easy accessibility compared to presence-absence or abundance data (Elith et al. 2006).

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[2] https://www.pangaea.de/, https://www.gbif.org/

Intent and methods of presence-only data are often unknown though, leading to potential biases (Hijmans et al. 2000, Reese et al. 2005, Elith et al. 2006). Due to sampling design, taking account of potential bias is important. Here, duplicates were removed in order to avoid spatial sampling bias (Fourcade et al. 2012, El-Gabbas and Dormann 2018). Presence-only models are commonly implemented in terrestrial habitats, where their use has gained much intension over past years, whereas SDMs of marine species are comparatively rare, though interest in their application has increased (Redfern et al. 2006, Valavanis et al. 2008, Robinson et al. 2011). Potentially, the comparably easy access to satellite data, which are often the basis of environmental data, lead to an increased use of SDMs (Palialexis et al. 2011). Many novel modelling methods have been proposed to be applied to marine species (see Palialexis et al. 2011 and references therein). A few methods that use presence-only data exist, amongst which there is MaxEnt (Phillips et al. 2006, Phillips and Dudik 2008). MaxEnt estimates the most uniform distribution of the species, by contrasting the sampling points against many background locations randomly sampled from the study area, with implementation of some constraints (Phillips et al. 2004, Phillips et al. 2006). It takes a list of species presences (locations) as input, as well as a set of environmental variables (e.g. salinity or temperature) across a user-defined geographical space, which is divided into grid cells. MaxEnt extracts a sample of background locations (where presences are unknown), which then are contrasted against the presence locations (Merow et al. 2013). The probability distribution of the species is estimated in terms of maximum entropy, which is the distribution that is closest to uniform across the study area (Phillips et al. 2006). Environmental variables (or predictor variables or covariates; hereafter: "EVs") are independent factors that can describe niche requirements of a species can be relevant to habitat suitability (e.g. temperature, bathymetry). The selection of environmental variables is based on *a priori* knowledge of the important ecological drivers of the focal species (Austin 2007). Often, the final choice of environmental variables is governed by their availability~~,~~ and collinearity (Bombosch 2013, Zeng et al. 2016). Collinearity often leads to overfitted models, so good practise is to remove correlated variables in the modeling process (Zuur et al. 2010). Since becoming available in 2004, the use of MaxEnt has grown extensively for modelling species distributions (Elith et al. 2011) and it became open source in 2017 (Phillips et al. 2017). It has become a popular tool for studying species distribution, because it is user-friendly, while at the same time its predictive performance is consistently competitive with the highest performing methods and even outperforms other methods in predictive accuracy (Elith et al. 2006, Merow et al. 2013).

According to Austin (2002), it is desirable to fit nonlinear functions, as species responses to environmental variables tend to be complex. This can be achieved by applying transformations of the environmental covariates, which are called features in Maxent (Elith et al. 2011, Merow 2013). MaxEnt's feature classes (FC) are linear (L), product (P), quadratic (Q), hinge (H), threshold (T), and categorical. According to Merow (2013) the definition of each feature class can be depicted as follows: 'Linear' represents the original EVs and constrains their mean, while 'quadratic' additionally constrains the variance of the environmental variables. 'Product' works as an interaction between pair wise combinations of EVs, where the covariances are constrained, when 'linear' is also used. 'Threshold' works as a step function, which is produced between each successive pair of data points. 'Hinge' works similar as 'threshold', though linear above the threshold value (Merow 2013). The FCs role reflects in the response curves, which plot the predicted relative occurrence rate against the values of a particular EV, thereby providing an important tool for evaluation (Merow et al. 2013). Response curves further aid in visualizing the model output and importance of environmental variables. To be concrete, they show the relationship between the occurrence habitat suitability and the EV. For each plot, the response is modelled for one EV, while the other EVs are held constant at their mean values at training presences[3]. By default, MaxEnt uses the number of presences to determine which feature classes to use, while more presences allow more features. An input of > 80 presences leads to all feature classes being used (Merow et al. 2013). This leads to limitations, though the user can also specify the feature classes manually (Merow et al. 2013).

Model performance can be assessed in several ways, amongst which are the value of the area under the receiver operating characteristic (ROC) curve (AUC). As a statistic assessment method for the discriminatory capacity of SDMs it is widely used (Jiménez-Valverde 2011). The AUC value enables the evaluation of model performance (Jiménez-Valverde 2011). In SDMs with presence-absence data, a value of 0.5 indicates that the model does not perform better than random, while a value closer to 1.0 indicates good model performance (Jiménez-Valverde 2011). When used without absences, the ROC plot is modified (see Jiménez-Valverde 2011 and references therein), models may still be assessed according to their AUC, in general the higher the better (Phillips et al. 2006). When the potential distribution of a species is the goal of the study, the AUC was suggested being a rather inappropriate performance measure, as weight of commission errors is

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[3] https://support.bccvl.org.au/support/solutions/articles/6000127046-interpretation-of-model-outputs

much lower than that of omission errors (Jiménez-Valverde 2011). Cross-validation is another method to evaluate the predictive performance of models, especially in situations in which an independent evaluation dataset is not available. Data can be partitioned into k folds, using one fold for testing and remaining folds (k-1) for fitting the model (Valavi et al. 2018 and references therein). This process is iterated until all folds were used for testing. However, non-spatial cross-validation does not ensure the spatial independence between training and testing dataset: training and dataset can be very close to each other (Dr. Ahmed El-Gabbas, personal communication). Concerning this matter, an attractive evaluation method is spatial block cross-validation, which enables spatially independent model evaluation (Valavi et al. 2018). Spatial blocks are geographical units, in which species and environmental data are treated together either for model training or testing (Fig. 2). Several blocks may be allocated to one cross-validation fold (Valavi et al. 2018). Spatial block cross-validation further enables accounting for spatial autocorrelation. As spatial autocorrelation is a measurement of correlation of observations between nearby locations and can negatively impact the model output, it is important to account for it (Moran 1950, Valavi et al. 2018).

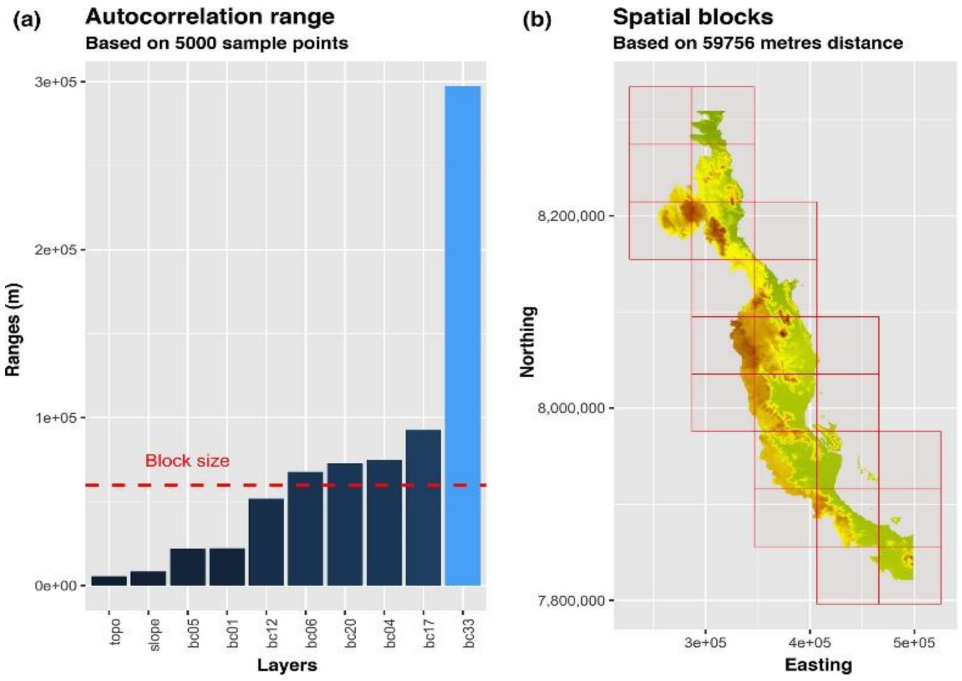

Fig. 2: (a) Exemplary spatial autocorrelation ranges of the environmental variables and (b) corresponding spatial blocks (Source: Valavi et al. 2018).

MaxEnt provides tools to assess the relative importance of environmental variables used to train the model, including Jackknifing and permutation importance (PI). Jackknifing is used to assess the relative importance of each EV by fitting two sets of models: 1) models run using all environmental variables, except each environmental variable in turn; 2) models run exclusively using each of the variables alone (Brown 2004, Robinson et al. 2011). Comparing AUC / training gain values amongst these two sets of models indicates variable importance. Values based on models run with a single environmental variable ("with only variable") indicate the predictive power/model performance of using this variable, whereas values for models run without this variable ("without variable") indicate its relative importance. To calculate permutation importance, MaxEnt iteratively shuffles values of each environmental variable at presence and background locations, then models are re-run and re-evaluated. Changes in training AUC, compared to the AUC of the original model, is used to indicate the relative importance of each EV. A decrease in AUC indicates the higher relative importance of the variable, while an increased AUC indicates that the variable is rather unimportant (Phillips et al. 2006).

1.4. Aim of the thesis

In past years, SDMs have become a popular tool for studying the spatial distribution patterns and ecology of animal and plant species (Elith et al. 2006, Redfern et al. 2006, Dormann et al. 2010 & 2011), while studies on marine species are increasing (Kaschner et al. 2006, Reiss et al. 2011, Bombosch et al. 2014, Schleimer et al. 2019). To guide conservation actions effectively, using SDMs has been recommended (Guisan et al. 2013), e.g. for monitoring biological invasions, identification of critical habitats for endangered species and more (Borja et al. 2014). This master thesis aims at identifying areas of suitable fin whale habitats in the Nordic Seas summer, by singling out which environmental variables are driving its observed distribution. Comparably few species distribution studies include data from polar regions (e.g. Zerbini et al. 2006, Bombosch et al. 2014, Nottestad et al. 2014, Zerbini et al. 2016, Prieto et al. 2017, Storrie et al. 2018) and this is one of the first studies to use SDMs to model suitable habitats of fin whales in the Arctic Ocean. By using SDMs, I will point out which areas, other than observed, might be suitable for fin whales, discuss underlying potential reasons and evaluate how potential threats can influence the distribution of fin whales in the Arctic. I further emphasize important environmental variables that potentially drive the distribution of the species or at least are important for habitat suitability.

2. MATERIAL AND METHODS

2.1. Study Area

The study area encompasses the Nordic Seas with a spatial extent from N60° to N81° and W45° to E55°, covering main parts of the Greenland-, Norwegian- and the Barents Sea (Fig. 1). The Baltic Sea was left out of the analysis, as fin whales are not native to these waters and the ecosystem differs significantly from the rest of the study area (see Fig. 3). The study area was mainly determined by inspecting fin whale distributional data available (see below), with a buffering area around available sightings. Models were calibrated at an equal-area projection, as if covariate grids were unprojected, a region covering a larger range in latitude of e.g. > 200 km, would have grid cells of varying areas (Elith et al. 2011). This happens especially away from the equator and must be avoided as MaxEnt implicitly assumes equal area cells, when randomly sampling cells (Elith et al. 2011). Optimum projection for the study area was determined using the project wizard tool (Savric et al. 2016)[4]: Polar Lambert azimuthal equal-area projection WGS 1984: EPSG 8326 with a central meridian of 005º 00' E. I used a grid cell size of 100 km^2 (10 x 10 km) to run the models due the large size of the study area. Further, this resolution seems to be suitable for the high mobility of the species. Land area and the Baltic Sea were masked out from study area, yielding a total of 51595 cells (area in blue in Fig. 3). All species occurrences and EVs were identically projected.

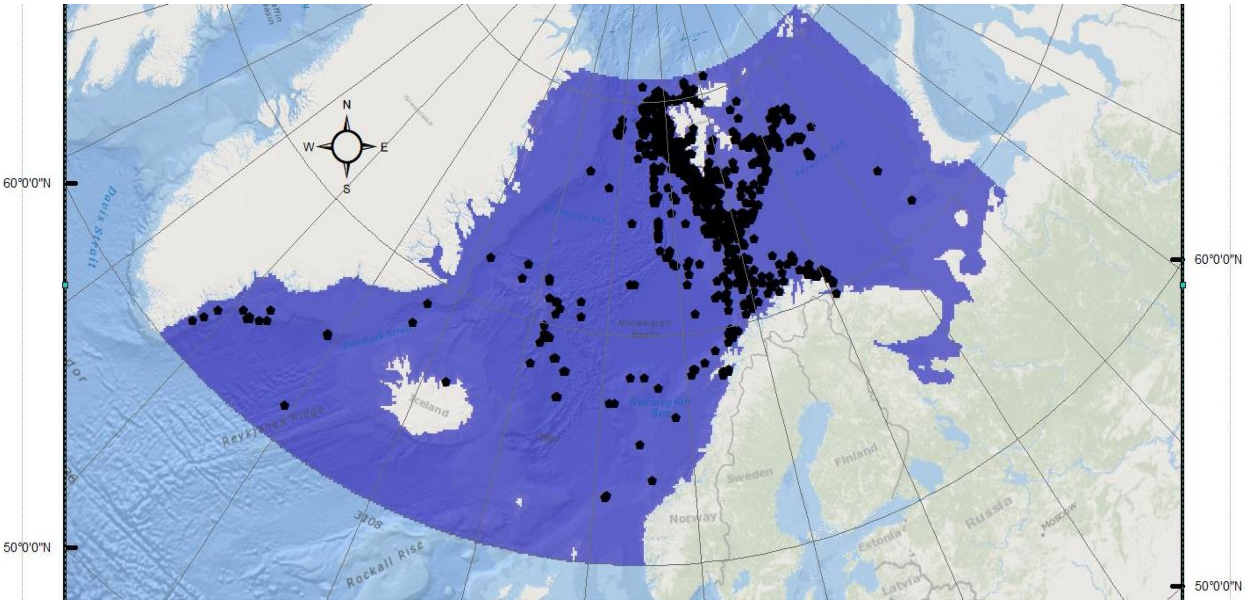

Fig. 3: The study area, covering N60° - N81° and W45° - E55°, including Svalbard and Iceland

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[4] http://projectionwizard.org

2.2. Data and Sampling Design

Opportunistic sightings were collected from available data sources: RV Polarstern cruises[5] (unpublished), GBIF (Global Biodiversity Information Facility)[6] and iOBIS (Ocean Biogeographic Information System)[7]. Only occurrences between 2004 and 2018 and from an extended definition of summer (May to September) were selected, as summer is the main feeding season of fin whales in the region. Yearly time span was determined according to availability of the Polarstern sighting data. Polarstern data were collected from 27 multidisciplinary research cruises to the Arctic from 2007 to 2018, but with an intermission in data acquisition between 2009 and 2011. Identification of cetaceans was conducted by several nautical officers, and sightings with date and group size were recorded systematically and electronically using 'WALOG software' developed by AWI (WALOG vers. 1.3) (Burkhardt 2009). Species were identified to the lowest taxonomic level possible (ranging from species level to "unidentified whale"), associated with a certainty level of identification. Occurrence position was recorded as the position of the vessel at the time of observation. Sightings are considered opportunistic, as no dedicated sighting effort was taken, and no dedicated survey design was implemented. The GBIF data were downloaded from the GBIF website at the desired time span (months/years) and study area extent. Similarly, the iOBIS data were downloaded using *robis* R-package (Provoost and Bosch 2019). Before running models, sighting data were plotted and occurrences outside of the study area or erroneous (e.g. on land) were removed. After thorough quality control, a total of 1,229 unique sightings remained.

2.3. Environmental Variables

Potential environmental variables were determined based on their ecological relevance for fin whales and their availability (Woodley and Gaskin 1996, Panigada et al. 2008, Druon et al. 2012, Duengen et al. 2018). Initial dynamic variables encompass chlorophyll-a concentration (mean and standard deviation 'sd'), temperature and salinity at surface and 100 m depth (mean and sd), sea ice concentration (mean and sd), and velocity & sea surface height (mean and sd). Mean and sd represents per grid cell statistically calculated values for the period from 2004 to 2018 and from May to September, when possible (see Table 2 for details).

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[5] https://www.pangaea.de/expeditions/cr.php/Polarstern

[6] www.gbif.org; access date: 01/30/2019

[7] https://obis.org; access date: 07/09/2019

Static environmental variables include bathymetry, slope, aspect and distance to shore, sea ice edge and isobaths (100 m, 200 m and 500 m). In total, 24 environmental layers were prepared at a consistent projection, extent and resolution to be ready to be used by MaxEnt, using ArcGIS (ArcMap 10.6.1, ESRI), QGIS (Version 3.4.5, QGIS Development Team) and R (R Development Core Team 2008). Environmental layers were projected into an equal area projection of Polar Lambert azimuthal equal-area proj.4 of WGS 1984: EPSG 8326 with a central meridian of 005º 00' E (Budic et al. 2015), using *spTransform* function of raster R-package (Hijmans 2019). For dynamic EVs, standard deviation and climatological mean were calculated for five months (May to September) over the respective (available) amount of years. While for sea ice concentration there was a data gap between May and June 2012, averaged sea ice data for 2012 was based upon July to September data only. Values of grid cells with missing environmental data were interpolated using "Kriging" tool in ArcGIS. Layers were first transformed into points "Raster to Points", then kriging was implemented with a search radius range between 60,000 and 400,000 m, using a minimum of eight points. Distance to isobaths and shore were calculated using the "Contour" and "Near" tools in ArcGIS, based on bathymetry. In the settings, the default method "planar" was selected. For the distance to sea ice edge, the ice edge was determined as the major polygon that encompass grid cells with >15% sea ice concentration (Meier and Stroeve 2008 and references therein, Spreen et al. 2008). Values for grid cells intersected with the ice edge line were assigned 0, while grid cells with sea ice concentration < 15% (outside the ice edge) were assigned positive values and grid cells with sea ice concentration > 15% (inside the ice edge) were assigned negative values (Williams et al. 2014). Some grid cells close to land had conspicuous sea ice concentration values, which is termed "land-spillover" or "land contamination of water pixels" (Dr Marcus Huntemann, personal communication, Markus and Cavalieri 2009). To avoid the influence of spurious value of sea ice close to land, a buffer of two grid cells was applied and values at these grid cells were re-estimated using Kriging. Many of the static variables were obtained from the general bathymetric chart of the oceans (GEBCO)[8], which provides publicly available bathymetry data of the world's oceans. Temperature and salinity data were obtained by the world ocean atlas (WOA) A5B7[7] dataset (Boyer et al. 2018). A5B7 refers to the time span 2005 – 2017 and includes a global coverage of Argo floats from 2005. Chlorophyll-a data were obtained from Ocean Color CCI[5] (Sathyendranath et al. 2018).

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[8] https://www.gebco.net/

Table 2: Covariates, source and time frame of raw data, * indicates temporal resolution, ** spatial resolution

Covariate	**Unit**	**Statistic**	**Time Frame**	**Resolution**	**Source**
Aspect	°			30-arc-sec**	GEBCO[8]
Bathymetry	M			30-arc-sec**	GEBCO[8]
Chlorophyll a	mg / m^3	sd	2004 – 2018	8-day composite*	OCCI[9]
Distance to SIE	Km		2004 – 2018	6.25 km**	AMSR2[10] calculation
Distance to Shore	Km			30-arc-sec**	GEBCO[8]
Distance to Isobath 500	Km			30-arc-sec**	GEBCO[8]
Salinity (0, 100 m)	unitless	mean, sd	2005 – 2017	0.25 x 0.25°**	WOA A5B7[12]
Sea Ice Concentration	%	mean	2004 – 2018	6.25 km**	AMSR2
Sea Surface Height	M	sd	2004 – 2018	0.25 x 0.25°**	COPERNICUS[11]
Slope	°			30-arc-sec**	GEBCO[8]
Temperature (0, 100 m)	°C	sd	2005 – 2017	0.25 x 0.25°**	WOA A5B7[12]
Velocity	m/s	mean	2004 – 2018	0.25 x 0.25°**	COPERNICUS[6], calculation

Box-Cox Transformations

To maximize uniformity and obtain normal distribution of variables, potential variable transformations were checked using box-cox transformations (Box and Cox 1964), following Dormann and Kaschner (2010). Accepted transformations that have improved the distribution of variables were distance to 500 m isobath, sea surface salinity (sd), sea surface height (sd), temperature at 100 m depth (sd) and velocity (mean) (Table 3). Transformations of other variables did not improve their distribution and were therefore not implemented.

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[9] https://esa-oceancolour-cci.org/

[10] https://seaice.uni-bremen.de/

[11] http://marine.copernicus.eu/services-portfolio/access-to-products/?option=com_csw&view=details&product_id=SEALEVEL_GLO_PHY_L4_REP_OBSERVATIONS_008_047

[12] https://www.nodc.noaa.gov/OC5/indprod.html

Tests for Multicollinearity

Multicollinearity, the strong correlation between two or more predictor variables, can cause instability in parameter estimation and affect model predictions (Graham 2003, Dormann et al. 2013), then the least correlated variables should only be used. Only candidate variables with a variance inflation factor (VIF) of <4 were included in the analysis to avoid collinearity, following Zuur et al. (2009). This led to the rejection of nine out of 24 variables. Further, the correlation coefficient between the filtered variables (with VIF <4) was calculated to examine other potential correlation problems. One variable (distance to 200 m isobath) was found to cause correlation issues (correlation coefficient > 0.7) and hence was removed from the analysis. Three environmental variables (mean temperature at 0 and 100 m depth and sd of sea ice concentration) were, based on literature research, expected to be of ecological importance to the species, and were consequently forced in after the removal of highly correlating variables. Since these three candidate variables were still causing collinearity problems, they were excluding from the analysis. In total, nine variables were excluded due to multicollinearity, which resulted in 14 variables to be used in the model (Table 2 and 3, Fig. 4).

Table 3: Overview of transformations and VIF of final EVs used in the model, sd = standard deviation, m = mean

Variable	Abbreviation	Transformation	VIF
Aspect	Aspect		1.06
Bathymetry	Bathy		3.27
Chlorophyll a sd	ChlaSTD		1.38
Distance to Sea Ice Edge	Dist2Ice		2.59
Distance to Isobath 500	Dist2Iso500SQRT	square root	3.53
Distance to Shore	Dist2Shore		2.82
Salinity 0 sd	Sal0STDlog	log	2.63
Salinity 100 m	Sal100mean		2.18
SIC m	SICmean		2.64
Slope	Slope		1.17
SSH sd	SSHSTD1BY	inverse	3.28
Temp 0 sd	Temp0std		3.00
Temp 100 sd	Temp100STDlog	log	1.80
Velocity m	VelocityMeanLog	log	2.07

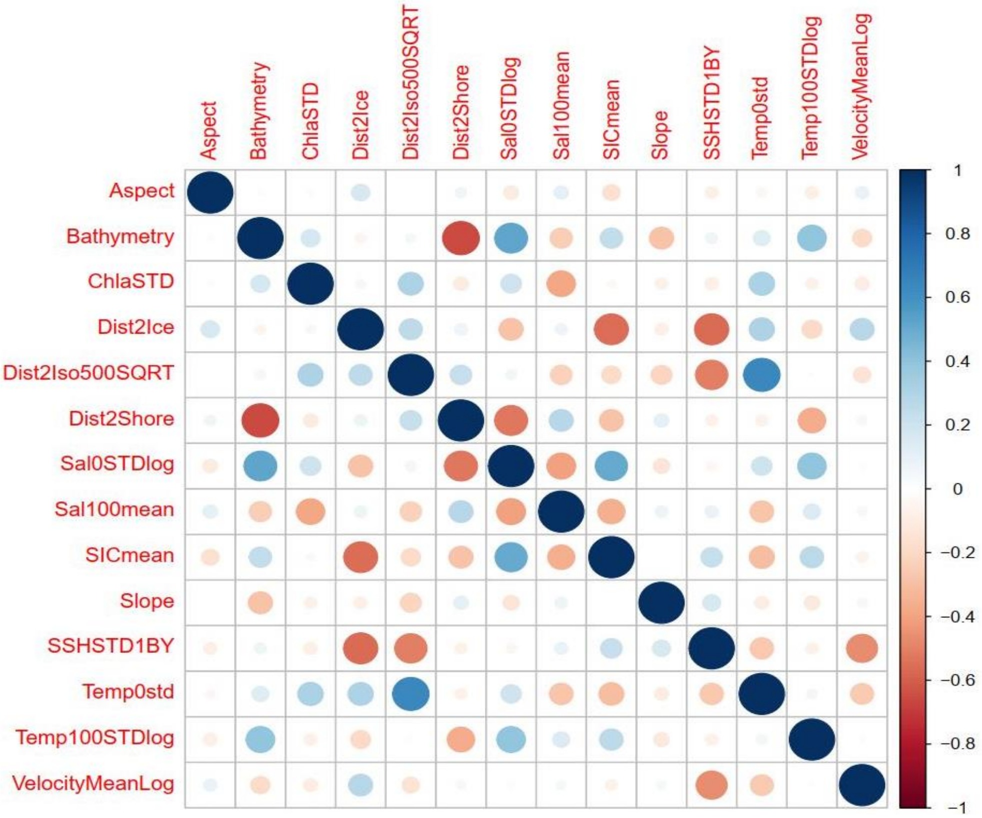

Fig. 4: Correlation plot of all variables. Blue is depicting a positive, red a negative correlation, the intensity of shading and size of the circles is indicating the intensity of correlation.

2.4. Modelling procedure

Models were fit using the software MaxEnt v3.4.1 (Philipps et al. 2006, Dudik 2007) available at http://www.cs.princeton.edu/~schapire/maxent. Two modelling approaches were implemented. First, without accounting for sampling bias: duplicated occurrences in each grid were allowed ($\text{model}_{\text{duplicates}}$). Second, to correct for sampling bias, duplicated occurrences in each grid were removed before running the model ($\text{model}_{\text{noduplicates}}$). This represents a special form of spatial thinning (e.g. *spThin* R package, Aiello-Lammens et al. 2019). In order to identify which combination of feature classes and regularization multiplier (RM) lead to the highest performing model, the function *ENMevaluate* of the ENMeval R package was used (Muscarella et al. 2014), following recommendations from recent literature; e.g. Merow et al. (2013) and Radosavljevic and Anderson (2014). Combinations of six feature classes and eight values for regularization multipliers (ranging from 0.5 to 4, with an increment of 0.5) were selected, leading to 48 models in total. Maxent’s best model parameters were picked according to testing AUC. Spatial blocks were created using the R-package “blockCV” (Valavi et al. 2018).

Spatial blocks based on presence and background data, where 0 was assigned to background points and 1 to presence locations. Block size was estimated as the median spatial autocorrelation range of the environmental variables, using "*spatialAutoRange*" function (see Fig. 2). Blocks were then distributed randomly into 4 cross-validation folds using "*spatialBlock*" function (iterations = 500). This function tries to find the best allocation of blocks into cross-validation folds, in a way that balances the number of presence and background locations between folds. The same procedure was run separately for each model.

2.4.1. Duplicates Model ($\text{model}_{\text{duplicates}}$)

The implemented blockCV mask layer mean range was 471,571 meters (see Fig. 5). This is the specified range by which blocks were created and training/testing data were separated. Data was then manually separated into four spatially cross-validated folds, resulting in four cross-validated models and one full model. For details on model settings see Table 4.

2.4.2. Removed Duplicates Model Arguments ($\text{model}_{\text{noduplicates}}$)

The implemented blockCV mask layer mean range was 453,767 meters (see Fig. 5). Data were manually separated into four spatially cross-validated folds, resulting in four cross-validated models and one full model. To account for spatial sampling bias, any duplicates within the occurrence data were removed. The removal of duplicates (a duplicate being one or more sightings per grid cell) led to a remainder of 746 occurrences. For details on model settings see Table 4.

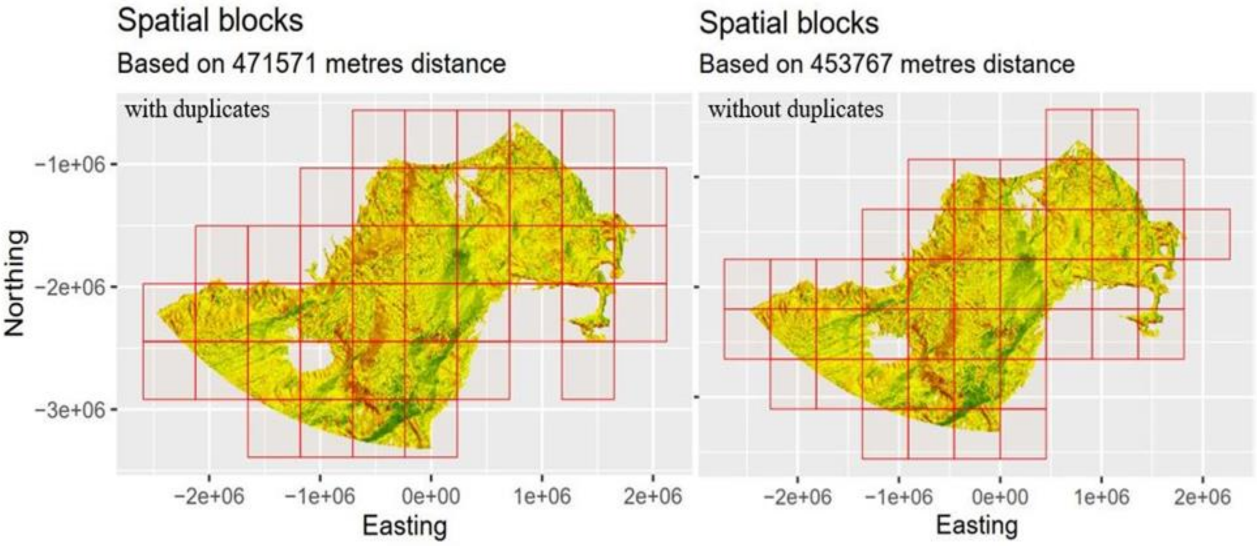

Fig. 5: Spatial blocks for model versions with and without duplicates

Arguments ENMevaluate

Algorithm = maxent.jar

Max. iterations = 3000

Method = user

Overlap = true

Bin.output = true

Parallel = true

Table 4: Overview of the settings for $\text{model}_{\text{duplicates}}$ and $\text{model}_{\text{noduplicates}}$

Settings	**Duplicate Model**	**Removed Duplicates Model**
Add samples to background	false	false
Maximum Iterations	3000	3000
Jackknife	true	true
Write background predictions	true	true
Response curves	true	true
Pictures	true	true
Total number of background points	51,595	51,595
Total number of occurrences	1229	746

Afterwards, models were run in R using the *maxent* function of "dismo" R-package (Hijmans et al. 2017) (for details see the R-script in the appendix). Predictions were made using *predict* function of the "dismo" package. There are four types of output in MaxEnt: logistic, cumulative, raw and cloglog. Cloglog was chosen as the output form for the analyses, as it is considered to have a stronger theoretical justification than e.g. logistic output (Philipps et al. 2017). All models were stacked and saved. The niche overlap between all models was calculated using *calc.niche.overlap* function of ENMeval R package (Muscarella et al. 2014).

The niche overlap metric used was the Schoener's D (Schoener 1968), which is a statistic for map congruence between pairs of prediction maps, and ranges from 0 (no overlap) to 1 (identical). It was used to identify how much similarity there is between model predictions (Schoener 1968, Warren et al. 2008). Jackknifing and PI were conducted in all model runs, as it enabled the assessment of the relative importance of each of the environmental variables within the respective model.

2.4.3 Visualization of predictions

All prediction maps were prepared using R, describing habitat suitability for each grid cell of the study area, ranging from 0 to 1 (0 being unsuitable, 1 being highly suitable).

3. RESULTS

Ten models with the best combination of MaxEnt's FC and RM estimated based on spatial-block cross-validation (with keeping and removing duplicated occurrences located at each grid cell: model$_{\text{duplicates}}$ and model$_{\text{noduplicates}}$, respectively) were constructed. Two full models and 8 spatially cross-validated models. The two full models of model$_{\text{duplicates}}$ and model$_{\text{noduplicates}}$ show a similar pattern of habitat suitability, though habitat suitability seems to be rather extensive and not so clustered in the model$_{\text{noduplicates}}$ (see Fig. 6). Progression of the response curves are similar, though varying in values, while the ratio between variables seems to be somewhat similar (Fig. 13 - 15). The top important variables of model$_{\text{duplicates}}$ and model$_{\text{noduplicates}}$ vary in their composition (see Fig. 9 - 12). In both full models, the seasonal variability (sd) of Chlorophyll-a, sea surface height, variability of temperature at 100 m, aspect, velocity, sea ice concentration, salinity at 100 m, and distance to isobath 500 m were the least contributing variables, with permutation importance less than 6% (see Fig. 11 and Fig. 12). Therefore, their response curves are not discussed further as they are presumed to not have a significant influence on habitat suitability of the fin whale. These variables are only shown in the supplementary (see appendix A).

3.1 Model with duplicates ($\text{model}_{\text{duplicates}}$)

Five different models were built for the $\text{model}_{\text{duplicates}}$ including four cross-validated models built on spatial blocks and one full model. The $\text{model}_{\text{duplicates}}$ had an average testing AUC of 0.855 ± 0.016. Habitat suitability is highest along the southwestern coast of Svalbard. Another peak in suitability is on the eastern side of Svalbard, though not as high as on the southwestern coast. This is followed by the north of Norway and on the eastern coast of Greenland up to Iceland (Fig. 6). The standard deviation of the predicted distribution of different cross-validation folds of $\text{model}_{\text{duplicates}}$ is comparably low. It is highest in the southeast of Svalbard, with patterns similar to general habitat suitability in the prediction map (see Fig. 7).

3.2 Model without duplicates ($\text{model}_{\text{noduplicates}}$)

Five different models were built for the $\text{model}_{\text{noduplicates}}$ including four cross-validated models built on spatial blocks and one full model. The $\text{model}_{\text{noduplicates}}$ had an average testing AUC of 0.862 ± 0.0098. The pattern of habitat suitability in the $\text{model}_{\text{noduplicates}}$ prediction map is broader and stronger than that of $\text{model}_{\text{duplicates}}$, especially around Svalbard and Norway (Fig. 6). Highest habitat suitability, here too, is along the southwestern coast of Svalbard, though a lot more extensive in the South and southeast of Svalbard. In northern Norway habitat suitability is high as well, higher than in the $\text{model}_{\text{duplicates}}$. Throughout the rest of the study area, patterns do not differ dramatically, though generally habitat suitability seems to be higher in areas of former predicted medium habitat suitability (Fig. 6). Standard deviation is higher than in $\text{model}_{\text{duplicates}}$, mainly in the areas of increased predicted habitat suitability compared to the standard deviation of $\text{model}_{\text{duplicates}}$ (Fig. 7 and Fig. 8).

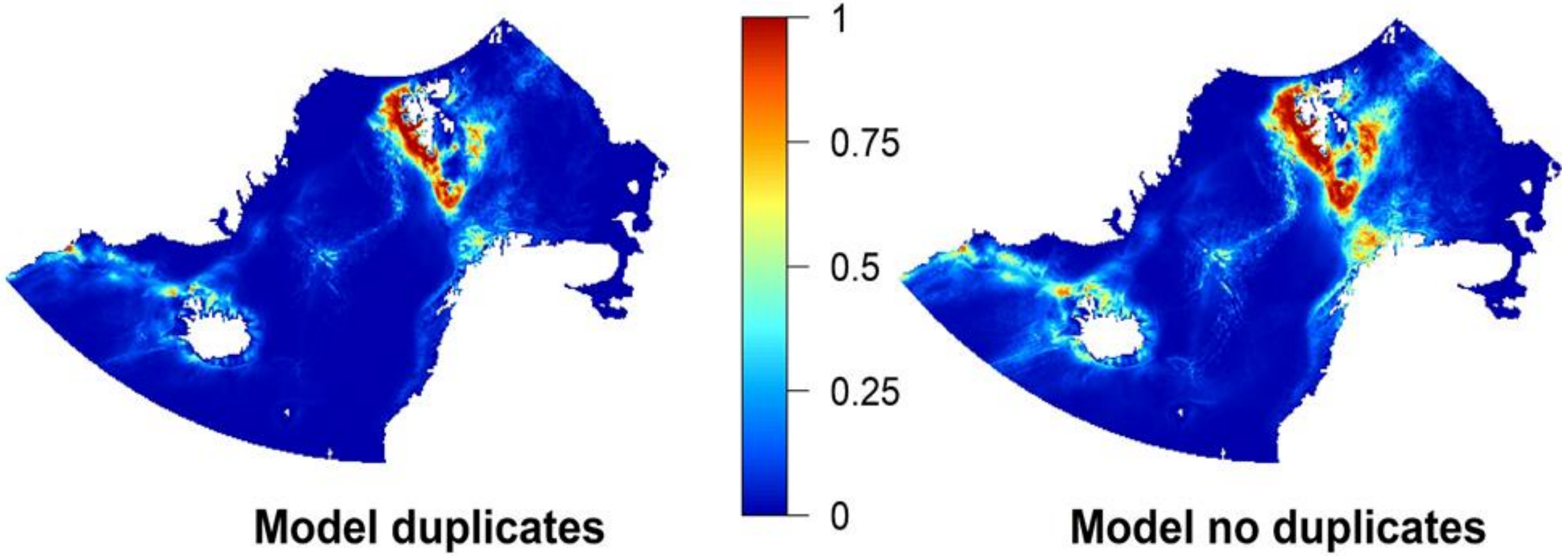

Fig. 6: Prediction maps of model$_{duplicates}$ and model$_{noduplicates}$. Habitat suitability ranges from 0 (blue; low) to 1 (red; high).

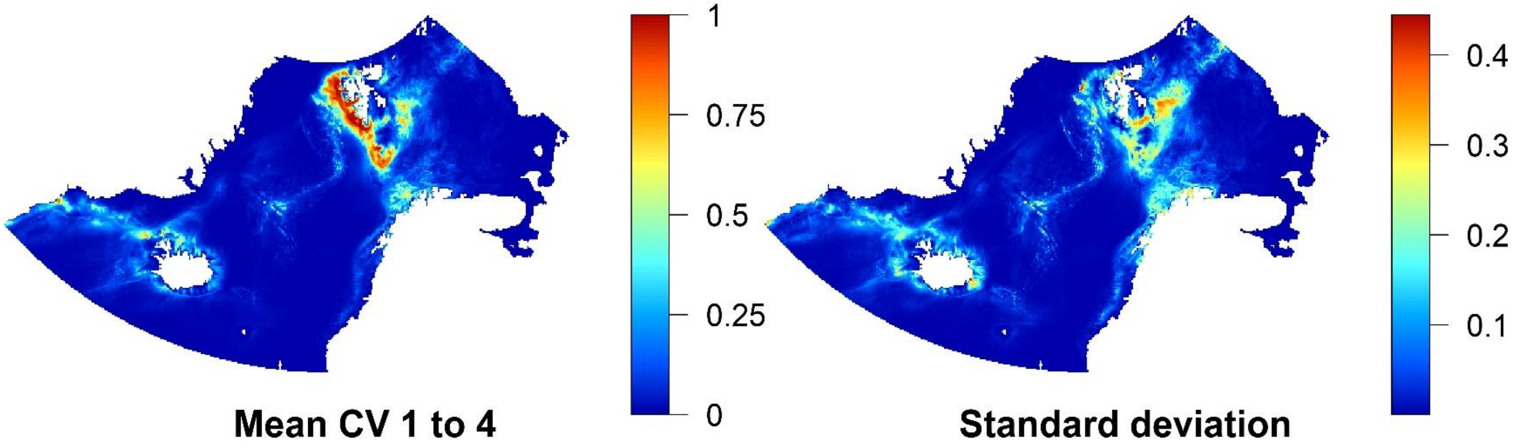

Fig. 7: Mean prediction map of the four cross-validated folds of model$_{\text{duplicates}}$ and the according standard deviation. Habitat suitability ranges from 0 (blue; low) to 1 (red; high).

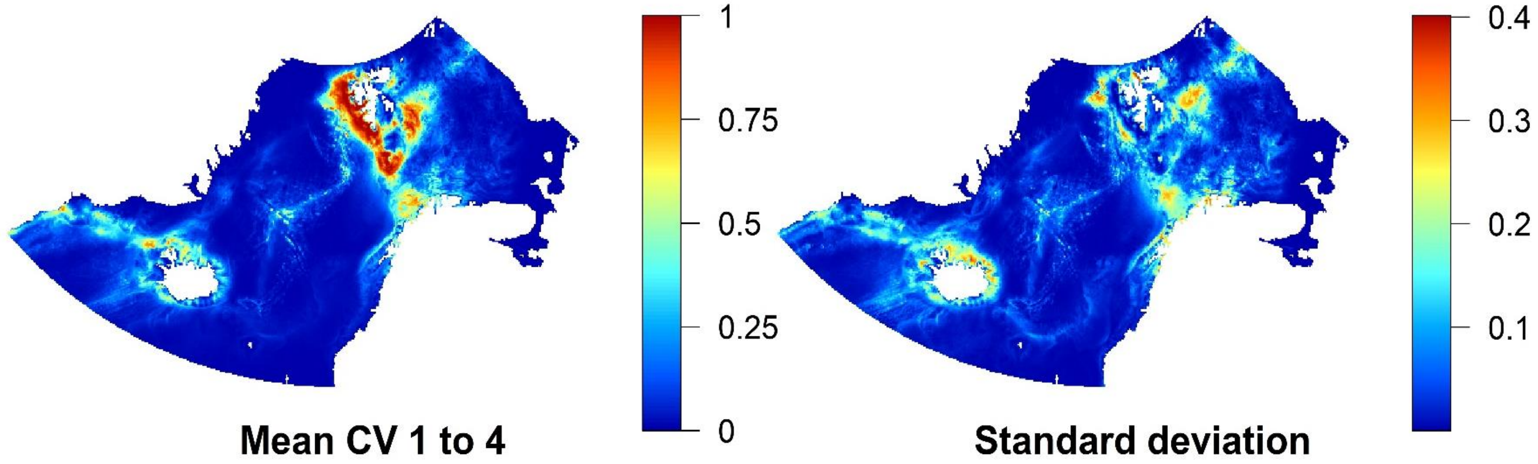

Fig. 8: Mean prediction map of the four cross-validated folds of model$_{\text{noduplicates}}$ and the according standard deviation. Habitat suitability ranges from 0 (blue; low) to 1 (red; high).

3.3. Jackknife of regularized training gain

When used alone to run models of type model$_{duplicates}$, distance to ice had the highest predictive power, followed by the variability (sd) of sea surface temperature, the variability (sd) of sea surface height, distance to shore and mean salinity at 100 m. Whereas, the model$_{duplicates}$ showed the least performance when bathymetry, distance to shore, and slope were excluded (see Fig. 9).

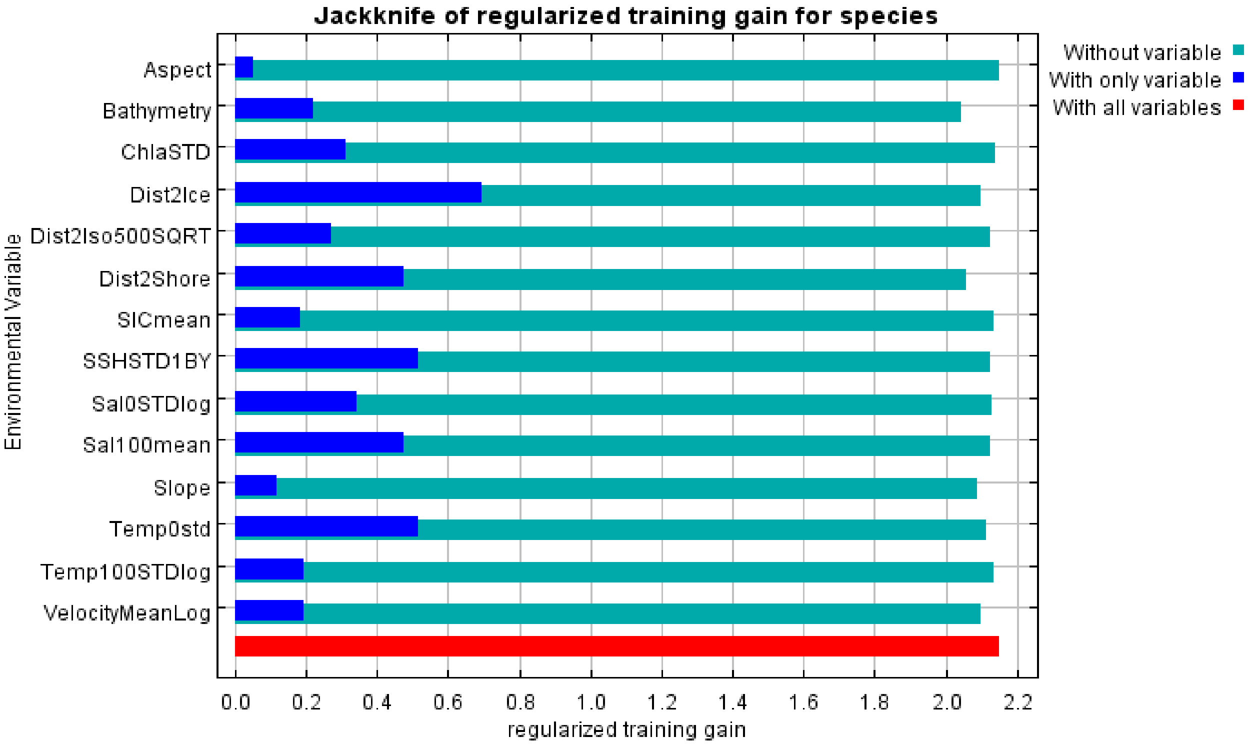

Fig. 9: Jackknife of regularized training gain for the full model$_{duplicates}$. Green indicates model performance without respective variable, blue indicates model performance with only variable. Red indicates model performance when all variables were used.

For the model$_{noduplicates}$, with only variable, distance to ice had the highest predictive power, followed by the variability (sd) of sea surface height, salinity at 100 m, variability (sd) of sea surface temperature and distance to shore. The model$_{noduplicate}$s showed the least performance when bathymetry, distance to shore, distance to ice and slope were excluded. While without variable, the model was weakest without bathymetry, distance to shore, distance to ice and slope, indicating a relative importance of these variables (see Fig. 10).

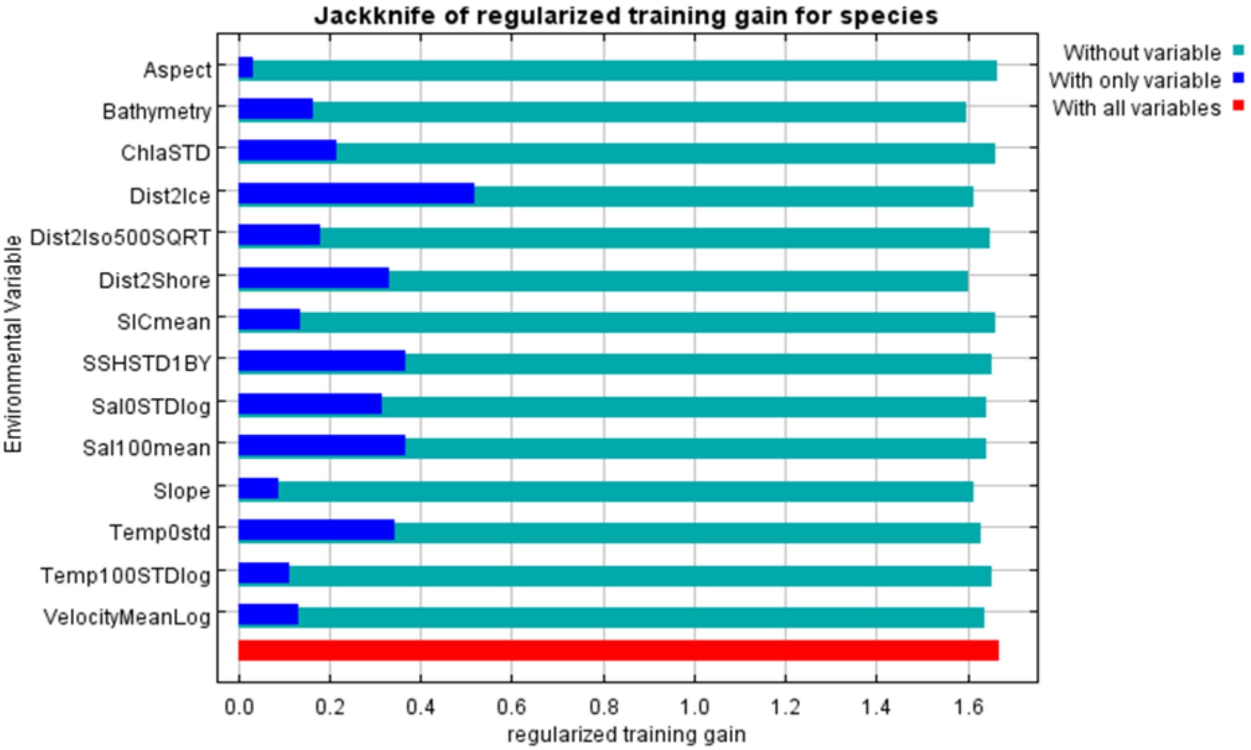

Fig. 10: Jackknife of regularized training gain for the full model$_{noduplicates}$. Green indicates model performance without respective variable, blue indicates model performance with only variable. Red indicates model performance when all variables were used.

3.4 Permutation Importance

The most contributing variables in terms of permutation importance in the full model$_{\text{duplicates}}$ were distance to shore, distance to sea ice edge, slope, salinity at 100 m depth, bathymetry, and variability of sea surface temperature (see Fig. 11).

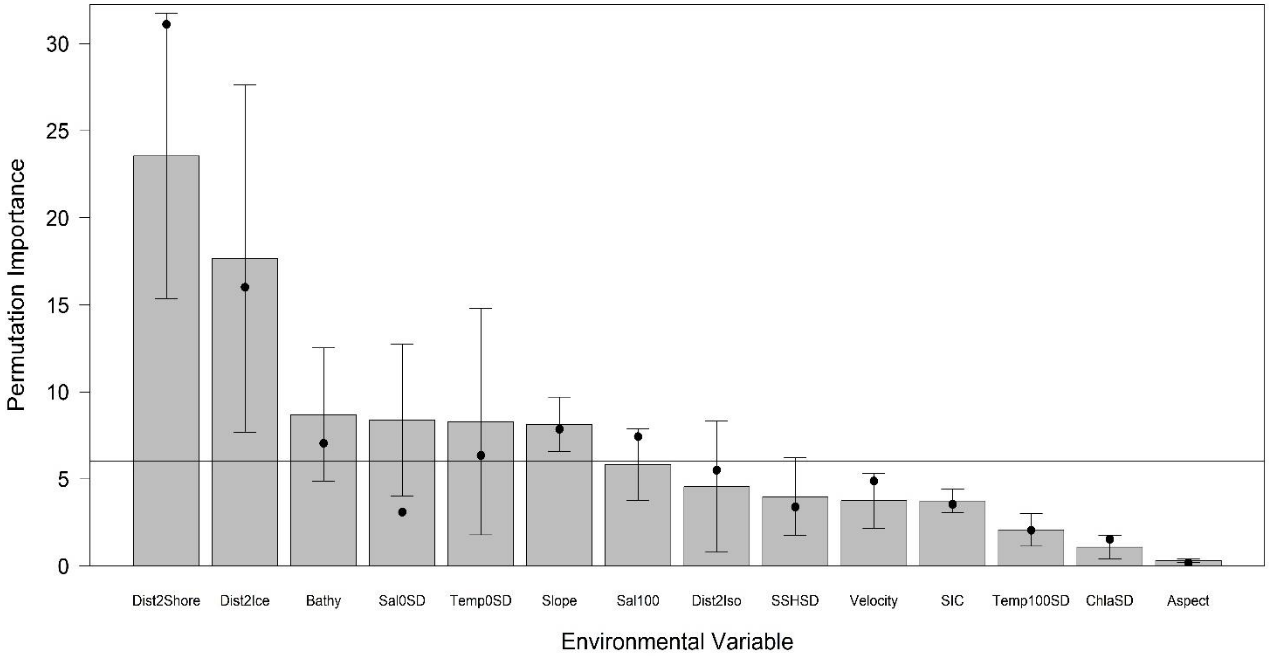

Fig. 11: PI for all EVs of the model$_{\text{duplicates}}$~~,~~ in a descending order. Dots resemble the full model, while bars indicate the mean PI of all four models. Error bars represent the standard deviation of PI. The solid horizontal line indicates a threshold of 6 below which EVs were of low interest.

The most contributing variables in terms of permutation importance in the full model$_{noduplicates}$ were distance to shore, distance to sea ice edge, bathymetry, variability of sea surface temperature, slope and salinity at 100 m depth (see Fig. 12). In all four model folds and the full model$_{noduplicates}$, both distance to shore and sea ice edge contributed most, varying only in magnitude. Aspect was the least contributing variable, both in jackknifing and permutation importance (see Fig. 10 and Fig. 12).

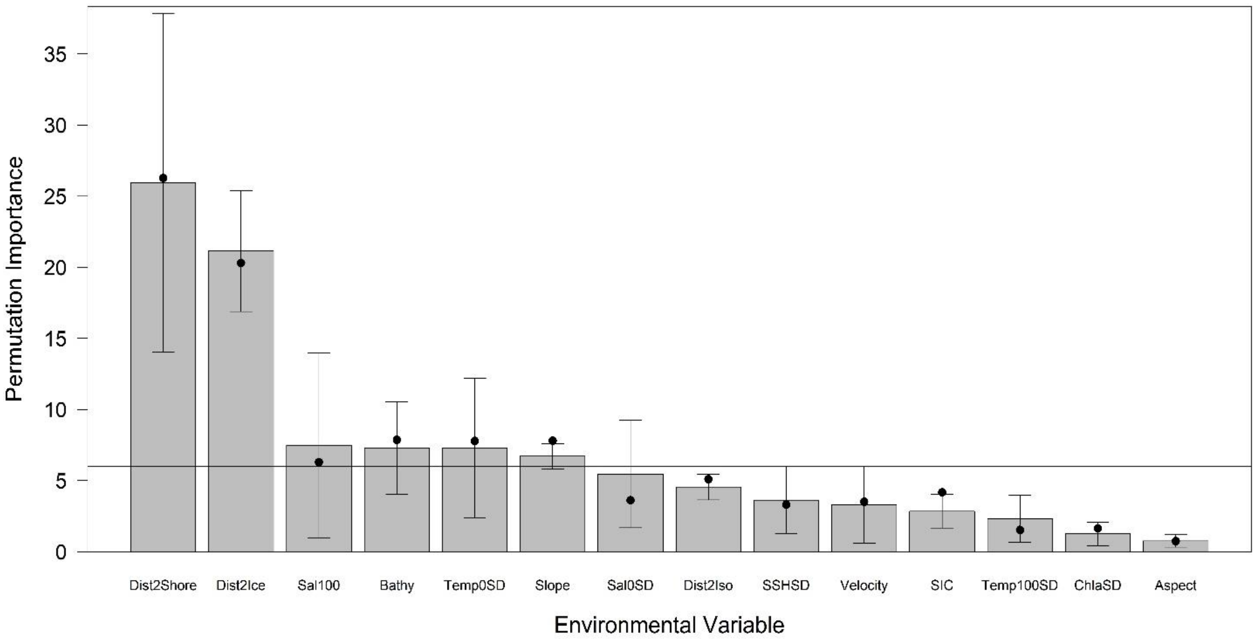

Fig. 12: Permutation importance for all EVs of model$_{noduplicates}$, in a descending order. Dots resemble the full model, while bars indicate mean PI values of all four model. Error bars represent the standard deviation of PI. The solid horizontal line indicates a threshold of 6 below which EVs were of low interest

3.5 Niche Overlap

Depicted below is the congruence between predictions of each pair of the four cross-validated models (with duplicates and without duplicates; Table 5 and Table 6, respectively). Overall, the Shoener's D index, which represents the similarity between each pair of maps, was somewhat larger in the model without duplicates than in the one with duplicates.

Table 5: Niche overlap (prediction congruence) between predictions of each pair of the four cross-validated models of model$_{\text{duplicates}}$

Model	**CV1**	**CV 2**	**CV 3**	**CV 4**
CV 1				
CV 2	0.793			
CV 3	0.762	0.709		
CV 4	0.803	0.740	0.717	
Full Model	0.892	0.834	0.813	0.844

Table 6: Niche overlap (prediction congruence) between predictions of each pair of the four cross-validated models of the model$_{\text{noduplicates}}$

Model	**CV1**	**CV 2**	**CV 3**	**CV 4**
CV 1				
CV 2	0.753			
CV 3	0.768	0.805		
CV 4	0.742	0.797	0.770	
Full Model	0.831	0.879	0.865	0.851

3.6 Response curves for all models

Depicted below is the comparison of all response curves for the respective full model of model$_{\text{duplicates}}$ and model$_{\text{noduplicates}}$ (Fig. 14). Only response curves of the most contributing variables (PI > 6) are shown.

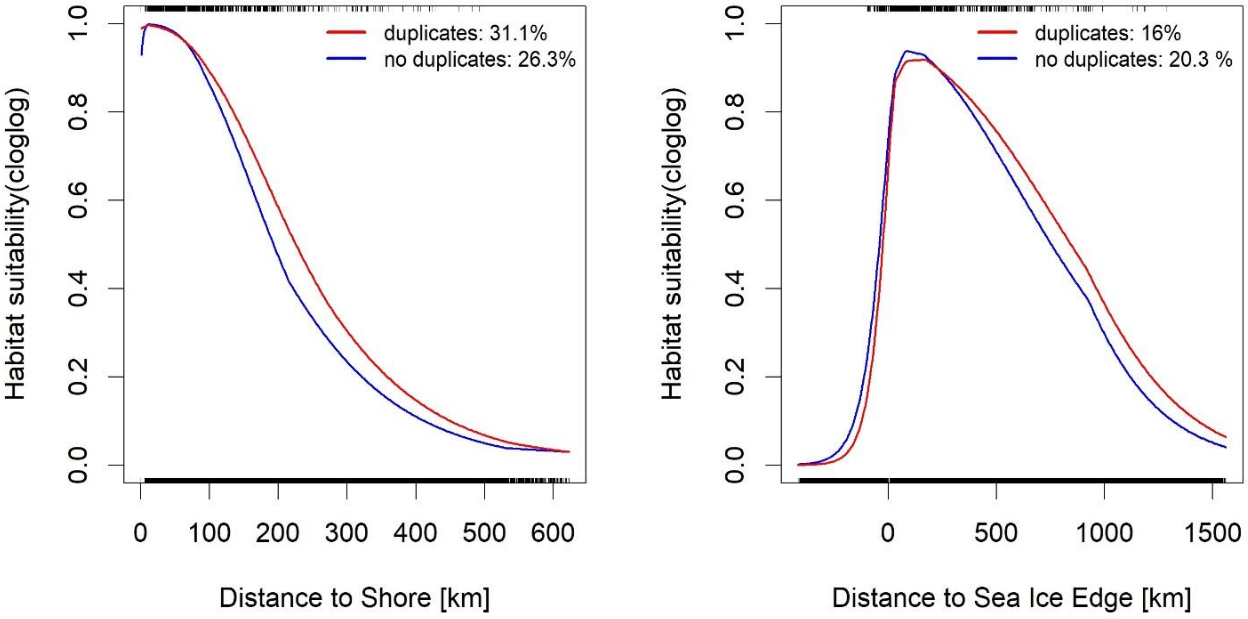

Fig. 13: Response curves for distance to shore (left) and sea ice edge (right). Ticks on the upper axis represent values at occurrences, while ticks on the lower axis represent values at background locations. Number after model name indicates the permutation importance of the respective variable.

The ticks of the rug in Fig. 13 show that most occurrences were recorded closer to shore. Similarly, models predict high habitat suitability within ~ 80 km from the shore, which then sharply decreases and stabilizes at low suitability beyond ~ 300 km from the shore (Fig. 13). Models show a unimodal relationship with distance to ice edge, with a peak suitability at ~ 170 km from the ice edge, in ice-free areas, then decreases sharply at higher distances. Habitat suitability is low to very low on the ice edge and in ice-covered areas (Fig. 13).

For bathymetry, models show a peak preference at a depth around 200 m, with much lower preference for shallower areas (Fig. 14), though the ticks show that most occurrences occur in rather shallow areas. Further, fin whales seem to avoid locations with very low slopes (Fig. 14). Habitat suitability increases sharply with increasing slope then stabilise (see Fig. 14). Contrastingly, most occurrences were noted at lower slope.

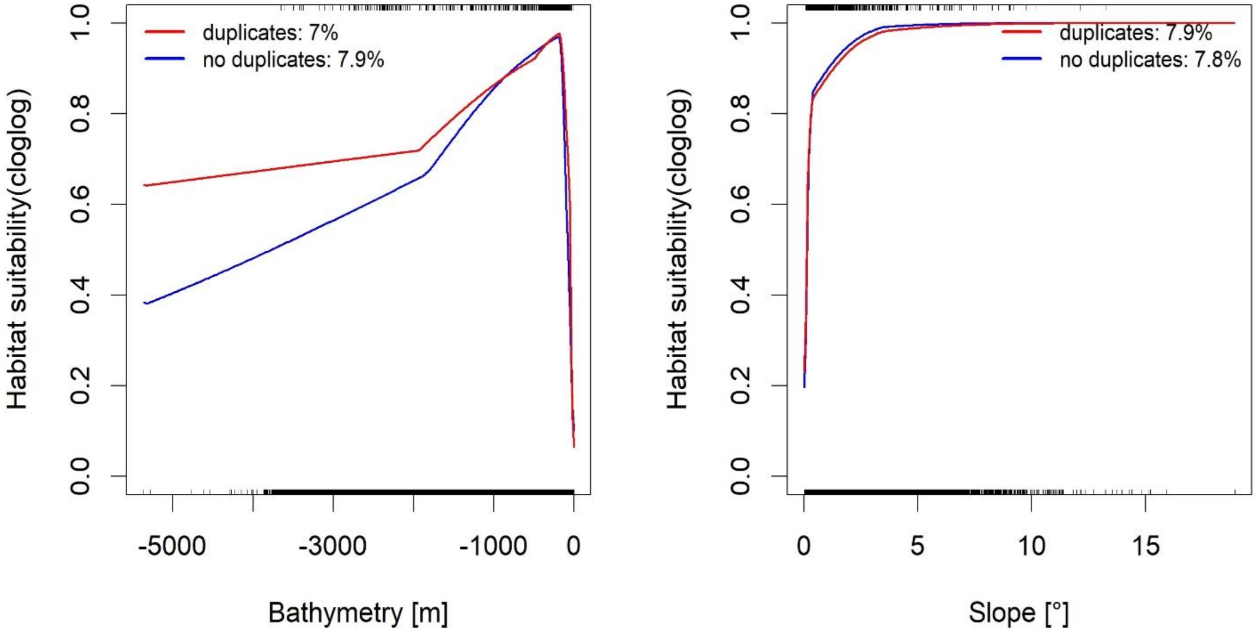

Fig. 14: Response curves for bathymetry (left) and slope (right). Ticks on the upper axis represent values at occurrences, while ticks on the lower axis represent values at background locations. Number after model name indicates the permutation importance of the respective variable.

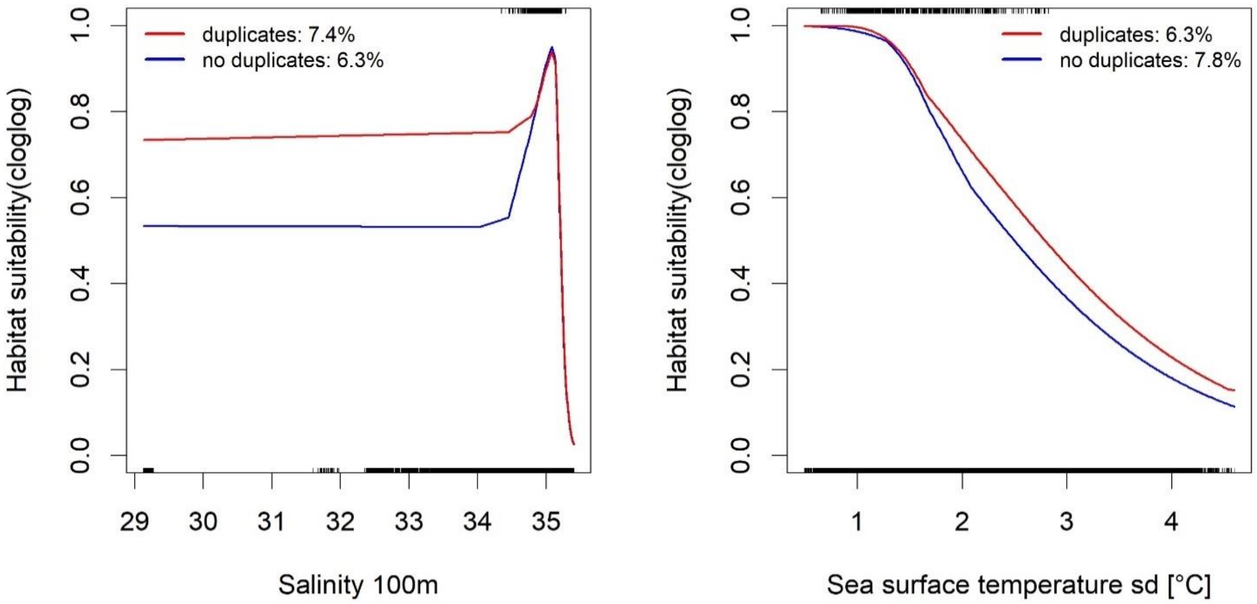

Fig. 15: Response curves for salinity at 100 meters depth (left) and variability of sea surface temperature (right). Ticks on the upper axis represent values at occurrences, while ticks on the lower axis represent values at background locations. Number after model name indicates the permutation importance of the respective variable.

There is no apparent relationship between fin whale suitability and mean salinity at 100 m depth up to a value of ~ 34.4 (although still having a moderate suitability), then suitability increased with a peak at ~ 35 then sharply decreased (Fig. 15). Most sightings occurred around these values.

There is a predicted peak in habitat suitability at locations with very low variability of sea surface temperature (<1.5°) (Fig. 15). Highest habitat suitability here seems to lie between a standard deviation of 0 and 1 (see Fig. 15), though with a much broader range of occurrences.

4. DISCUSSION

The aim of this master thesis was to predict habitat suitability of fin whales in the Nordic Seas using opportunistic sighting data and SDMs. A further aim was to identify underlying drivers of habitat suitability in terms of environmental variables. Two types of spatially cross-validated models, one with and one without duplicates, were constructed. This led to the identification of six environmental variables having an impact on fin whale habitat suitability in the Nordic Seas (permutation importance >6 %), with the two most contributing variables being distance to shore and distance to sea ice edge.

4.1. Comparison to other studies

The habitat preferences of fin whales are mainly reflected by six environmental variables. These variables are distance to shore, distance to sea ice edge, bathymetry, sea surface temperature (sd), salinity at 100 m depth (mean), and slope. In order to compare results of this study with others, some studies around the study area with similar approaches were regarded. Storrie et al. (2018) recently published a study on species assemblage and habitat use of cetaceans in the Svalbard Archipelago using MaxEnt. The predicted distribution of fin whales reported by Storrie et al. (2018) largely agrees with our results. Areas with particularly shallow and flat bathymetry were modelled to be unsuitable habitats (below 20 %) (Storrie et al. 2018). Very deep areas beyond the slope and areas with dense ice cover were also found to be unsuitable (Storrie et al. 2018). Fin whales were detected in a broad array of depths there, with a median depth of 250 m. This resembles our results, though here, rather than seeing a distribution over a broadband of depths, we found highest habitat suitability to be at depths of 180 to 240 m. Fin whales prefer areas with open water afar from sea ice, and most suitable habitats were identified to be steep areas of the continental slope around the 500 m isobath (Storrie et al. 2018). In some other studies, fin whales occupied a narrow zone along and north of the polar front, with some individuals also occurring at the shelf edge and southwestern Barents Sea (Skern-Mauritzen et al. 2011). Here, too, areas along the polar front, which run southwestwards of Svalbard, were modelled highly suitable for fin whales (Fig. 6). Fin whale habitat suitability seems to be especially high north of the polar front, along the shelves of Svalbard (Fig. 6 and Fig. 16). The position of the polar front and associated productivity gradients are to a large degree determined by bathymetry, particularly in the western Barents Sea (Harris et al. 1998, Ingvaldsen 2005).

As prey availability may be more predictable in productive areas, prey predictability has been suggested to impact the distribution of pelagic predators (Gende and Sigler 2006, Skern-Mauritzen et al. 2011). Hence, productive areas, such as in the polar front (Fig. 16), may be quite predictable spatially and temporally and seem to serve as suitable foraging areas (Fall and Skern-Mauritzen 2011), which reflects in the current study.

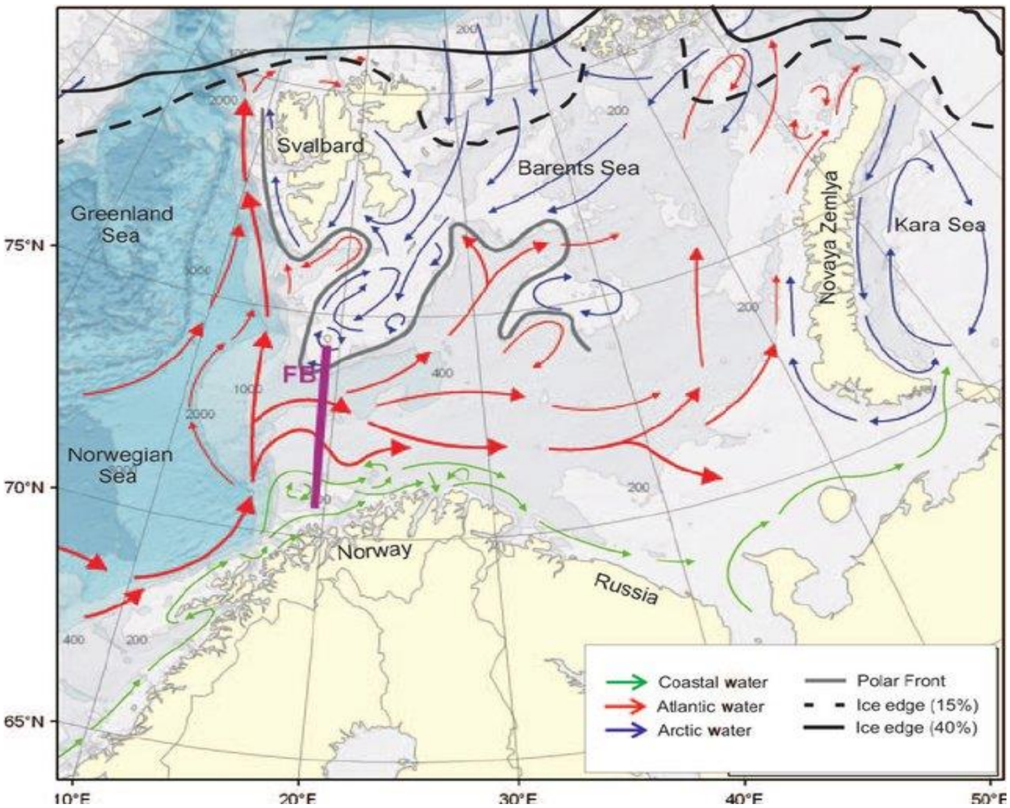

Fig. 16: Main circulation and water masses in the Barents Sea. The mean ice edge, using 15% (solid) and 40% (dashed) ice concentration, in September (black) and the Polar Front (grey) (Source: Johannesen et al. 2012).

4.2. Model Performance

Model performance has been comparably high, with convincing output (see Fig. 6). In general, $\text{model}_{\text{duplicates}}$ (AUC 0.855 ± 0.016) and $\text{model}_{\text{noduplicates}}$ (AUC 0.862 ± 0.0098) had high AUC values and showed reasonable patterns of habitat suitability. As has been discussed in the introduction, the usual way of calculating AUC does not maintain spatial independence between training and testing dataset, so spatial-block cross-validation has been used. Standard deviation of the averaged predictions from the four cross-validated models of both model types shows reasonable values, indicating good model performance (see Fig.7 and Fig. 8). The use of spatial-block cross-validation which accounts for spatial autocorrelation and the estimation of best combination of Maxent's settings may also explain the consistent predictions of the cross-validated models. To avoid spatial sampling bias, as is often the case when using opportunistic sighting data (El-Gabbas Dormann 2018), duplicated occurrences were removed. This resulted in a convincing prediction map, with a slightly higher AUC, and a lower standard deviation as compared to the other model. Main difference between both model types is the broader or “smoother” modelled distribution in model$_{\text{noduplicates}}$. This model predicts areas of suitable habitats in under-sampled areas (see Fig. 6). This is not the case in model$_{\text{duplicates}}$, where highest habitat suitability agglomerates around the places of highest occurrence data. Nevertheless, both models showed -high performance.

4.3. Potential distribution of fin whales in the Nordic Sea

The predicted distribution from the full (and mean cross-validated) model$_{\text{noduplicates}}$ seemed to be slightly more realistic than the model$_{\text{duplicates}}$, due to the much smoother modelled habitat suitability (Fig. 6) and former mentioned arguments. The modelled distribution is in concordance with other studies of fin whale occurrences and their favored prey distribution (Kovacs et al. 2009, Vikingsson et al. 2015, Storrie et al. 2018). Unsurprisingly, along the East Greenland coast, habitat suitability was rather low, compared to Svalbard, though former studies have shown high fin whale occurrences here (Heide-Jørgensen et al. 2007, Vikingsson et al. 2009, Hansen et al. 2018). Due to low occurrence data within this area, it is not surprising that habitat suitability was estimated lower than around Svalbard. Some areas in front of the southern East Greenland coast were modelled to be highly suitable, which is convincing and indicate good model performance as it is consistent with prior studies documenting the occurrence of fin whales in this region (see Fig. 6).

4.3.1 Distance to shore

Distance to shore was the most important environmental variable in both full models with permutation importance ranges from 26.3% to 31.1%. The response curves show a clear preference of fin whale to locations closer to shore than farther away, with highest suitability at around 10 km up to 80 km (Fig. 13). Within the study area, fin whales were mostly found in dense aggregations offshore, e.g. along the East Greenland coast (Heide-Jørgensen et al. 2007). Other studies show somewhat contrasting findings. In Iceland, fin whales were virtually absent from shallow coastal waters (Vikingsson et al. 2015), while in the Mediterranean Sea, fin whales were found beyond the continental shelf (Forcada et al. 1996). In the Northern Hemisphere, fin whales tend to occur in temperate offshore to subpolar waters south of approximately 60–70° N (Mizroch et al. 2009, Edwards et al. 2015).

Compared to earlier years, they were observed more frequently in near-shore areas (Storrie et al. 2018) though Zerbini et al. (2016) found fin whale occurrence to increase linearly with distance to shore in the Eastern Bering Sea (Zerbini et al. 2016). Results here suggest that fin whales do not favor shallow waters, as habitat suitability increases around 8 to 80 km away from shore. Offshore areas do not seem to be suitable either, because modelled habitat suitability thereafter sinks again.

4.3.2 Distance to sea ice edge

In the Arctic, several cetaceans such as bowhead whales (*Balaena mysticetus*), narwhals (*Monodon monoceros*), and minke whales are known to be closely associated to the ice edge, areas of light ice cover or in open water within the ice (Ribic et al 1991, van Franeker 1992, Ainley et al. 2007, Scheidat et al. 2011). In the Antarctic, the presence of fin whales showed a negative correlation with sea ice concentrations on weekly to monthly time scales and it was suggested that fin whales were absent in ice-covered areas (Širović et al. 2004). In the study area, some observations in areas with loose drift ice were made in a different study, though modelling suggested general unsuitability of areas with dense ice cover (Storrie et al. 2018). In this study, results showed an optimum habitat suitability for fin whales at distances between 80 and 170 km from the ice edge in ice-free areas (Fig. 15). These findings are supported by the modelled highest habitat suitability in mean sea ice concentrations of < 20% (see Fig. 2 in Appendix A). An increase in habitat suitability from 0 to 18 % sea ice concentration indicates some tolerance according to sea ice though. In a former study in the Antarctic only minke whales were observed within the ice, while fin whales were exclusively observed in open waters, which fits to these findings (van Franeker 1992). In the Gulf of St. Lawrence, fin whales were found to shift their arrival dates at feeding grounds at a rate of 1 day earlier each year per 3 decades, which was linked to an earlier sea ice break up and higher sea surface temperature (SST) (Ramp et al. 2015). Tsjuii et al. (2016) also suggested that fin whales arrive in the Chuckchi Sea only after sea ice has melted and water temperature has elevated. Furthermore, they were noticed to stay longer when the ice-free period was longer, and their presence seems to be related to higher water temperature and zooplankton abundance (Tsjuii et al. 2016). In Davis Strait, some fin whale individuals do not migrate south until sea ice forms from the north in November or December (Širović et al. 2004, Simon et al 2010). All in all, these findings, supported by the results of this study, suggest a strong temporal relationship between the occurrence of fin whales and sea ice melting/formation: fin whales seem to avoid ice-covered areas and rather roam in ice-free or -limited areas, avoiding the sea ice edge.

4.3.3 Salinity

Results suggest no relationship between fin whale habitat suitability and salinity at 100 m up to a value of 34.4, then increased to reach a peak at a value of around 35 then reduced sharply at high salinity values (Fig. 16). As to my knowledge, no studies have related the distribution of fin whales to salinity, despite Tsujii et al. (2016), who found that fin whales leave the southern Chukchi Sea after the decrease in water temperature and salinity. Their findings suggested that the physical environment may trigger the movement of fin whales towards their wintering area, though the role of salinity in this remains unclear. It is likely, that salinity acts as a proxy for other variables, such as temperature, which affects sea ice conditions, which again leads to fluctuations in salinity. Interestingly, within this study, salinity had the highest correlations (around -0.4) with the variability of chlorophyll-a concentration.

4.3.4 Bathymetry and Slope

Fin whales have been previously found to be feeding offshore and/or at large deep-water bays (Perkins and Whitehead 1977, Parsons and Brownlie 1981). Woodley & Gaskin (1996) observed that fin whales tend to aggregate where bottom topography is heterogeneous, and water is well mixed. It was further found that fin whales utilize currents modulated by sea bottom topography (Woodley and Gaskin 1996, Panigada et al. 2005). Water depth and slope act as important predictors of fin whale occurrence in the North Atlantic (Woodley and Gaskin 1996, Ingram et al. 2007, Vikingsson et al. 2015, Schleimer et al. 2019*)*. In the Bay of Fundy, Canada, a modelled fin whale sighting rate indicated an increase in the sighting rate of fin whales with increasing depth, which clearly contrasts our results (Ingram et al. 2007). There is a direct relationship between bathymetric characteristics and fin whale habitat suitability though, here, fin whales do not favor the deepest regions. A preferred depth of around 200 m has been noted, while at deeper areas habitat suitability decreased again (Fg. 14). In Svalbard and Iceland, fin whales were found to generally occupy steeper and deeper regions (Vikingsson et al. 2015 and 2017, Storrie et al. 2018), which is only partly in contrast to our findings. Our modelled highest habitat suitability according to slope on the other hand, does well agree with prior findings of other studies. Slopes are known to act as an important predictor of fin whale occurrence in the North Atlantic (Woodley and Gaskin 1996, Ingram et al. 2007, Vikingsson et al. 2015, Schleimer et al. 2019).

In Svalbard, fin whales were observed with greatest densities amongst others along the continental slope to the west and north of Spitsbergen before (Storrie et al. 2018). The front between polar and Arctic water, around the slope of the Greenland Plateau, attracts many fin whales (Joiris 2012). Here, slope had a strong impact on habitat suitability, which increases with increasing slope, demonstrating steeper regions to be favored. By contributing to the model with a PI of 7.8 and lower model performance when left out of the model, it indicates an important environmental variable, underlying fin whale distribution.

4.3.5 Sea Surface Temperature

The variability of sea surface temperature throughout summer months had a relatively high impact on the distribution of fin whales (PI = 7.8). When used alone, it was among the most contributing variables, while when excluded it does lead to a decrease in regularized training gain (see Jackknifing results; Figures 9 and 10). Highest habitat suitability was predicted at locations with very low sea surface temperature variability (Fig. 15), indicating a preference of fin whales to areas with homogenous sea surface temperature (SST) during summer. Though mean SST or deeper in the water column were not included in the model, a preference for rather cooler water, given other studies and the other results of this study, is likely. In other areas, highest densities of fin whales were significantly higher in relatively cool waters than elsewhere (Forcada et al. 1996). Fin whales are distributed in ice-free areas of Arctic water masses and the colder parts of Atlantic water masses (Nottestad et al. 2014). Due to only small differences in temperature throughout the water column, currents within the Barents Sea are barotropic and stratification is mainly determined by salinity changes (Ingvaldsen and Leong 2009, Tomczak and Godfrey 2013). The fresher, lighter waters stay in the upper layer and form the Polar Mixed Layer, one of the three water masses of the Arctic Ocean (Tomczak and Godfrey 2013). Stratification is generally weak in winter, but increases in spring, due to increasing temperatures and freshwater inflow (of sea ice melting). The timing of this stratification has a clear impact on the timing and development of spring phytoplankton bloom (Ingvaldsen and Loeng 2009), which might make water temperature a direct link or indicator to prey resources. Therefore, an interrelation between the preference of low variability in SST and prey is likely, though, here, it is not clear to which extent.

4.3.6 Other variables

Several environmental variables were of negligible importance within the habitat suitability model. These variables comprise: variability of sea surface salinity, distance to 500 m isobath, variability of sea surface height, mean velocity, mean sea ice concentration, variability of temperature at 100 m depth, variability of chlorophyll-a, and aspect. A potential explanation for differing important environmental variables are of course the variability of the ecosystem and different ecological needs in different regions. As whales are migratory, breeding in lower latitudes in winter while mainly feeding at higher latitudes in summer (Stern 2009, Silva et al. 2019), environmental variables underlying their distribution probably deviates according to their needs. One would, for instance, expect environmental variables that act as proxy to feeding in summer, while in winter, during breeding season, it would be EVs that are linked to breeding. In the Arctic, northward expansion of fin whales has been noted, with increasing sightings in coastal environments and occasionally habitat shifts into deeper waters (Vikingsson et al. 2015, Storrie et al. 2018). This might lead to fluctuations within favored habitats of fin whales during the past decade and could potentially mask the effectiveness of habitat suitability models, due to temporal variation. This, of course, complicates modelling and might lead to an underestimation of important covariates. Observations of environmental change in the study area extend these issues and include increased water temperatures, a temporal shift in phytoplankton bloom and a general decrease in zooplankton biomass (Rey 2004, ICES 2010 a,b, Huse et al. 2012). As effects of anthropogenic activities are spatially heterogeneous, the intensity of the responses of marine predators to human activities may vary, such as some species being more vulnerable in specific areas of their range (Trathan et al. 2007). Predicting the effects of anthropogenic changes on marine predators is complex and does largely depend on individual responses of the species towards changes in the environment (Harley et al. 2006, Brook et al. 2008). Former SDMs indicated that fin whale distribution was characterized by water depth, distance to 200 m and 2000 m isobath, SST and SSH and chlorophyll-a concentration (Vikingsson et al. 2015, Zerbini et al. 2016). While distance to 200 m and 2000 m isobath were not included in the model and therefore not linked to fin whale occurrence, all other variables were in some form included. The predicted highest abundance of fin whales around 2000 m isobaths and virtual absence from shallow coastal waters of Iceland in a previous study were in accordance with the preference of fin whales' regional main prey *M. norvegica* to deeper waters (Vikingsson et al. 2015). Within this study though, no tendency towards any isobath was found. Important to note though, is the potential correlation of variables, as e.g. distance to shore or bathymetry might act as proxies for other EVs such as distance to isobath. The fact that no relation was found between fin whale occurrence and chlorophyll-a concentration or sea surface temperature might also be due to differences in between studies of temporal and/or spatial resolution. Here, for example, an 8-day-composite of chlorophyll-a concentration was used. Despite deviances in data sources, it should be considered that fin whales might favor different habitats linked to different EVs, not only in their feeding or mating habitat, but potentially between different longitudes and/or latitudes.

4.4. General considerations

As the distribution of whales at their summer feeding grounds is most likely linked to food sources, different environmental variables can be of higher importance than others. Especially because prey often forms the missing link between oceanographic variables and higher-trophic level predators (Croll et al. 2005, Friedlaender et al. 2006, Doniol-Valcroze et al. 2007, Anderwald et al. 2012). Additionally, at small spatial scales (e.g. metres to few kilometres), highly dynamic avoidance by prey could result in hardly noticeable, dynamic spatial associations between predators and prey (Fauchald 2009). Ergo in pelagic systems, beyond environmental variables, predator-prey associations are likely important effects that are scale-dependent (Fall and Skern-Mauritzen 2014). Another important fact when considering scales in SDMs is the temporal variability in prey preference: Schleimer et al. (2019) found evidence that habitat use of fin whales in the Gulf of St. Lawrence changed as the season progressed, which might be linked to switched prey preferences. Euphausiids are an integral part of the generalist diet of fin whales, though these whales were suggested to be flexible feeders, as they are known to switch prey depending on availability and sex (Gavrilchuck et al. 2014, Ressler et al. 2015). If fin whales vary in prey preferences, most likely different EVs favor the occurrence of these prey species. Unravelling the mechanisms that lead to the formation of a species ecological niche requires small-scale habitat research, investigating both prey distribution and associated predatory behavior, as well as potential predator avoidance strategies by the prey (Bombosch et al. 2014). To gain a better understanding of the influence of prey on habitat models and their feeding ecology, it is important to have high spatiotemporal synchrony in the collection of prey and cetacean data, to quantify their relationship (Laidre et al. 2010). Especially threshold values at which prey switching occurs could be an important factor to which models need to be adjusted spatially and /or temporally. As the distribution of highly mobile marine predators, to which fin whales belong, is not static, temporal variation needs to be taken into account. For instance, habitat suitability of humpback and minke whales in the Antarctic was found to be highest in coastal areas at the end of the season (Bombosch et al. 2014). Even at smaller temporal scales, the resolution might be of high importance: Fin whales are known to dive longer and most likely deeper during the day than the night (Watkins et al. 1984, Stone et al. 1992), therefore a temporal variation in habitat suitability of environmental variables is possible.

4.5. Limitations

Citizen science has provided useful insight into the abundance and distribution of cetaceans (Cheney et al. 2013, Beck et al. 2014, Bruce et al. 2014) and is expected to be helpful for many more studies in the future. The data logging software 'Walog' (Burkhardt 2009), which was used for the collection of Polarstern data, enabled high-quality acquisition of species data and is considered a useful tool for citizen science. After appropriate instructions to the user, similar approaches could be used on whale-watching boats and research vessels. However, it is important to note that Polarstern sightings were not part of systematic surveys and typically come from independent, random survey designs, so one cannot estimate sampling effort using similar datasets. Using Polarstern data alone, due to small data, would not have been sufficient for the analysis. Therefore, it was important to include open source data, such as GBIF or iOBIS, without which model performance would have most likely been weaker. To obtain more reliable data and to be independent from open-source data, surveys such as from Polarstern, should be dedicated or compromised towards a general research goal. For example, personnel could be employed to constantly whale watch and log. Also, investigating an unsampled part of the study area to address a larger variety of environmental variables could be a reasonable addition. As possibly different environmental variables are linked to different prey types, this could ideally complement the model, as it is possible that different prey is targeted in different areas. The suggestions above could make SDMs in the Arctic or Antarctic much more robust and accurate.

Some considerations should be taken into account when interpreting the results, though, as biases do exist according to study design (e.g. in the form of easily accessible areas for citizens). There is the possibility of species misidentification, though this uncertainty can be considered low for the Polarstern data, as only sightings of high certainty of identification were used.

Also, habitat models can only estimate the part of a species „niche", which was captured by the sighting, therefore the applicability to unsampled areas is depending on the representativeness of the prevalent environmental conditions (Bombosch et al. 2014). This study, as well as other modelling studies, suggests that fin whales occupy a broad range of habitats, with the most suitable ones occurring along the steeper areas of the continental slope and around the 500 m depth contour (Storrie et al. 2018). Even though the latter did not significantly contribute to model performance, we found highly important factors, such as distance to shore and distance to sea ice edge or mean salinity at 100 m depth, bathymetry, standard deviation of SST and slope. It is conspicuous that many of these variables are static variables. This might be of various reasons and potential errors in remotely sensed data should always be considered. One reason to think of is that oceanographic processes are often tightly coupled to the physical environment, such that upwelling is often linked to bathymetry or slope. Environmental conditions that allow dense aggregations of prey occur in coastal zones, upwelling areas, fronts and/or offshore regions of high productivity (Croll et al. 2005, Johnston et al. 2005, Doniol-Valcroze et al. 2007, Gill et al. 2011, Visser et al. 2011), which might have enhanced habitat suitability within this study. Another reason might be spatially and/or temporally too coarse environmental variables. A limitation within this work was the circumstance that no directly prey-linked variables were available and could therefore not be included in the analysis. It would have been interesting to see if there was a link between e.g. krill or fish abundance and habitat suitability of fin whales. Especially, as fin whales are known to target krill, capelin and blue whiting depending in the region (e.g. Skern-Mauritzen et al. 2011, Nottestad et al. 2014). In a recent study by Schleimer et al. (2019), a positive correlation was found between krill biomass and fin whale numbers. Anyhow, another model, comprising bathymetric and oceanographic variables, was built in the same study and was proven to be more robust than the krill model (Schleimer et al. 2019). This demonstrates the necessity of a comprehensive consideration of model input and combination of environmental variables as well as model settings optimization. Further, it is important to note that fin whales distribution in the study area could also be linked to EVs not currently available at appropriate spatial and/or temporal resolution. After all, it is important to note that the results of this study are only valid within the study area and must not be transferred for other areas, e.g. such as the Mediterranean. The model is trained with a specific range of values for environmental variables, so that projecting this beyond the study area can be subject to high uncertainty. Additionally, the model is only valid in summer for the same reasons.

4.6 Outlook

Overall, environmental changes, such as increasing SST or the decline in sea ice extent, which were observed over the past decades (e.g. Stroeve et al. 2012, Overland and Wang 2013, Pistone et al. 2014), most likely have affected cetacean distributional patterns. If environmental variables are thought to have a direct influence on cetacean distribution, a change in EVs will most likely lead to a change in distribution. For example, water masses, fronts, pack ice and ice edge are known to be the main hydrographic factors influencing the distribution of the upper trophic levels in the ocean (Joiris et al. 2014 and references therein). Fluctuations in the usage of habitat is mostly determined by multiple oceanographic variables and their effects on prey distribution and abundance (Croll et al. 2005, Doniol-Valcroze et al. 2007, Gill et al. 2011). If sea ice-loss extends, and the increases in water temperature and inflow of the water mass from the Bering Sea continue, the distribution range of fin whales in the Arctic Sea will extend (Tsjuii et al. 2016). Therefore, temporal resolution of EVs should play an important role in SDMs. Baleen whales constitute important top-down regulators of the marine ecosystem (Bowen 1997, Simon et al. 2010). It has been argued that as significant regulation of zooplankton and fish occurs, top predator responses to different prey regimes determine both structure and functioning of an ecosystem (Dalpadado et al. 2003, Gjosaeter et al. 2009, Skern-Mauritzen et al. 2011). These relationships should therefore, especially in times of climate change, be investigated and built into future models. Machine learning methods can be very powerful and helpful tools to protect marine species due to above stated reasons. In this study, it was possible to identify areas of high interest for fin whales and model their potential distribution accordingly. Opportunistic sighting data has proven its suitability for using in SDMs. Important EVs were identified, and possible mechanisms, underlying distribution, were unravelled. It can be expected that many more of these studies will emerge in the future, either using citizen science or other scientific studies. Our study further demonstrates the utility of species distribution modelling in hardly accessible areas, where sighting data is scarce. It is an important tool to model the distribution of marine species that is cost-effective and can aid in conservation measures. This might include prediction maps for mitigation of fisheries, seismic surveys, etc. It can enhance research in forms of informative prediction maps, inspiring studies of rather restricted areas, where species occurrence is expected to be high. This provides researchers with the opportunity to confirm on habitat suitability maps, as yet unsampled areas could be investigated. In general, this study has shown that citizen science and open source data can enhance and supplement research, if data are treated accordingly.

APPENDIX

Appendix A

Response curves of all environmental variables < 6 % permutation importance

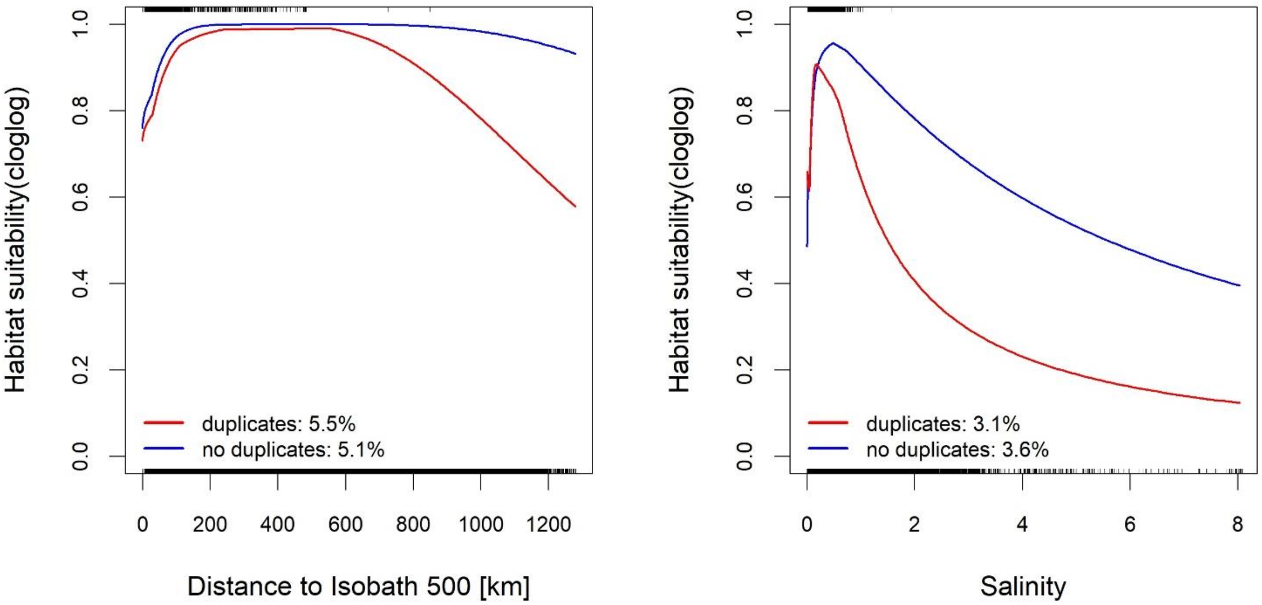

Fig. 1: Response curves for distance to isobath 500 (left) and sd of salinity (right). Ticks on the upper axis represent values at occurrences, while ticks on the lower axis represent values at background locations. Number after model name indicates the permutation importance of the respective variable.

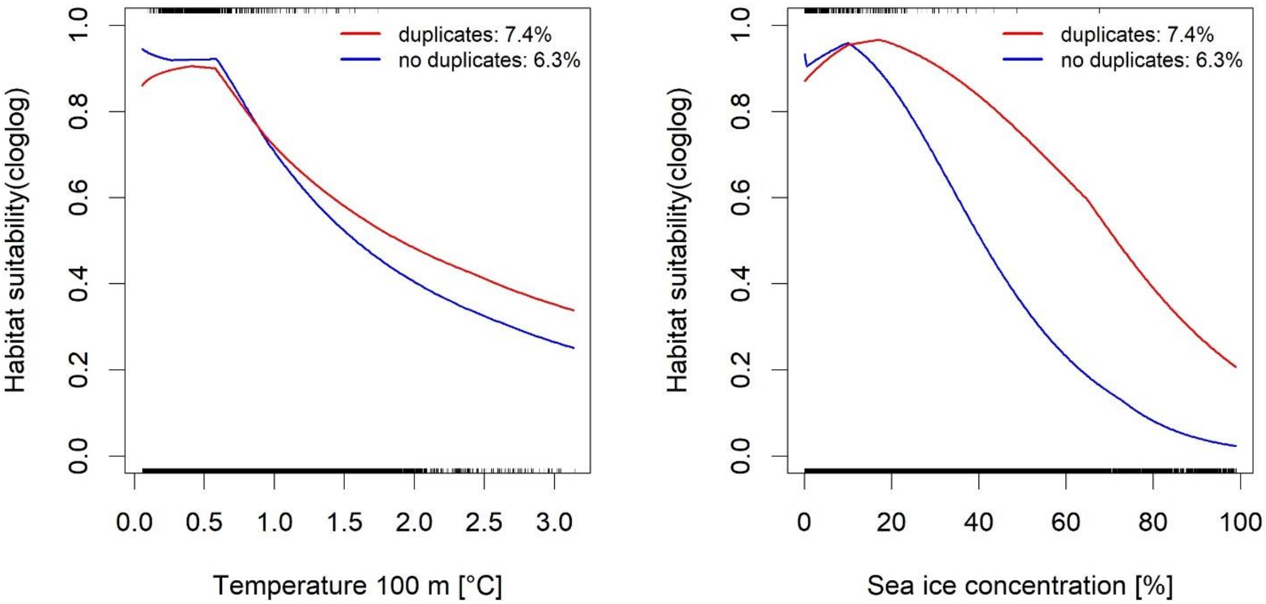

Fig. 2: Response curves for temperature at 100 m (left) and sea ice concentration (right). Ticks on the upper axis represent values at occurrences, while ticks on the lower axis represent values at background locations. Number after model name indicates the permutation importance of the respective variable.

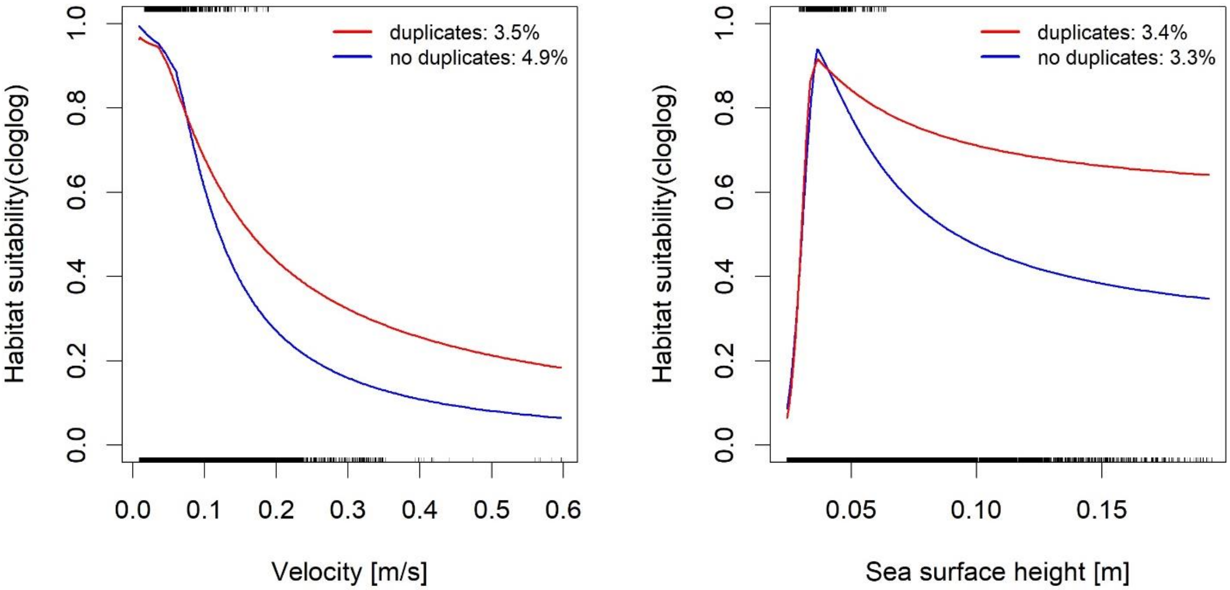

Fig. 3: Response curves for velocity (left) and sea surface height (right). Ticks on the upper axis represent values at occurrences, while ticks on the lower axis represent values at background locations. Number after model name indicates the permutation importance of the respective variable.

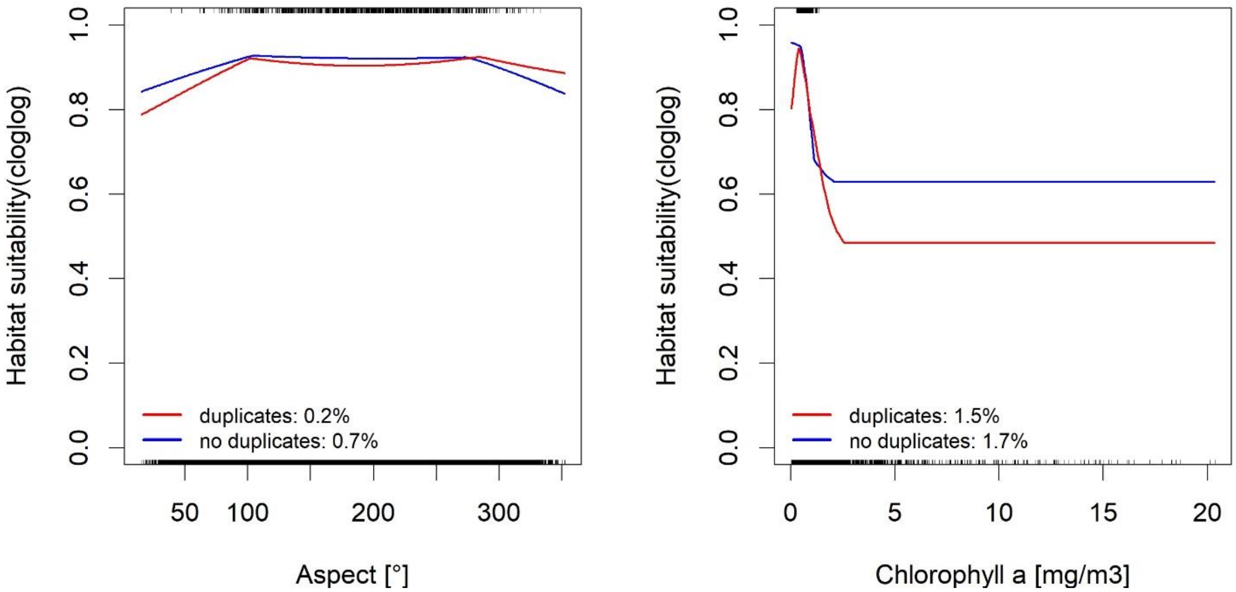

Fig. 4: Response curves for aspect (left) and chlorophyll-a (right). Ticks on the upper axis represent values at occurrences, while ticks on the lower axis represent values at background locations. Number after model name indicates the permutation importance of the respective variable.

Appendix B

R Scripts

 # Protocol for assessing multicollinearity

```
evs_vifstep <- vifstep(evs,th=4)
# 9 variables from the 24 input variables have collinearity problem:
#   Temp0mean Sal0mean Temp100mean Dist2Iso100SQRT SSHmean Sal100STDlog VeloSTD ChlaMean SICstd
# After excluding the collinear variables, the linear correlation coefficients ranges between:
#   min correlation ( Slope ~ SICmean ):  0.003267862
# max correlation ( Dist2Iso200SQRT ~ Bathymetry ):  -0.7261775
evsSmall <- evs[[as.character(evs_vifstep@results$Variables)]]
evs_vifcor2 <- vifcor(evsSmall,th=0.7)
evsSmall2 <- evs[[as.character(evs_vifcor2@results$Variables)]]
evsSmall2 <- stack(evsSmall2, evs$Temp0mean, evs$Temp100mean, evs$SICstd)
evs_vifstep2 <- vifstep(evsSmall2, th=4)
evs_vifcor3 <- vifcor(evsSmall2, th=0.7)
AA <- sort(as.character(vifcor(evsSmall2, th=0.7)@results$Variables))
BB <- sort(as.character(vifcor(evs,th=0.7)@results$Variables))
AA[-which(AA %in% BB)]
BB[-which(BB %in% AA)]
evsD <- as.data.frame(evs,na.rm=T)
evsD <- cor(evsD)
class(evsD)
corrplot(evsD,method="circle")
```

 # spatialBlock function protocol

```
ValsOcc <- extract(x = evsub$Aspect, y = Occ)
ValsNAs <- which(is.na(ValsOcc))
spRange <- spatialAutoRange(rasterLayer = evsub, speciesData = Occ) # distance 453767
sb2 <- spatialBlock(speciesData = FinSP,species = "species",rasterLayer = evsub, maskBySpecies=F,
        theRange = 453767, k = 4,  selection = "random",  iteration = 500)
```

```
foldExplorer(sb, evs, FinSP)

foldExplorer(sb2, evsub, FinSP)

save(spRangeRMDUPS, sbRMDUPS, sbRMDUPS2, FinSPRMDUPS, file = "D:/MA real Arctic AWI/Analysis_R/SAC_RMDUPS.RData")

BlockMaskRMDUPS <- rasterize(sb2$blocks[, "folds"], evsub$Bathymetry, field = sb2$blocks$folds)

BlockMaskRMDUPS <- mask(BlockMaskRMDUPS, evsub$Bathymetry)


# ENMeval function protocol

PresXY <- sp::coordinates(OccRM)

PresCV <- raster::extract(BlockMaskRMDUPS, PresXY)

BackXY <- raster::as.data.frame ( x = BlockMaskRMDUPS,  xy = T, na.rm = T)

BackCV <- BackXY$layer

BackXY <- BackXY[, c("x", "y")]


It3000RMDUPS <- ENMevaluate(occ = PresXY, env = evsub, bg.coords = BackXY, occ.grp = PresCV, bg.grp = BackCV, algorithm = "maxent.jar", method = "user", overlap = T,  bin.output = T, parallel = T,progbar = T, numCores = 4, maximumiterations = 3000,  removeduplicates = "false")

Save (It3000RMDUPS, file="D:/MA real Arctic AWI/Analysis_R/It3000RMDUPS.RData")


It3000RMDUPS@models

max(sapply(1:48, function(x){  It3000RMDUPS@models[[x]]@results[4]}))

It3000RMDUPS@algorithm

It3000RMDUPS@results

It3000RMDUPS@predictions

Max_TAUC_ID <- which.max(It3000RMDUPS@results$avg.test.AUC) #the item with the highest T.AUC

Plot (It3000RMDUPS@predictions[[Max_TAUC_ID]], main="AUC")

AA1 <- as.character(It3000RMDUPS@results$settings[Max_TAUC_ID])

plot(It3000RMDUPS@predictions[[AA1]], main="AUC")

It3000RMDUPS@results[order(It3000RMDUPS@results$avg.test.AUC, decreasing = T),]

It3000RMDUPSsubset <- It3000RMDUPS@results

It3000RMDUPSsubset <- It3000RMDUPSsubset[-which(It3000RMDUPSsubset$features == "LQHPT"),]

save(It3000RMDUPSsubset, file="D:/MA real Arctic AWI/Analysis_R/It3000RMDUPSsubset.RData")
```

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Hiermit versichere ich, dass ich diese Arbeit selbstständig verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Außerdem versichere ich, dass ich die allgemeinen Prinzipien wissenschaftlicher Arbeit und Veröffentlichung, wie sie in den Leitlinien guter wissenschaftlicher Praxis der Cal von Ossietzky Universität Oldenburg festgelegt sind, befolgt habe.

Oldenburg, den 24.09.2019

Diandra Düngen