

Spatiotemporal distribution of killer whales
(*Orcinus orca*) along the Norwegian coast: A MaxEnt
species distribution model including citizen science data

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Norwegian Orca Survey



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A citizen science approach: assessing environmental influences on seasonal distribution of killer whales (*Orcinus orca*), in Norwegian waters

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Abstract

In Norway, killer whales (*Orcinus orca*) are known to mainly prey on the Norwegian Spring Spawning (NSS) Stock of the Atlantic herring (*Clupea harengus*), following their migration up north during the winter. This has led to large assemblies of killer whales and herring, which has instigated research on killer whales in the northern regions. However, little is known about the distribution of killer whales in the central and southern parts of Norway. This study examines the value of citizen science in complementing data for killer whale distribution, while using this data for the creation of a species distribution model that produces relevant ecological knowledge on the distribution of killer whales. This was done by collecting observational data on killer whales through a variety of sources, including citizen science, to create a species distribution model using the maximum entropy (MaxEnt) method. Three different season-specific models were fitted, based on the seasonal migration patterns of the NSS herring (season 1 = Sept - Jan, season 2 = Feb - March, season 3 = April - August). In addition, a questionnaire survey was generated to investigate new distribution patterns in the two largest fjords in Norway, Sognefjord and Hardangerfjord. This study demonstrates that citizen science can be used to map and document the presence of cetaceans and that data derived from citizen science can be used as a part of ecological modelling applications. Citizen science together with other sources, synthesized a large amount of data with a broad spatial coverage, resulting in a dataset of 4372 observations. Results from the questionnaire indicated that the presence of killer whales in Hardangerfjord and Sognefjord is a new phenomenon. The MaxEnt model, which used 3536 of observations from the dataset, was able to successfully discriminate distribution patterns for killer whales in Norway with AUC levels > 0.9 (season 1 = 0.909, season 2 = 0.907, season 3 = 0.901). The most important environmental variables contributing to killer whale distribution in the MaxEnt model were herring, distance to coast, salinity, sea bottom temperature and chlorophyll *a* concentration. In addition, this research has highlighted the value of citizen science as a tool in ecological research, and established a baseline for the distribution of killer whales in Norway, with new knowledge on important environmental parameters that can be used in future research.

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1. Introduction

Understanding the distribution patterns of a species is an important topic in biology and biogeographic research. Species distribution is dependent on specific factors such as prey resources and direct physical effects (e.g. temperature and pH) which make a habitat suitable (Miller, 2010). Monitoring the species distribution of wide-ranging marine predators can be challenging due to the logistical difficulties and high cost associated with the tracking of highly mobile species. An approach to mitigate these challenges is by collecting data from citizen science initiatives. Additionally, Species distribution models (SDMs) constitute a valuable tool, as they provide information on distribution and habitat preferences. SDMs can be used in conservation research to determine whether any conservational actions are needed (Evans and Hammond, 2004).

1.1 Citizen science

Citizen science is aid from the general public to scientific research, with the guidance of professional scientists (Earp and Liconti, 2020a). Collecting data using citizen science has several benefits for a project, including increased sample size from a larger workforce, while reducing cost effects. It's a beneficial tool that enlists the general public in scientific discovery and it is particularly important in biodiversity research as large numbers of abundance and density taxa are determined by citizen science projects. It is particularly useful in the marine environments, to track widely mobile megafauna across larger regions and habitats (Theobald et al., 2015, Burgess et al., 2017). As marine legislations are becoming more complex, the use of citizen science to collect and obtain data can help with the increased need for larger datasets (Hyder et al., 2015). Studies have shown that the use of citizen science can provide data on various species, and can help manage populations, e.g., by establishing the need for marine protected areas (MPAs) and later monitoring them (Van Strien et al., 2013, Sullivan et al., 2009). Citizen science can also provide data at a large spatial and temporal scale which is helpful in the research on distribution of far ranging coastal cetaceans (whales), like the killer whale (Earp and Liconti, 2020b, Delaney et al., 2008, Silvertown, 2009). It additionally generates trust and increases interest for a topic in

the general public, which can indirectly lead to efficiency in future decision making of management and conservation, by motivation fulfilment (Hyder et al., 2015, Glenn et al., 2012, Weichselgartner and Kasperson, 2010).

An ongoing citizen science program by the Cornell Lab of Ornithology (CLO) and the National Audubon Society called eBird was launched in 2012, and uses the internet as a tool to gather information on birds. A network of human observers provides bird observations to monitor the distribution, abundance and potential patterns across spatiotemporal scales (Sullivan et al., 2009). This program later developed into a collective enterprise with partners of experts within fields of conservation biology, population and distribution biology, statistics and quantitative ecology (Sullivan et al., 2014). Another ongoing citizen science initiative is the Norwegian Biodiversity Information Centre (NBIC), "Artsdatabanken". The NBIC was established in 2005, as a respond to the Norwegian governments increased focus on biodiversity. The program was previously a part of the Ministry of Education and Research, but has since 2018 been independent, under the Ministry of Climate and Environment, but with their own board (Artsdatabanken, 2014a). The NBIC collects data from a wide range of sources, and collaborate with several experts within the field of biology. The program leverages the general public's observations to gather observational data on species in Norway. These observations are then verified by experts. Several million geospatial observations have been gathered by the NBIC and are available through maps and lists, for everyone to use (Artsdatabanken, 2014b).

Even though it's not a new tool, citizen science has recently gained significant popularity, as shown by the increased number of studies utilizing it (Earp and Liconti, 2020b, Burgess et al., 2017). Despite this, it is not fully embraced by the scientific community, and guidelines for best practices remain undefined (Cohn 2008; Silvertown 2009; Bonney et al. 2014; Burgess et al. 2017). One of the main concerns and a frequent discussion around the topic of citizen science is the quality control of collected data (Crall et al., 2010, Ellwood et al., 2017). Another concern is the lack of structure which can disrupt the requirements of strict assumptions for data used in statistical analysis. To address this, precise protocols can be implemented when validating sampling data to reduce sampling biases and eliminate the need for such strict assumptions (McDuffie et al., 2019). Providing quality data is crucial to create

credibility, and previous studies have shown that citizen science projects can provide sufficient data, where maximum dividend is achieved after data validation and verification (Hyder et al., 2015). Another challenge involves engaging the general public in a project. Motivating participants to actively get involved is important for the success of citizen science projects (Prestopnik and Crowston, 2012, Rotman et al., 2012).

When studying the wide ranged distribution of killer whales with daily migrations of several kilometres (5-98 km/day) (Dietz et al., 2020), collecting information can require large workforces. The Norwegian Orca Survey (NOS) has since 2013 had an ongoing monitoring project, recording the year-round occurrence of killer whales in Norway. Additionally, they established a citizen science initiative in 2016 to gather observational data on killer whales, with an online platform to invite various wildlife enthusiasts, photographers and the general public to contribute their killer whale images and observations (Jourdain and Karoliussen, 2021). With NOS' research activities being mostly limited to northern Norwegian regions, help from the general public made it possible to extend their ongoing monitoring of Norwegian killer whales to also include encounters from all parts of Norway (Eve Jourdain, 2017). A part of their project has been to photo-identify killer whales, using the Bigg (1982) method, examining the individual's shape and natural markings of the dorsal fin and adjacent saddle patch. Each individual killer whale was given a specific ID-code and the results were put in an extensive ID-catalogue that constitutes the foundation of past and ongoing studies (Jourdain and Karoliussen, 2021).

1.2 Species distribution models

Species migration is found in all major animal groups of fish, invertebrates, turtles, pinnipeds, sharks, and cetacean's to track temporal and/or spatial changes in e.g. climate, feeding resources and breeding areas (Dingle and Drake, 2007). To examine the potential geographic range of a species and the environmental drivers behind its spatial distribution, the use of Species distribution models (SDMs) have become widely popular (Jones et al., 2019). SDMs are known as habitat suitability models or ecological niche models, and have become a fundamental tool in ecology, biogeography and conservation (Merow et al., 2014, Guisan et al., 2013, Zimmermann

et al., 2010, Franklin, 2010). They have rapidly increased concurrent with the rise of good statistical techniques and Geographic Information System (GIS) tools, as well as increased availability of ready-to-use environmental datasets (Phillips et al., 2006b, Guisan and Zimmermann, 2000). SDMs relate the geographical distribution of a species to its present environment, to map suitable habitats and/or distribution (Guisan and Zimmermann, 2000). Most of the SDMs approaches rely on both presence and absence data to create regression-based models using general statistical methods, like the generalized linear model (GLM), the generalized additive models (GAM), or classification and regression trees (CART) (Guisan and Zimmermann, 2000). However, there is limited availability of absence data, making modeling techniques that require only presence data very valuable (Graham et al., 2004). Obtaining absence data for cetaceans is particularly difficult as they are highly mobile species. Additionally, they can be hard to identify, as encounters often occur from far distances. The lack of absence data is particularly found in areas where conservation actions are needed and sampling data has been insufficient (Anderson et al., 2002, Ponder et al., 2001, Soberon, 1999). Detecting a species can be difficult due to the complexity of marine habitats, leading to the requirements of e.g. expensive equipment. This is particularly the case for offshore and sub-surface studies (MacLeod et al., 2008), which specifically regards the cetacean species. Therefore, the interest in SDMs with presence-only data has increased (Pearce and Boyce, 2006), and been used in several studies researching distribution of cetaceans (Jones et al., 2019, Edrén et al., 2010).

A technique using only presence data to model the geographical distribution of a species is the Maximum Entropy (Maxent) method by Phillips et al. (2006b). The method combines the species environmental requirements from spatial occurrence data together with specific environmental parameters. Based on these, the method describes important factors impacting distribution of a species and/or its preferred habitat (Phillips et al., 2006b). The model assumes that for a short period of time the distribution is at equilibrium with relevant environmental factors, while experiencing only small disturbances (Hirzel and Guisan, 2002). The MaxEnt algorithm requires a collection of geographical occurrence data, such as observational data, and a set of ecologically relevant environmental predictors. From this, it generates pseudo-

absence data from the background points to replace absence data (Phillips et al., 2006a).

The principle of the Maximum entropy model is derived from E.T Jaynes (1957) approach to finding the best way to estimate the unknown probability of distribution. He proposed that the best approach is to ensure that any limitations on the unknown distribution are met and the distribution should have maximum entropy within those limitations. This is known as the maximum-entropy principle, and the MaxEnt machine learning algorithm searches for the probable distribution with the highest entropy (defined as a measure for randomness or disorder in a physical system) (Phillips et al., 2006b, Jaynes, 1957, Ignatov, 2011).

1.3 Killer whale (*Orcinus orca*, Linnaeus 1758)

Killer whales (*Orcinus orca*) are apex predators and the most widely distributed species of marine mammals, with patchy distribution across all of the Earth's oceans (Forney et al., 2006). They are most common in coastal areas, particularly in cold to temperate waters of high latitudes, nonetheless they also occur in offshore and tropical waters (Forney et al., 2006). Killer whales are highly social animals with group structures tightly knitted around females in so called matrilineal pods, i.e., the pod is based around mothers and their offspring (Bigg et al., 1990, Brent et al., 2015). A pod usually consists of mature females, their offspring and a varied proportion of males and post-reproductive females (Brault and Caswell, 1993a). Social pods use clicks, pulsed calls, and whistles to communicate. These differ from each other in vocal repertoire where different pods have special dialects of whistles (Brault and Caswell, 1993b, Ford, 1991, Au, 1993, Simon et al., 2007). The size of a killer whale pod can range between approximately 5 and 63 individuals (Brault and Caswell, 1993a, Katona et al., 1988, Hoelzel, 1991), and vary in relation with target prey and prey abundance (Nøttestad et al., 2002, Nøttestad et al., 2014, Jourdain et al., 2017).

Killer whales are considered generalists due to their broad diet consisting of over 140 known prey species, including mammals, fish, squids, birds and reptiles (Forney et al., 2006, Jourdain et al., 2017, Ford, 2009). However, regional populations often adopt specialized diets and behavior based on prey availability (Nichol and Shackleton, 1996,

Ford et al., 1998, Ford and Ellis, 2014, Jourdain, 2020). Behavioral adaptations to foraging on a narrow range of prey may, in some cases, lead to social segregation caused by cultural barriers. That is, individuals may prefer interacting with others that adopt similar feeding behaviors, further restricting social contacts and leading to reproductive isolation among ecotypes (Riesch et al., 2012). Ecotypic forms documented so far differ in behavior, morphology, pigmentation, acoustics and genetics (LeDuc et al., 2008, Ford et al., 2011, Hoelzel et al., 2007, Foote et al., 2011, Pilot et al., 2010). In the North Pacific Ocean three distinct ecotypes have been described based on these factors: the “resident”, “transient” and “offshore type” (Dahlheim et al., 2008, Foote et al., 2009, Ford et al., 1998, Herman et al., 2005). The “resident” ecotype primarily feed on fish, and more specifically salmonids, the “transient” ecotype specializes on marine mammal prey and the “offshore” ecotype appears to primarily feed on sharks and other high trophic level fish (Herman et al., 2005, Ford et al., 1998). Ecotypic differentiation is less clear in other parts of the world (Foote, 2023).

In the North Atlantic Ocean (NA) two distinct killer whale ecotypes have been suggested by Foote et al. (2009), based on tooth-wear and analysis of nitrogen stable isotopes. Type 1 is the generalist killer whale, feeding mainly on fish, but also on marine mammals to some extent. Type 2 is the potential exclusive mammal eater, where the main part of their diet may consist of baleen whales (Foote et al., 2009). It has been suggested that the Type 1 fish eating killer whale consists of three different populations based on available prey resources: herring (*Clupea harengus*) - feeding, mackerel (*Scomber scombrus*) - feeding and tuna (*Thunnus* spp.) - feeding (Foote et al., 2011). However, recent research highlighted that classifying North Atlantic killer whales into these two ecotypes was over simplistic, in the light of much dietary variation occurring within populations. Consequently, these ‘types’ should no longer be used (Foote, 2023).

Killer whales are found throughout Norwegian coastal waters with higher abundance in areas where the Norwegian spring spawning (NSS) stock of Atlantic herring is also abundant, for e.g., at herring wintering and spawning grounds (Similä et al., 1996). NSS herring is one of the largest fish stocks in the world and are found in large parts of the Norwegian Sea during their feeding period (April-August) (Bachiller et al., 2016).

During their wintering period (September-January) the herring gather in northern Norwegian fjords. For the last decades, assemblies of killer whales have gathered here to feed on the overwintering stock, creating a large aggregation of herring and whales. This aggregation has since 2012 occurred off the coast of Troms (Dietz et al., 2020). After the wintering period in mid-January, the herring starts migrating southwards. This leads to the redistribution of the herring stock throughout several spawning grounds between Lofoten and Lista (69N - 58N), with main spawning ground off Møre (64-62) (Slotte, 1999). The NSS herring stock's population dynamics are highly fluctuating, and spawning, feeding, and wintering grounds may change from one year to the next (Huse et al., 2002, Huse et al., 2012).

Most of the studies on killer whales in Norway have been conducted in the north, where large assemblies of killer whales gather for seasonal feeding on the NSS herring (Similä et al., 1996, Bisther and Vongraven, 1995). However, recent studies have shown observational evidence of Norwegian killer whales preying on marine mammals like the harbour porpoise (*Phocoena phocoena*), grey seal (*Halichoerus grypus*) and harbour seal (*Phoca viulina*) (Cosentino, 2015, Vongraven and Bisther, 2014). One of these was a longitudinal study by Jourdain et al. (2017) that documented persistent feeding on seals in the Norwegian coastal waters for at least 30 years. Additionally, lumpfish (*Cyclopterus lumpus*) was newly documented by Jourdain et al. (2020b) as a prey species for Norwegian killer whales. Moreover, the study found behaviour of seasonal adaptations between prey resources and feeding strategies within the pods, where the pod size adapted over the year according to prey abundance. Another study from Jourdain et al. (2020a) further investigated the different dietary variations in Norwegian killer whales by looking at stable isotopic nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) ratios. The study found possible dietary patterns among Norwegian killer whales, ranging from fish eaters (herring and lumpfish) to seal-eaters. The seal-eaters were found to have a diverse diet consisting of both fish and marine mammals, eating from a higher trophic level throughout the year, with elevated nitrogen values in their skin (Jourdain et al., 2020a). Other prey species reported for the Norwegian killer whales include cod (*Gadus morhua*), lumpfish, Atlantic salmon (*Salmo salar*), Atlantic mackerel, saithe (*Pollachius virens*) and eider duck (*Somateria molissima*) (Nøttestad et al., 2014, Similä et al., 1996, Vester and Hammerschmidt, 2013, Jourdain et al., 2021). The population size of the Norwegian killer whale has been estimated to consist

of 15056 (CV = 0.29, 95% CI: 8423–26914) individuals, using line-transect surveys (Leonard and Øien, 2020). A study by Jourdain et al. (2021) further investigated the abundance of killer whales in Norway. The study highlights line-transect survey methods as insufficient for estimating Norwegian killer whale abundance during the last 20 years. Here, a smaller and more defined area was used to estimate the abundance of killer whales at herring wintering grounds in northern Norway, by using a capture-recapture model with photo-identification data spanning 32 years. The model estimated a peak in abundance in 2015 with an estimate of 1061 individuals (CV = 95% CI: 999–1127) and a drop to 513 whales (CV = 95% CI: 488– 540) in 2018.

1.4 Aims

The initial focus in this study was to analyse observations and acoustic recordings of killer whales in Hardangerfjord on the west coast of Norway, to investigate the migration patterns of two killer whale pods. The two pods are known to frequently enter Hardangerfjord. However, it turned out that the acoustic recordings were not suitable to reliably identify killer whales. Therefore, the aim of the study was changed, and the scale extended to instead look into the distribution of killer whales along the entire Norwegian coast. Because of the initial aim, some of the data collected in a media analysis were solely gathered from the west coast. The implications that this may have for the results are discussed in section 4.

Almost all studies on killer whales in Norway have been conducted in the northern region. The lack of studies in the southern part of Norway represents a missing piece in our understanding of the Norwegian killer whale spatial distribution and habitat use. Little research south of Lofoten is the consequence of the limited potential for dedicated fieldwork, due to logistical challenges like the rough waters outside the coast of e.g., Møre. Additionally, the unpredictable killer whale presence in the south, where there is no real distribution pattern, has made research challenging. Although there is evidence of killer whale occurrence along the entire Norwegian coastline (Christensen, 1988), there is no recent observational data to study their distribution. Therefore, observational data from a variety of sources were collected over the past 22 years, with the majority of observations collected from citizen science initiatives, to examine killer whale distribution in the south of Norway. A SDM based on these observations

and environmental data was applied to predict suitable locations for killer whales in Norwegian waters. Results from the SDM were compared to existing knowledge of factors that influence the distribution of killer whales in the north, to validate how the model performed.

The aim of this study is to assess the value of citizen science in complementing data on killer whales, combined with a species distribution model that produces relevant ecological knowledge on the temporal and spatial distribution of killer whales in Norway.

In assessing this aim, a two-step approach was conducted: (1) First, a comprehensive review of killer whale sightings along the entire Norwegian coast was generated using observational data, in large parts collected from citizen science, for the period 2000 – 2022, and (2) Secondly, the collected data were used to fit a maximum entropy model which identified the environmental factors that best predicted the presence of killer whales in Norway, with an emphasis on the distribution off the central and southern coast.

2. Method

2.1 Data collection

Data on killer whale sightings were collected from four different sources:

- 1) Media analysis (of newspaper and magazine archives)
- 2) The Norwegian Biodiversity Information Centre (NBIC)
- 3) The Norwegian Orca Survey (NOS) and
- 4) The Institute of Marine Research (IMR).

Media analysis

Web archives of newspapers, magazines, scientific papers and other publications hold valuable historical data that can be used for research purposes. Accessing these archives can be complicated due to copyright concerns and other limitations (Hurdeman et al., 2013). But in some cases, it may be possible to apply for research access. The use of archive methods (searching and extracting information from archives of newspapers and magazines) for researching killer whale distribution in Norway, have never been applied before. Hence, data on observed killer whales along the Norwegian coast between the years 2000 to 2022, were collected. The information gathered with the archive method were compiled in a large dataset.

The media analysis consisted of broad searches through three relevant archives: 1) “Bergens Tidende”, 2) “Nasjonalbiblioteket” and 3) “Atekst retriever”. The observational data were examined, and to exclude false positives and create a credible dataset, the following inclusion/exclusion rules were applied: Observations without information on date, time or place were not included. In e.g., sailboat magazines, some articles were found with limited information, stating observations of killer whales made earlier that year or month. In these cases, the encounters were not the central focus of the article, and so were considered less credible. Observations made from large distances, or longer than two weeks prior to publication were also not included. Photographic evidence, found in 2/3 of the articles, were also included in the dataset for verification. Unfortunately, due to a computer crash, photographs between the year 2020-2022, were lost and could not be restored.

1) *Bergens Tidene* - Since the initial focus was on the Hardangerfjord region, searches were conducted in *Bergens Tidende*, one of the biggest newspapers in the Vestland region. *Bergens Tidene* generously provided access to their archive for one month. In the search function, one or more words could be used simultaneously, where all the words used needed to appear in the same article. Therefore, using a single word in the search function generated a greater number of articles compared to using multiple words, as the latter required all the words to be present within the same article. A search with the word “spekkhogger*” was conducted with the symbol (*), indicating variation of the word’s ending, to provide as many outputs as possible.

2) Nasjonalbiblioteket - The main library institution in Norway, Nasjonalbiblioteket, provided access to their publication archive of books, newspapers, magazines and digitalized content. The structure of Nasjonalbiblioteket’s archive was different from *Bergens Tidende*. It allowed for multiple search words being used simultaneously, without the words being in the same article, by the operator “OR”. The search phrase «spekkhogger* OR orca* OR staurkval* OR killer whale*» was made to source as many observations as possible. The operator broadens the search by including several terms related to killer whales. The search parameter was limited to the Vestland region.

3) Atekst retriever - The third platform used in the media analysis was Atekst retriever, a comprehensive database that contains an extensive range of Norwegian newspapers, magazines, and other news sources. Atekst retriever generously provided access to their archive for one month. Here, the search functions were similar to the one in Nasjonalbiblioteket, where the use of multiple words in a single search could be generated by including the operator “OR”. The same phrase as in the Nasjonalbiblioteket search was used: «spekkhogger* OR orca* OR staurkval* OR killer whale*». Different parameters could be chosen to specify the search, where “web” and “Norwegian sources” were chosen.

The Norwegian Biodiversity Information Centre (NBIC)

Observational data on killer whales were also obtained from NBICs database (<https://artskart.artsdatabanken.no/>) for the study period 01.01.2000 - 31.01.2022.

The Institute of Marine Research

Additionally, observational data for 1984-2022 were provided by the Institute of Marine Research (IMR). Most of this was opportunistically sampled data, e.g., collected with IMR research vessels during any one of numerous IMR surveys. The IMR also routinely receives reports of marine mammal sighting from the navy and the coast guard. Additionally, as a national research institute with a high profile and large public visibility, the IMR occasionally receives pictures, videos and reports of marine mammal activity from the public. The latter could be considered citizen science, but records where this was the case were not practically possible to identify. All IMR data included the date of the observation, the number of whales and the longitude and latitude of where the whales were spotted.

The Norwegian Orca Survey

Lastly, observational data collected through citizen science were provided by the Norwegian Orca Survey (NOS), with observations from the year 2009-2023. The data included mostly observations from Vestlandet. Date, location and region for the study period were included in the final dataset.

2.1.1 Data processing

All observations from the abovementioned sources were compiled into a comprehensive dataset. The collected data were organized into “database”, “date”, “source”, “region”, “location”, “x” and “y” representing coordinates of latitude and longitude, and “comments” for additional relevant information. While data from Artsdatabanken and IMR already included coordinates, the remaining data sources (Bergens Tidende, Nasjonalbiblioteket, Atekst retriever and NOS) lacked this

information. In these cases, approximate coordinates were obtained from Google Maps, by using the “region” and “location” details (Figure 1).

To assess potential biases, and differences in these biases, in data collected through citizen science and by the IMR, plots/graphs were made showing the number of killer whales sighted per year, using data from 1) only citizen science, 2) only IMR, 3) the full combined dataset.

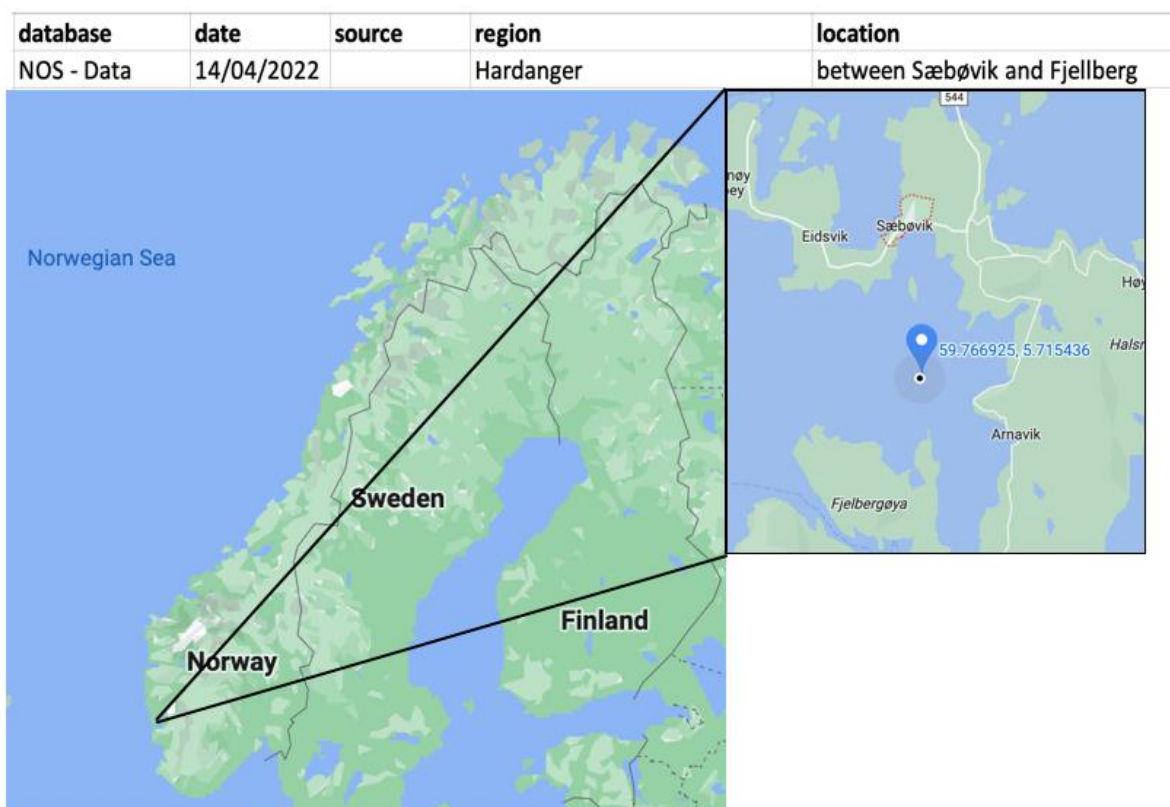


Figure 1: An example illustrating how corresponding coordinates of location and region described in the final dataset were obtained from Google Maps.

2.2 Questionnaire

A questionnaire was designed to focus on Norway’s two largest fjords, Sognefjord and Hardangerfjord, where the presence of killer whales has been well known for the past years through monitoring organized by the Norwegian Orca Survey (Jourdain et al., 2022). The two fjords are located in Vestland county, with Sognefjord being the largest fjord in Norway, and the longest open fjord in Europe stretching 205 km inland, with a

maximum depth of 1303 meter (Thorsnæs, 2021b). Hardangerfjord is the second largest fjord in Norway, with a length of 180 km and a maximum depth of 852 meter. Its main fjord has a width ranging from 2-10 km with many smaller fjords branching out (Thorsnæs, 2021a). The questionnaire was generated to assess whether the presence of killer whales in the two fjords is a new phenomenon. It was distributed to the citizens of Hardangerfjord and Sognefjord and consisted of six questions:

1. Have you ever observed killer whales in Hardangerfjord/Sognefjord?
2. When was the first time you observed killer whales in Hardangerfjord/Sognefjord?
3. What time of the year did you observe the killer whales?
4. How many times have you observed killer whales in Hardangerfjord/Sognefjord?
5. Have you ever observed killer whales attack porpoises in Hardangerfjord/Sognefjord?
6. Have you ever observed killer whales attack seals in Hardangerfjord/Sognefjord?

Regarding what time of the year observations were made, participants had the option to select multiple answers, in case some of them had observed killer whales at different times of the year.

The questionnaire was created using the online survey platform, Survio (<https://www.survio.com/Hardangerfjord/> <https://www.survio.com/Sognefjord/>) and distributed on the Facebook group “Spekkhoggara i Hardanger” on the 28th of May 2022, and again on the 23rd of January 2023. It was later distributed on a Facebook group that share information about killer whales in Sognefjorden, “Spekkhoggere i Sognefjorden” on the 10th of February 2023. Results were gathered from the online platform and summarized in Microsoft excel.

2.3 Modeling with Maximum Entropy

Data Requirements & Pre-processing steps - Since the collected data on killer whales consisted of presence-only data, a MaxEnt model (version 3.4.3) (Phillips et al., 2006a) was chosen to estimate the habitat and distribution most suitable for killer whales. Collected data on observed killer whales between 01.01.2000 – 31.12.2022, that remained after applying all quality checks described previously and that remained within the study area, were used in the model as data points to represent presence-only records.

Study area – The study area for the MaxEnt model was defined within the geographical extent that included all but seven of the gathered observational data points. These seven data points were located significantly outside the bounds of the other observations, and were therefore not included. In accordance with Phillips et al. (2006b) limiting the data to fit within the bounds of other data can improve the model performance, as background data is subjected to observational data. The study area covers the entire coast of Norway, extending nearly to Iceland, including almost the entire Norwegian Sea and the Greenland Sea, as well as areas of the Barents Sea, North Sea and parts of the Atlantic Ocean. It ranges from the latitudes 56.5°N - 80°N and longitudes -10°E - 34°E (Figure 2). The Norwegian Sea stretches around 1.1 million square kilometres. It has a very deep pool, with large parts being more than a 1000 meters deep and with a maximum depth of nearly 4000 meters (Sælen, 2021).

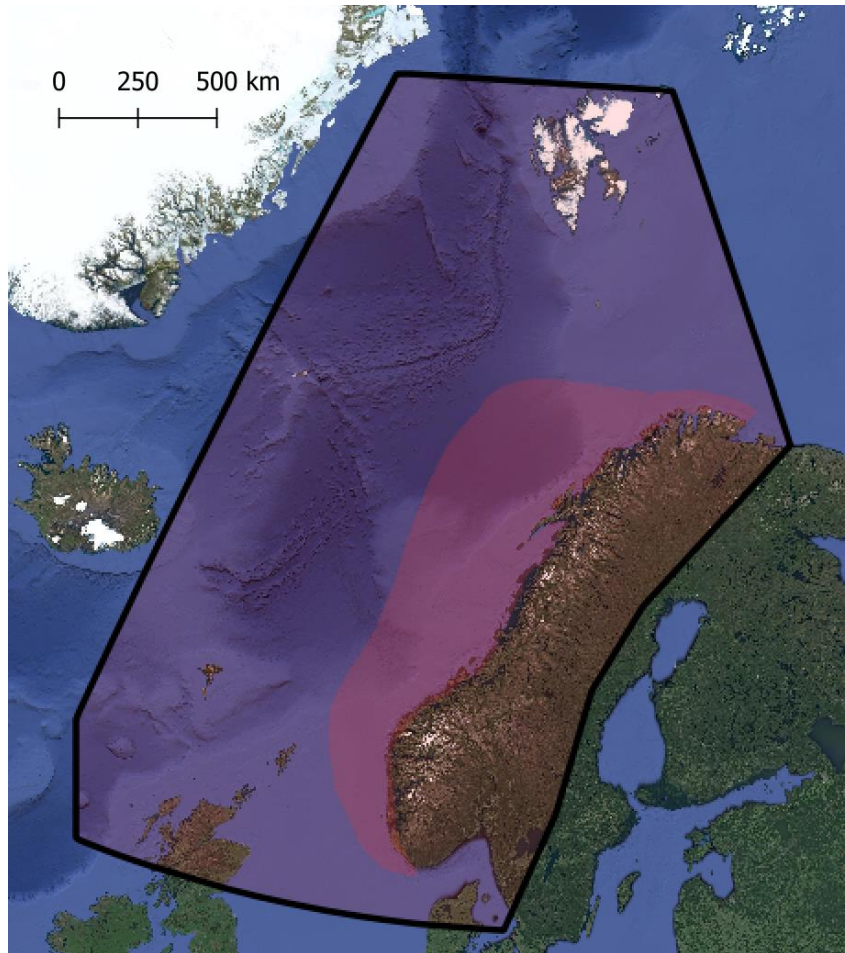


Figure 2: Map of the study area covering the entire Norwegian coast. The map was created using the Quantum Geographic Information Systems (QGIS) software program (QGIS, 2022). Here a Google satellite layer is displayed in the background with a template layer covering the study area on top. All observational points within the outer boundary were used in the model. The coastal area, where the highest amount of observational data were collected, is marked with a brighter red colour.

2.3.1 Environmental predictor variables

Generally, the accuracy of a MaxEnt model depends on the specific environmental predictors included in the model (Sutton and Martin, 2022). In this study, the choice of environmental parameters was selected based on a review of previous studies on the spatial distribution of killer whales (Jones et al., 2019, Viddi et al., 2010, Sahri et al., 2021). Some of these variables were selected as they presumably influenced the killer whales directly, and some because they could have an indirect effect, e.g., mediated through the killer whale's prey.

Fourteen environmental variables were chosen for the model: herring, sea bottom temperature (SBT), sea surface temperature (SST), salinity, ocean mixed layer thickness (OMLT), depth, seabed substrate, chlorophyll a concentration (chl-*a*), vessel density (VD), stratification, stratification roughness (rstrat), rugosity, seafloor slope and distance to coast (DTC) (Table 1). The next sections will explain the environmental variables in turn.

Table 1: Overview of the fourteen environmental variables considered for inclusion in the MaxEnt model.

Variable	Source	Unit	Spatial resolution	Temporal resolution	Year
Herring catch	Fiskeridirektoratet	Kg	1/2°	NA	2000-2022
Sea bottom temperature	Copernicus marine service	°C	1/12°	Daily	2000-2019
Sea surface temperature	Copernicus marine service	°C	1/12°	Daily	2000-2019
Salinity	Copernicus marine service	‰	1/12°	Daily	2000-2019
Ocean mixed layer thickness	Copernicus marine service	m	1/12°	Daily	2000-2019
Chlorophyll a concentration	Copernicus marine service	mg/m ³	1/4°	Daily	2000-2019
Depth	EMOD net	m	100m	NA	2022
Seabed substrate	EMOD net	NA	500m	NA	2019
Vessel density	EMOD net	km ²	1 km ²	Monthly	2017-2022
Stratification	Calculated from temperature	°C	1/12°	Daily	2000-2019
Stratification roughness (rstrat)	Calculated from stratification	°C	1/12	Daily	2000-2019
Rugosity	Calculated from bathymetry	°C	125m	NA	2022
Seafloor slope	Calculated from bathymetry	m	125m	NA	2022
Distance to coast	Calculated from bathymetry	m	125m	NA	2022

Herring - Herring was thought to be an important environmental parameter in the model, as the killer whale presence and seasonal distribution correlate with the movements of its prey (Similä et al., 1996, Condy et al., 1978, Ford et al., 1996, Jourdain et al., 2021), and their main prey along the Norwegian coast is known to be the Norwegian spring spawning herring (NSS). NSS herring performs large scale seasonal migrations along the Norwegian coast and into the Norwegian Sea. These seasonal migrations occur as herring move between wintering grounds (September-January), spawning grounds (February-March) and feeding grounds (April-August) (Similä et al., 1996, Røttingen, 1992, Slotte, 1999). Such species-specific considerations are important to include in the MaxEnt model, as it biologically motivates the studied species (Araújo and Peterson, 2012). To account for seasonal patterns in the spatial distribution of herring, three separate MaxEnt models were fitted, each corresponding to one “biological season”. Since distributional data on herring were not available for the study area, herring catch data were used as a proxy for the presence of herring. Catch data from 2000 to 2020 were downloaded from The Norwegian Directorate of Fisheries (fiskeridir.no). The data contained all catch across all fishing gears from Norwegian fishing vessels and foreign vessels landing fish in Norway. It also included the catch from research and education purposes, as well as first hand sales of recreational fishing (Hopland; and Aasheim, 2022).

Chlorophyll a, Sea surface temperature, Stratification, Ocean mixing layers & Stratification roughness (rstrat) - High primary production and upwelling zones have been speculated to correlate with the spatial distribution of fish prey (Edrén et al., 2010). For this reason phytoplankton could presumably influence the prey of killer whales through bottom-up mechanisms (Frederiksen et al., 2006). Following Jones et al. (2019), mass concentration of chlorophyll *a* (chl-*a*) in sea water, together with sea surface temperature (SST), were used in the model as an indicator for the amount of phytoplankton near water surface. SST is one of the most influential parameters for oceanography, as it provides information on thermal features. Additionally, it plays an important role in the energy uptake, and moisture exchange between the atmosphere and sea surface (Sumner et al., 2003). Primary production depends on sufficient sunlight for growth. It also relies on nutrients such as sodium, phosphorus and iron being mixed up from the deep, while not being mixed down below the photic zone (Wafar et al., 1983, Murphy, 1998, Bristow et al., 2017). Stratification and ocean mixing

layer thickness were therefore included in the model. Chl-a, sea surface temperature and ocean mixing layers were downloaded from Copernicus Marine Environment Monitoring ocean map from the global ocean physics reanalysis for the years 2000-2019 (Table 1). Roughness of terrain (rstrat) was used in the model to find the maximum and minimum variation in stratification roughness of terrain, as it was thought to indicate where mixed and stratified waters meet as specified by strong heterogeneity (Fogg et al., 1985, Woodson and Litvin, 2015).

Depth, seabed substrate, slope, rugosity & distance to coast – Seabed substrate and depth can both be linked to the distribution of fish prey (Munk et al., 1995, Edrén et al., 2010) and were used as an indicator for seafloor relief (depth and height of terrain). Seafloor relief is recognized as the primary factor for determining the distribution and composition of fish populations. It relies on several abiotic factors like temperature, light and salinity that contributes to food availability through primary production and habitat availability through the amount of vegetation (Galaiduk et al., 2017, Hill et al., 2014, Borland et al., 2021). Seabed substrate and depth were downloaded from the European Marine Observation and Data Network (EMOD net) from the years 2019 and 2022, respectively. Spatial variation in terrain metrics is also linked to fish diversity and abundance, and therefore rugosity (index of seafloor complexity) and seafloor slope (degree of maximum change in elevation) were thought to be important (Hastie et al., 2004, Bailey and Thompson, 2009). As killer whales are common in coastal areas possibly due to higher ocean productivity (Forney et al., 2006), the distance to coast was included in the model to find how killer whale occurrences is related to the coast.

Sea bottom temperature, Salinity & Vessel density - Oceanographic parameters like sea bottom temperature and salinity play an important role in community composition and species distribution (Mayer and Piepenburg, 1996, Stransky and Svavarsson, 2010), and were therefore included in the model. Both parameters were downloaded from CMS for the years 2000-2019, whereas vessel density, the last variable included in the model, was downloaded from EMODnet for the years 2017-2022. EMODnet collected data on ship traffic through coastal stations and satellites to create a vessel density map, that displays the total monthly number of vessels per square kilometre (Falco et al., 2019). Vessel density was included in the model as it causes noise pollution that can disturb or attract killer whales leading to behavioural changes (Holt

et al., 2017, Barrett-Lennard et al., 1996, Williams et al., 2006, Holt et al., 2009, Mul et al., 2020).

Processing predictor variables – All environmental variables were downloaded as GIS raster layers from the European Marine Observation and Data Network (EMODnet), Copernicus Marine Service's (CMS) MyOcean Pro and The Norwegian Directorate of Fisheries (Table 1). They were processed separately in R Studio, (Version 2023.03.0+386) as they were downloaded from different platforms and had slightly different formats. Due to excessive file sizes, environmental data had to be split up into smaller parts within the study area before being downloaded, and later combined to a full layer by using the *mosaic function* in R (Hijmans, 2023). Some of the environmental covariates were calculated, from other environmental variables (Table 1). Stratification was calculated by subtracting sea bottom temperature from sea surface temperature. Stratification was then used to calculate the stratification roughness (*rstrat*) using the *roughness of terrain function* from the raster R package (Hijmans, 2023). Depth was downloaded in many parts and combined into a single raster layer in R, using the *mosaic function* (Hijmans, 2023). From depth, two additional parameters were derived; rugosity and seafloor slope, again by using the *terrain function* in R. Distance to coast was found using the *distance function* in the raster R (Hijmans, 2023) package based on the depth GIS layer.

A raster template covering the spatial extent of the study area was defined using coordinates of 56.5°N - 80°N and 10°E - 34°E. All environmental variables were projected to the coordinate system UTM33N (EPSG code 32633) with a resolution of 5000 x 5000 meters and saved as .tiff files. Since the environmental parameters were available with different temporal resolutions, varying between hours, days and months (Table 1) and downloaded for up to a 20-year period, a mean value for each predictor layer was calculated. For SST, SBT, Salinity, chl-a, ocean mixing layers and vessel density each of the mean variables were split up into the three biological seasons used for killer whales (September-January, February-March and April-August). This resulted in three mean predictor layers for each environmental covariate, where each layer represented the seasonal average for that covariate.

Catch data on herring were summed per season per location and used to create season-specific herring raster layers. However, locations given in the fishery data referred to cells in a coarse spatial grid used by the Directorate of Fisheries in Norway (DOF) to report fishing data, with a resolution of approximately 0.5 degrees (~53 km). Under the assumption that fishing effort in each cell was uniformly distributed, catch data were mapped from the grid used by the DOF to a new herring raster layer defined based on the template grid defined above. This was accomplished by assigning catches to raster cells in the herring grid based on the proportion of overlap of each template cell with the location cells in the DOF grid. Thus, the value of cells in the raster grid that overlapped multiple locations cells in the DOF grid received catches from all location cells with which they overlapped. More precisely,

$$H_i = \sum_j Z_j \times P_{i,j} \quad (\text{equation 1})$$

where H_i is the value of cell number i in the herring grid, Z_j is the total seasonal landed catch of herring in the j th location cell that intersected with cell i in the herring grid, and $P_{i,j}$ is the proportion of the total area of location cell j covered by herring cell i . Values for H_i were calculated separately for each season. For example, if a cell in the herring grid covered 5%, 4%, and 2% of the area in each of three location cells, with values 1000, 500 and 1500, respectively, for season 1, then the value of that cell in the herring raster for season 1 would be $0.05 \times 1000 + 0.04 \times 500 + 0.02 \times 1500 = 100$. Cells in the herring grid that did not overlap with the DOF grid were assigned a value of 0.

The seabed substrate data included seven different substrate categories: sand, coarse sediment, mixed sediment, rock & boulders, mud, sandy mud and muddy sand.

Extrapolating environmental variables – Since a proportion of the killer whale observations intersected cells with missing data in one or more of the environmental raster layers (e.g., due to differences in coverage and/or resolution), missing values in the environmental raster layers were replaced with the nearest non-missing values, on a cell-by-cell basis.

Collinearity and Jackknife test – To avoid collinearity that could result in uncertainties in model estimates, the model was tested for correlation between environmental variables using a method by Pearson (Lee Rodgers and Nicewander, 1988) (Figure 20). Before dropping any correlated layers from the model, a jackknife test was conducted to account for variable importance. The jackknife runs a series of models, excluding and isolating each variable in turn, before running the model with all variables together. From this, the variable importance of each variable can be estimated from the increase in model gain with and without each variable included, and by only including the isolated variable (Liu et al., 2018). After conducting the jackknife test, variables with high correlation and low ecological significance were dropped from the model, using the variance inflation factor for collinearity, *vifcor function* in R (Naimi et al., 2014). Any layers with highly correlated environmental variables above the threshold of 70% were dropped out from the model. 70% indicates when collinearity begins to severely mislead the model estimation and prediction (Dormann et al., 2013, Smith and Santos, 2020, Sony et al., 2018).

Sensitivity analysis – Leverage was calculated for each of the observational points used to fit the model. Following the method by Daniel (2014), the estimated leverage scores were used to determine if the impact of any one observational data point was so large that it should be considered as an outlier. Outliers could have a disproportionate effect on the model (McCullagh and Nelder, 1989). No outliers were identified this way; therefore, all observational data were included in the model.

Creating the MaxEnt model – The software package used to fit the MaxEnt model, was the *dismo* R package, version 1.3-14 (Hijmans et al., 2017). Coordinates from killer whale observations collected from citizen science were used in the model as presence data. The environmental prediction layers describing spatial variability in the three seasons were placed in a raster stack, so there was one stack for each season, to be used in three different seasonal MaxEnt models. Recommendations by Phillips (2008) and Fourcade et al. (2014) suggest to use 10000 background points, which is the default and common practice for MaxEnt. However, a study by Lissovsky and Dudov (2021) questions the representativeness of this default setting for the use in any territory, and exemplifies studies using 75000 – 300000 background points (El-Gabbas and Dormann, 2018). With the study area being of substantial size (309602 cells of

5000 x 5000 meter), it's possible that more random background points would be needed to fully capture the heterogeneity of the conditions in the study area. Therefore, the model was run with 10000, 15000 and 20000 background points, and the model that performed best, as measured by regularized training gain, was used for further analysis. With these settings, three different seasonal models were fitted using the MaxEnt function. A schematic overview with information on how the models were created is shown in Figure 3.

Model output - For each model, probability maps, threshold maps and variable response curves were generated. The probability map is represented by a Complementary Log-log (cloglog) transformation of the model's predictions. MaxEnt has four output formats for model values (raw, cumulative, logistic and cloglog), with cloglog being the default output (Phillips, 2005). Cloglog maps the predictions on a transformed scale between 0 and 1 of probability of presence, where higher values demonstrate areas with more suitable conditions for killer whales. The size of grid cells in the model plays an important role as the model is structured to estimate probability of presence by assuming that each cell holds one individual per cell (Phillips, 2005). The MaxEnt model produces response curves to represent probability of presence (POP) for each environmental variable. The response curves plot POP (y-axis) against a series of values within each parameter (x-axis). Each plot ranges between a threshold where the suitability for presence is highest (Fitzgibbon et al., 2022). The response curves provide information on how each variable influence the model. Furthermore, the model will predict suitability in areas where most of the parameters have highest suitable conditions. If the response curve is flat it implies that the parameter will not influence the POP. However, higher ranging curves implies that the parameter is important for POP in the model, where the model is able to distinguish between suitability and not (Fitzgibbon et al., 2022).

Model testing – Some methods are established to evaluate SDMs, like the MaxEnt model. This includes evaluations within the receiver operator curve (ROC), which finds the Area Under the Curve (AUC) and the True Positive Rates (TPR) (Fitzgibbon et al., 2022). The AUC ranges from 0 to 1, where 1 is perfect performance and 0.5 is equivalent to a random prediction. A random prediction would mean that the model is indifferent and does not help with identifying presence and absence. Well performing

models are recognized to have AUC values above 0.9 (Swets, 1988). Recommendations from (Swets, 1988) were followed to assess the AUC values, where > 0.90 = excellent, $0.80-0.90$ = good, $0.70-0.80$ = fair, $0.60-0.70$ = poor and < 0.60 = fail. To assess the accuracy of the three models, each dataset was split up into two subsamples, one with training data (80% of the observations), used to fit the model and one with testing data (20% of the observations), used to create predictions on “unseen” data.

In accordance with Phillips et al. (2006b), the model performance was tested using the *evaluate function* in R (Hijmans et al., 2023) and analysed using the Area Under the Curve (AUC) of the Receiver Operator Characteristic (ROC) analysis to evaluate its success. ROC and AUC were chosen to measure the accuracy of the models because of its popularity within SDMs and especially within MaxEnt literature (Elith et al., 2006, Ma and Sun, 2018, Yuan et al., 2015). They measure the rate of classification error when applying a model to the test data (Hastie et al., 2009). AUC is a threshold independent evaluator that provides a single measure of accuracy. It traditionally evaluates how well the model predictions can distinguish between locations of presence data and absence data, but for presence-only data used in this model, it compares presence data with background points (pseudo-absence data) (Fielding and Bell, 1997, Merow et al., 2013). From the evaluation of each model, a threshold map was made using the best performing threshold given by ROC, to identify potential areas of high occurrence. The threshold finds the lowest value for predicted occurrence by finding the lowest suitable value point from where an observation of a killer whale has been made and uses it to make a map to predict killer whale presence/absence (Phillips et al., 2006b). Each of the model performances were also tested by evaluating the true positive rate (TPR) at the specific threshold given by ROC.

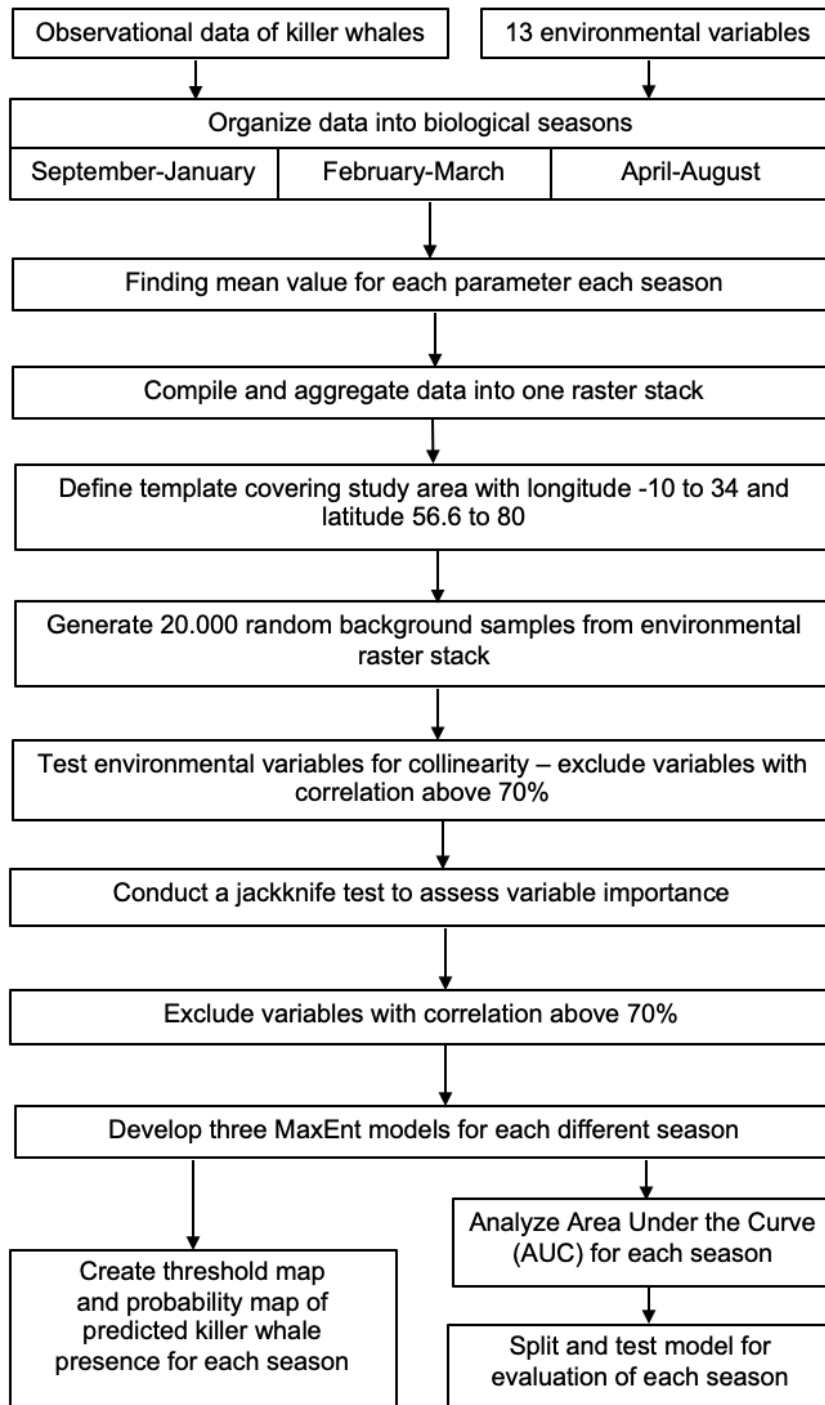


Figure 3: Schematic representation of procedure for making and testing MaxEnt model for killer whale distribution in Norwegian waters. Inspiration for schematic representation gathered from Pan et al. (2023).

2.4 Source for analysis

The full dataset containing all observations from the four different sources, as well as observations gathered from Atekst retriever, and all R-scripts used in the model analysis can be obtained from the available GitHub repository (<https://github.uio.no/ullaaf/Masterthesis>). Environmental data were downloaded from three sources: the Copernicus Marine Service (CMS), European Marine Observation and Data Network (EMODnet), and the Norwegian Directorate of Fisheries. The data contained varying temporal resolutions between days, months and years (Table 1). Sea bottom temperature, sea surface temperature, salinity, ocean mixed layer thickness and chlorophyll *a* concentration were obtained from CMS (<https://data.marine.copernicus.eu/products>), and contained daily records for the years 2000-2019. From EMODnet (<https://emodnet.ec.europa.eu>) depth was obtained with data from 2022, seabed substrate with data from 2019 and vessel density with data of monthly records for the years 2017-2022. Herring catch records was obtained from the Norwegian Directorate of Fisheries (<https://www.fiskeridir.no>) and contained data for the entire study period.

3. Results

3.1 Killer whale sighting

The final dataset of killer whale observations contained 4372 records (Figure 4 & 5). The highest sighting rates were recorded in 2020, with over 400 reported sightings (Figure 6). An overall increase can be seen in reported sightings of killer whales throughout the years of the study period (Figure 6).

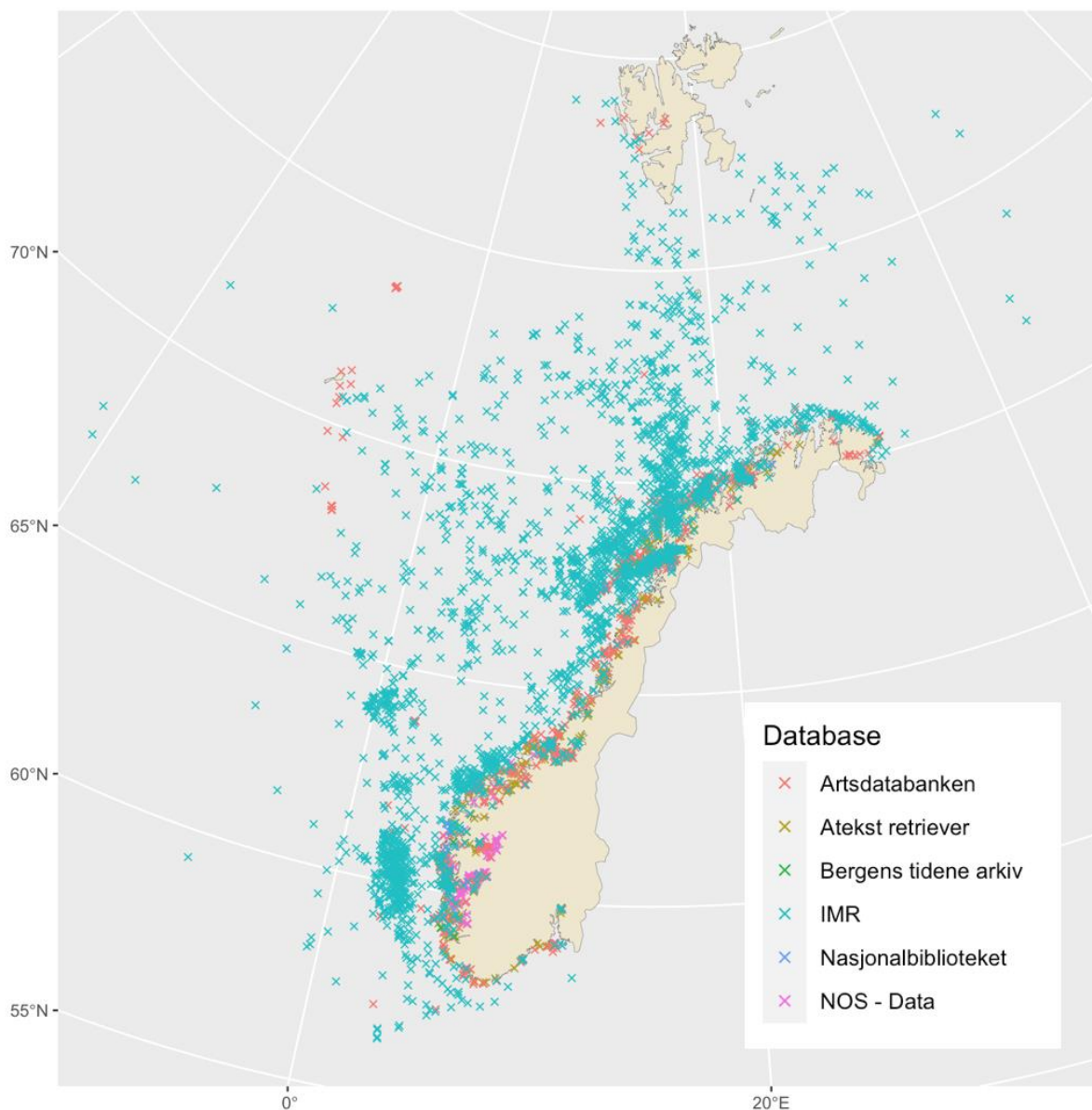


Figure 4: Map illustrating the distribution of 4372 collected observations of killer whales. Each source (Artsdatabanken, Atekst retriever, Bergens Tidende Arkiv, IMR, Nasjonalbiblioteket and NOS – data) is represented by a different colour.

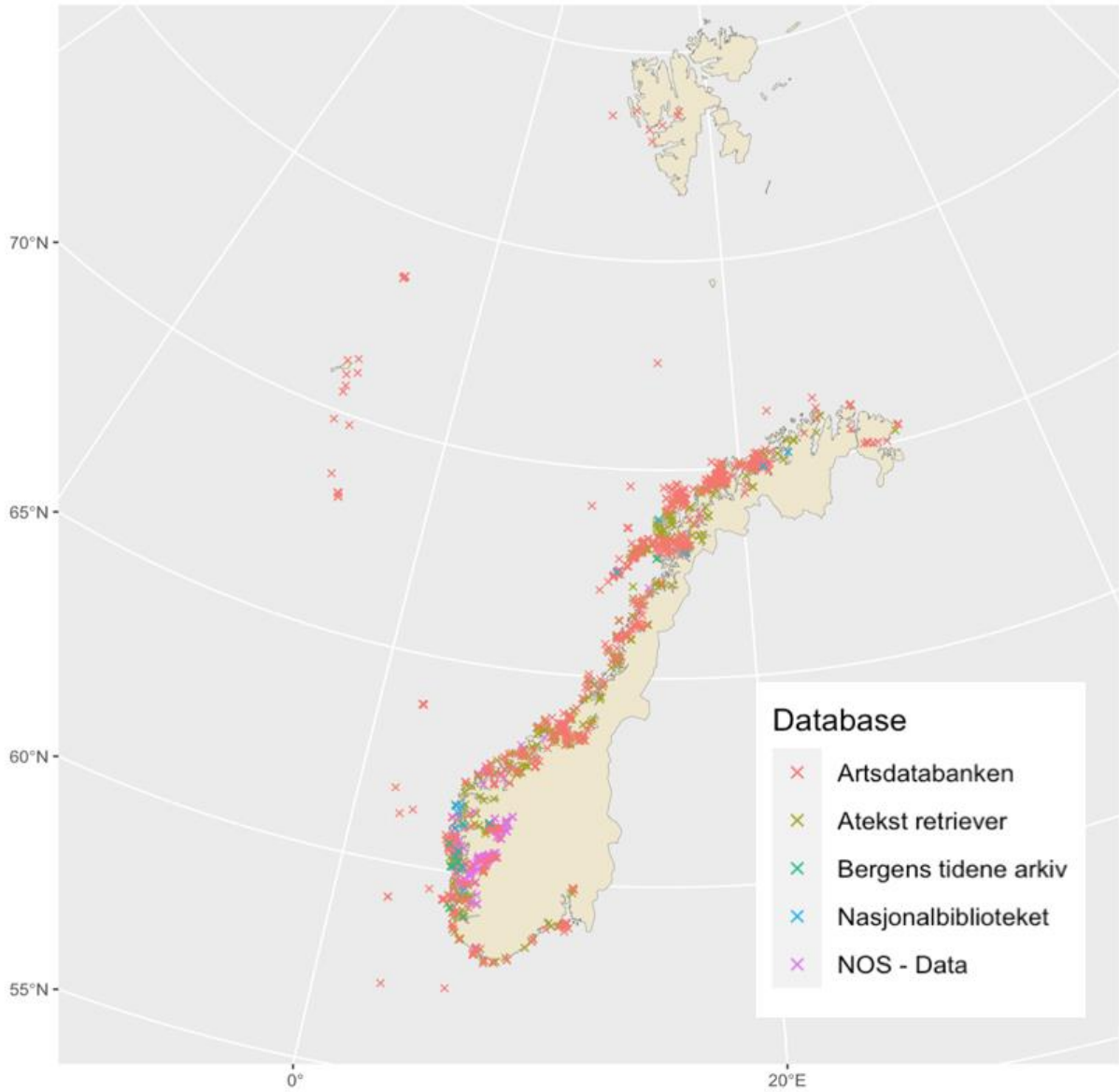


Figure 5: Map illustrating distribution of observed killer whales collected from citizen science, excluding observations from IMR, to better see the results. Each source (Artsdatabanken, Atekst retriever, Bergens Tidende Arkiv, Nasjonalbiblioteket and NOS – data) is represented by a different colour.

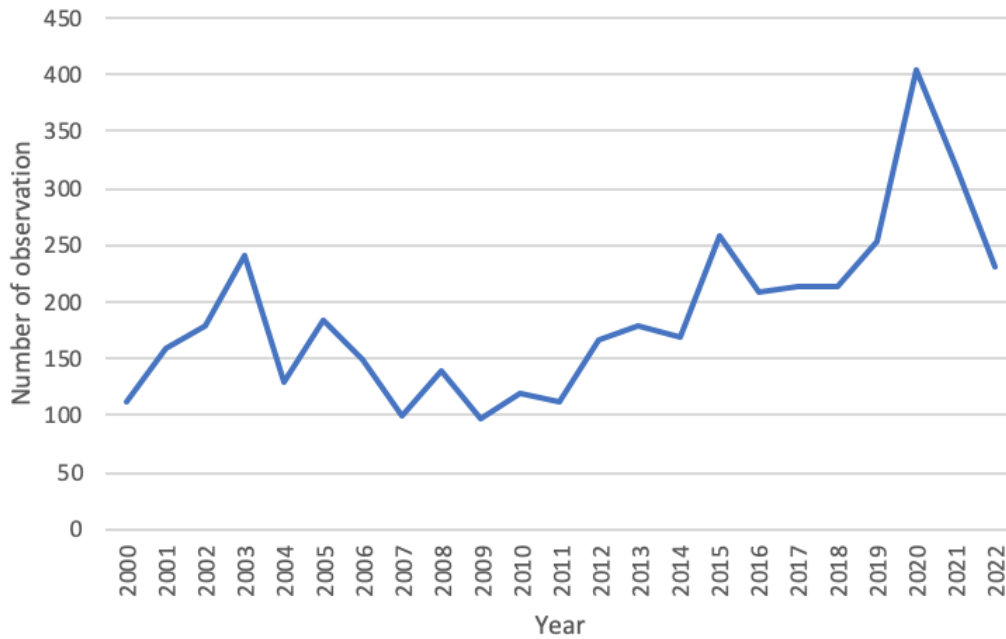


Figure 6: Observations of killer whales compiled from all collected data spanning from 2000 to 2022.

Media analysis – Of the total 4372 observations, 504 were gathered from the media analysis. 14 records were found in Bergens Tidende and 20 in Nasjonalbiblioteket. The most comprehensive media search was conducted in Atekst retriever and resulted in 6969 articles that matched the search keywords. 470 of these passed the inclusion criteria. More than half of these articles included photographs.

The Norwegian Biodiversity Information Centre (NBIC) – Observations collected from Artsdatabanken included reported sightings from two different research institutes and a biologist: “Norsk Zoologisk Forening,” “Global Biodiversity Information Facility” (GBIF) outside of Norway, and from biologist John Bjarne Jordal (JB Jordal) (Figure 7). The dataset yielded a total of 935 observational records.

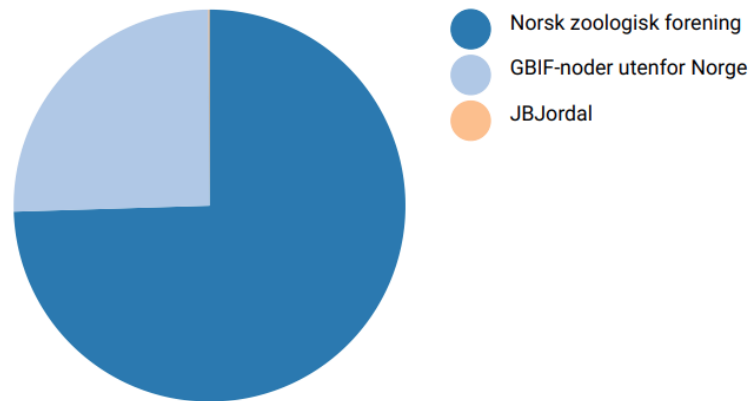


Figure 7: Picture collected from Artsdatabanken, illustrating observations of orcas made by three different sources, resolved by color “Norsk Zoologisk Forening”, “GBIF-noder outside of Norway” and “JB. Jordal”.

Norwegian Orca Survey (NOS) – NOS data contained records of 277 killer whale encounters, mainly from the Vestlandet region.

Institute of Marine Research (IMR) – Lastly, data provided from IMR contained a total of 2656 observations of incidental sightings.

The total number of observations per year, when excluding IMR data, exhibits a clearly increasing trend (Figure 8a). There was a limited number of observations reported before 2014, followed by a steep increase in observations starting in 2014. The largest increase was between 2019 to 2020, resulting in over 300 observations reported in 2020. Number of killer whale sightings per year only including IMR data showed a gradual decrease in observations collected during the study period (Figure 8b)

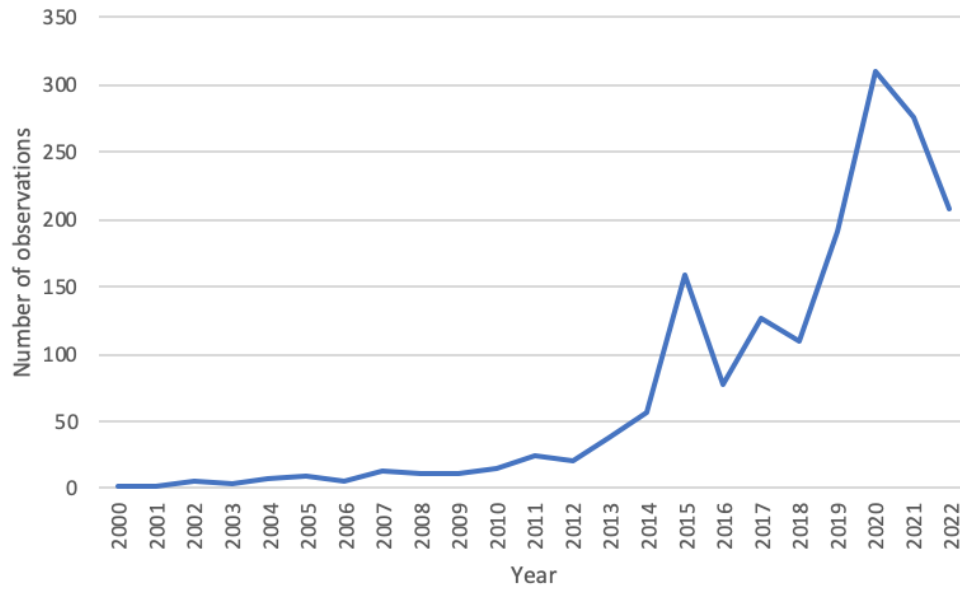


Figure 8a: Observations collected from citizen science **excluding IMR data** during the period of 2000 to 2022.

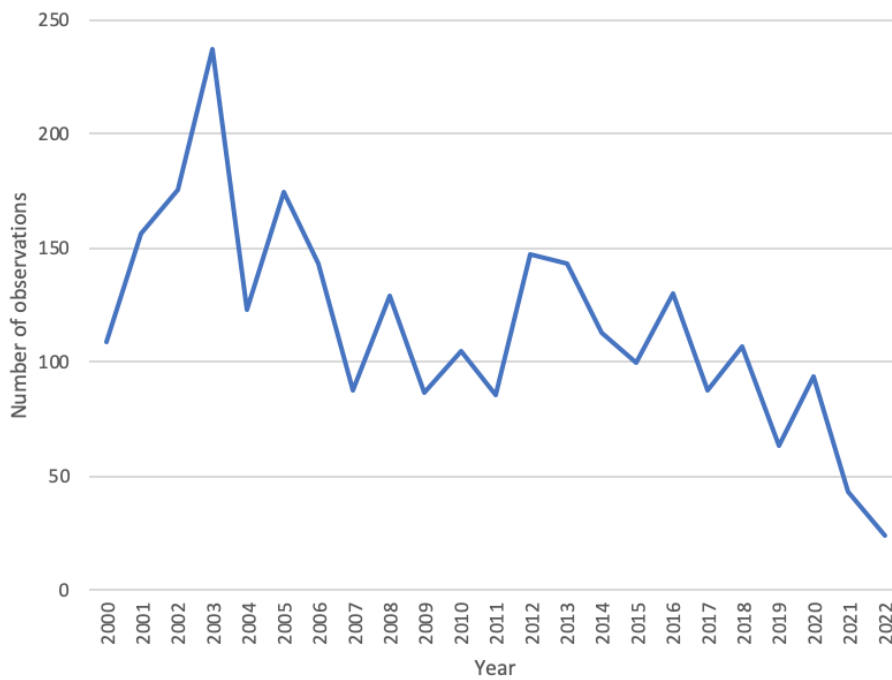


Figure 8b: Observations in **IMR data** during the period of 2000 to 2022.

The total monthly number of collected observations of killer whales was found to be spread evenly throughout the months of the year (Figure 9). Most observations were made in May, with around 500 observations. Slightly fewer observations were made in June and August, and in December, less than 200 observations.

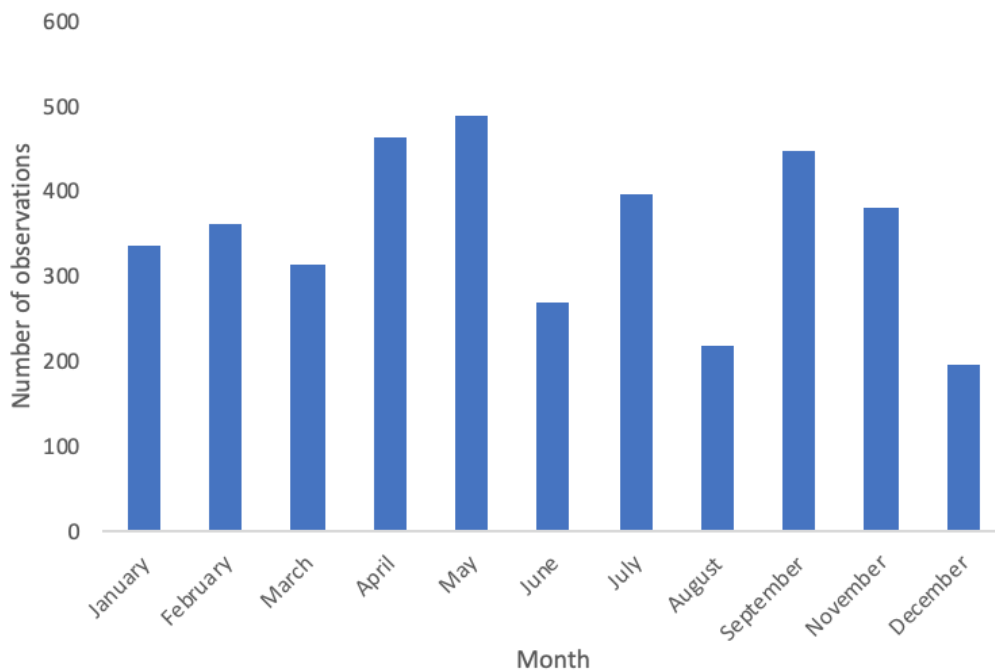


Figure 9: Number of monthly observations of Killer whales compiled from all collected data (Media Analysis, Artsdatabanken, NOS and IMR) spanning from 2000 to 2022.

3.2 Questionnaire

3.2.1 Hardangerfjord

116 participants responded to the questionnaire about killer whales in Hardangerfjord. Out of the contributing participants, 114 had observed killer whales in Hardangerfjord (Figure A1). Regarding the first time killer whales were observed, three participants responded that they were not sure (Figure A2), while one participant answered that an observation was made as early as in 1918 (Figure 10). Another answered that he/she had observed one for the first time in 1985. The observation from 1918 could be a potential source of error as it was not observed directly by the participant. When excluding these two observations, the majority of observations were made in the last

10 years, with a clear increase in observations reported in the past five years, between 2017-2022 (Figure 11).

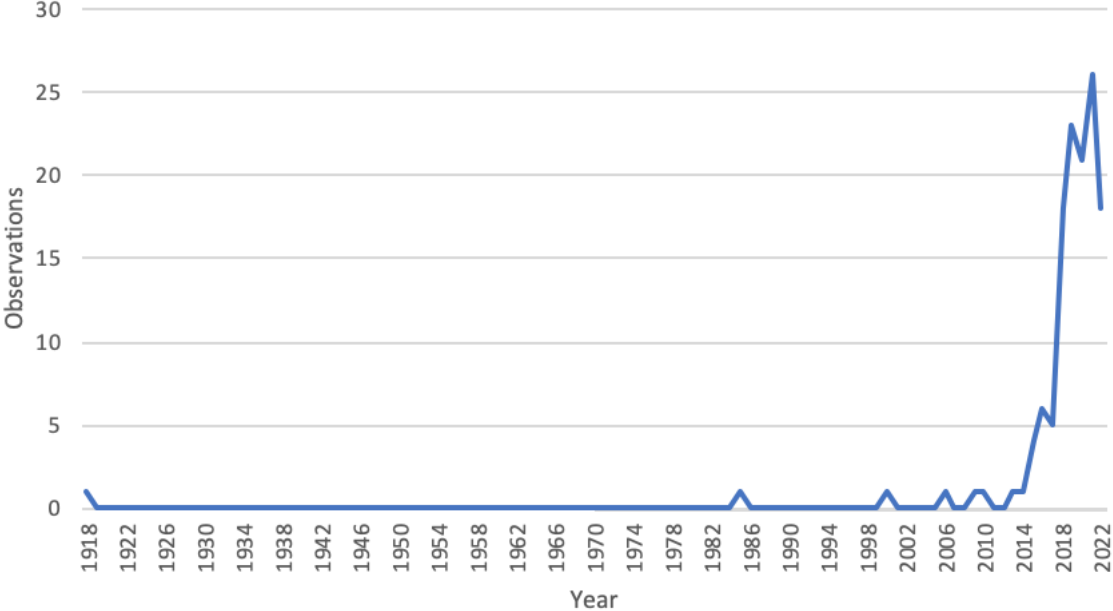


Figure 10: First observations of killer whales in the Hardangerfjord based on citizen science, including an observation from 1918 (could be a potential source of error).

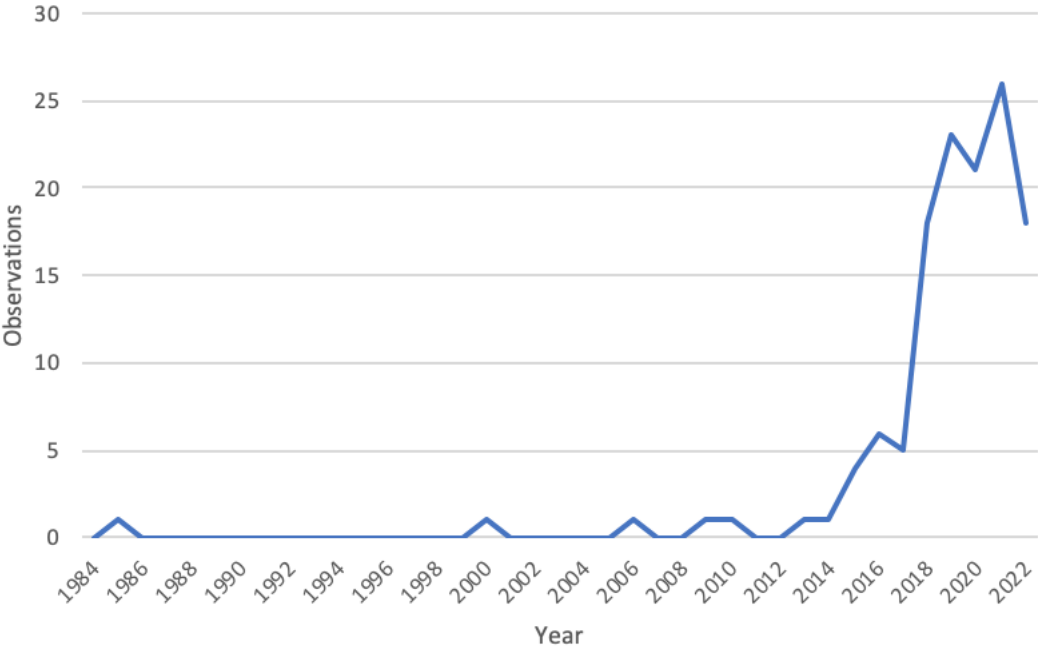


Figure 11: First observations of killer whales in the Hardangerfjord based on citizen science, not including an observation from 1918.

198 answers were given, regarding the month observations were made (Figure 12 & A3). The survey shows that the frequency of killer whale observations in the Hardangerfjord is higher during the winter and early spring months, with the highest number of observations being recorded in April (Figure 12). In contrast, very few observations were reported between June and November, with no observations recorded in October.

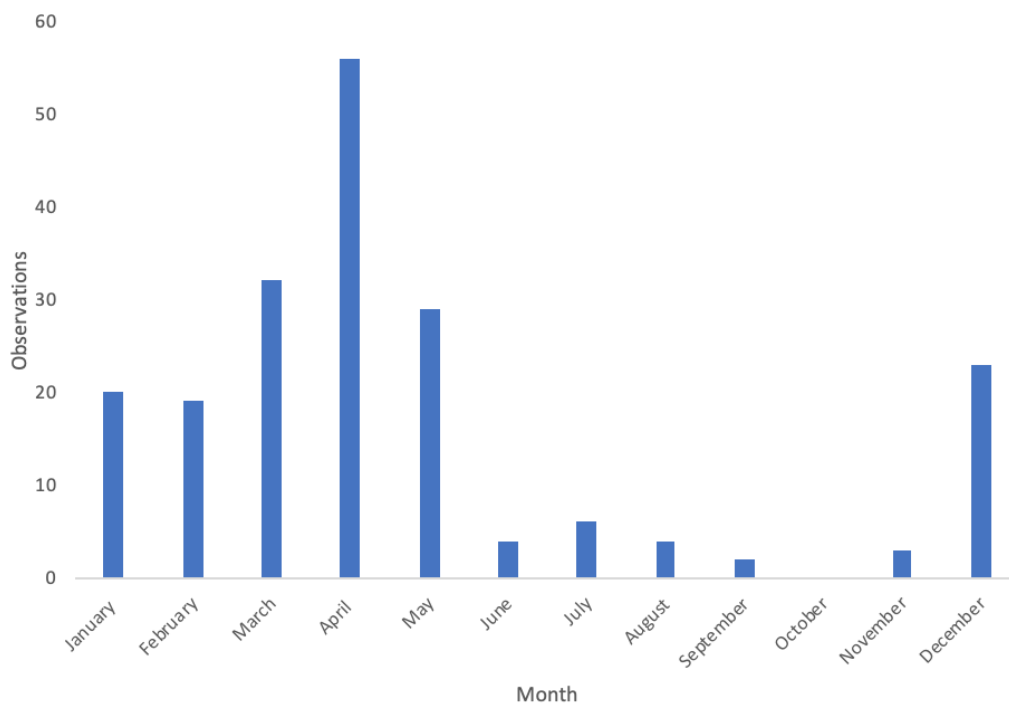


Figure 12: Monthly observations of killer whales recorded in Hardangerfjord.

The majority of participants had encountered killer whales in the Hardangerfjord multiple times. Specifically, 24 participants had observed them more than 10 times, while 20 had observed them twice (Figure 13 & A4).

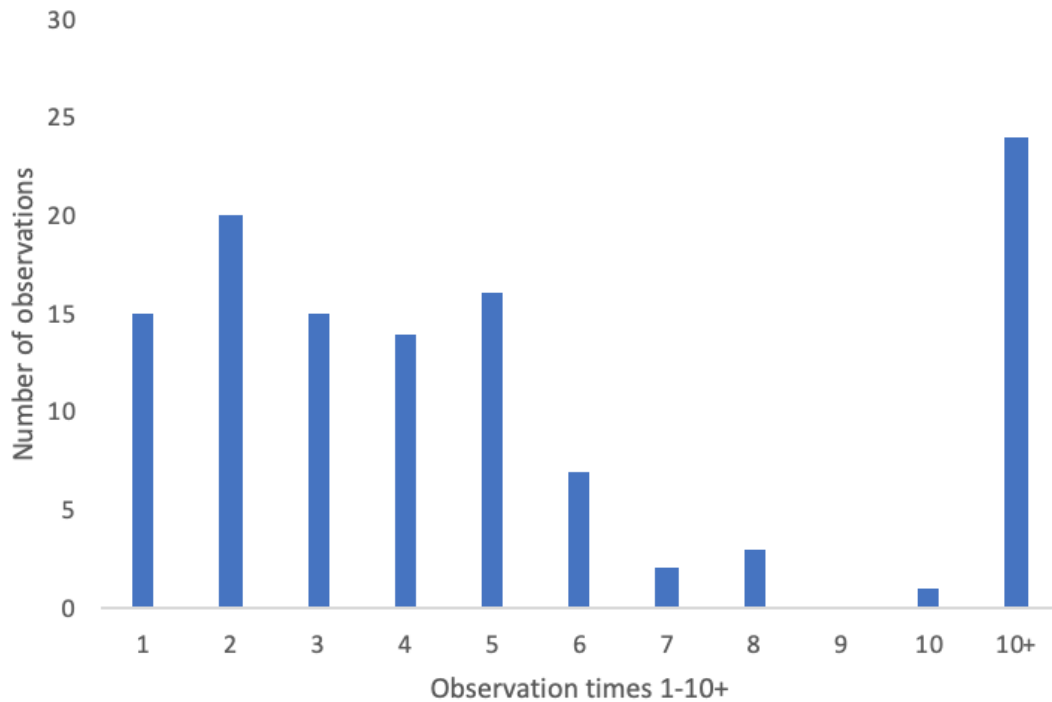


Figure 13: Histogram illustrating number of times each participant has observed killer whales in Hardangerfjord.

The last two questions concerned attacks on marine mammals by killer whales in Hardangerfjord (Figure A5 & A6). Out of the 198 observations made by the 114 observers, 38 had observed attacks on harbour porpoises and 11 had observed attacks on seals. This correlates with the high abundance of harbour porpoises in the Hardangerfjord, which appears to be the reason the whales frequently move in and out of the fjord, to feed on the porpoises (Åslein, 2023).

3.2.2 Sognefjord

40 participants contributed to the questionnaire on killer whales in the Sognefjord. Here, 39 reported having observed killer whales in Sognefjord, and only one had not (Figure A7). Regarding first-time killer whales were observed in Sognefjord, one participant answered having observed one in 1986. This record was made in Leikanger and the participant responded to also having observed killer whales in Sognefjord “the last four years”. Another participant answered with “I’ve seen them every year the past years”, which was considered to be the last three years. Besides the record from 1986,

all other observations were made the last nine years, with no observations made between the years 1986 and 2015 (Figure 14). A clear increase in observations were made in 2016 and another again in 2020 (Figure 14 & 15). This trend in observations argue that killer whales in Sognefjord could be a new phenomenon.

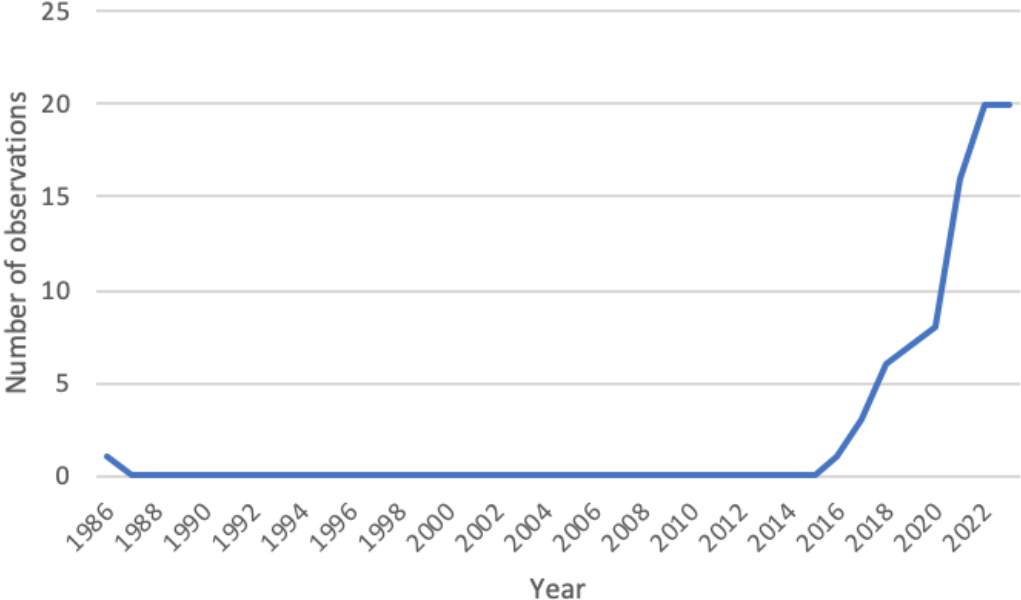


Figure 14: Yearly observations of killer whales in Sognefjord based on citizen science, including the observation from 1986.

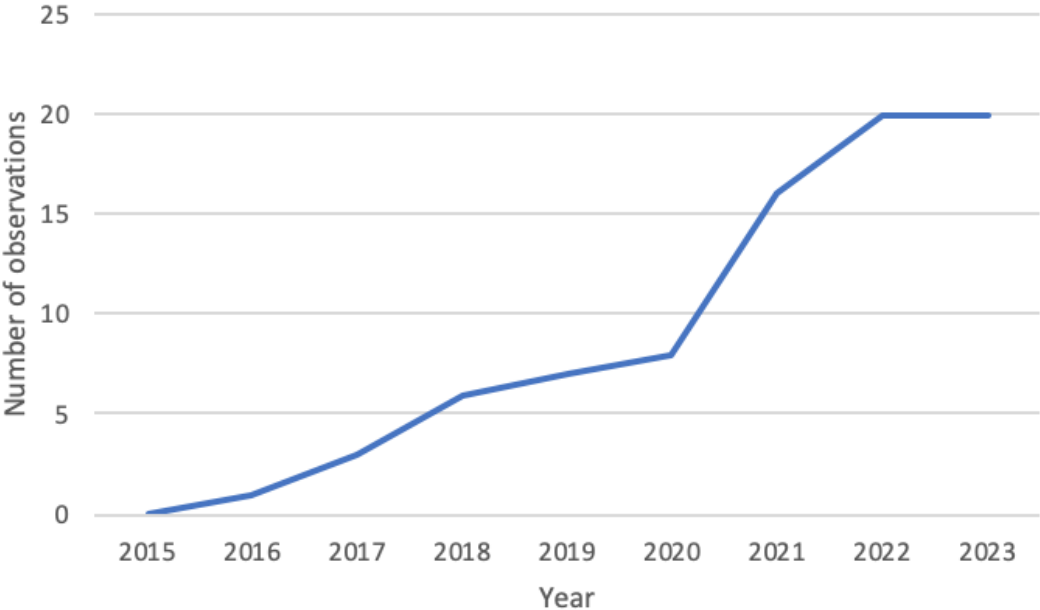


Figure 15: Yearly observations of killer whales in Sognefjord based on citizen science, excluding the observation from 1986 (could be a potential source of error).

Concerning the timing of observations, participants had the option to select multiple answers, resulting in 76 answers (Figure A9). The results show a clear trend towards increased observations of killer whales during the winter months, between November and March, with the highest number of observations counted in January (Figure 16). Few observations were made between April and October.

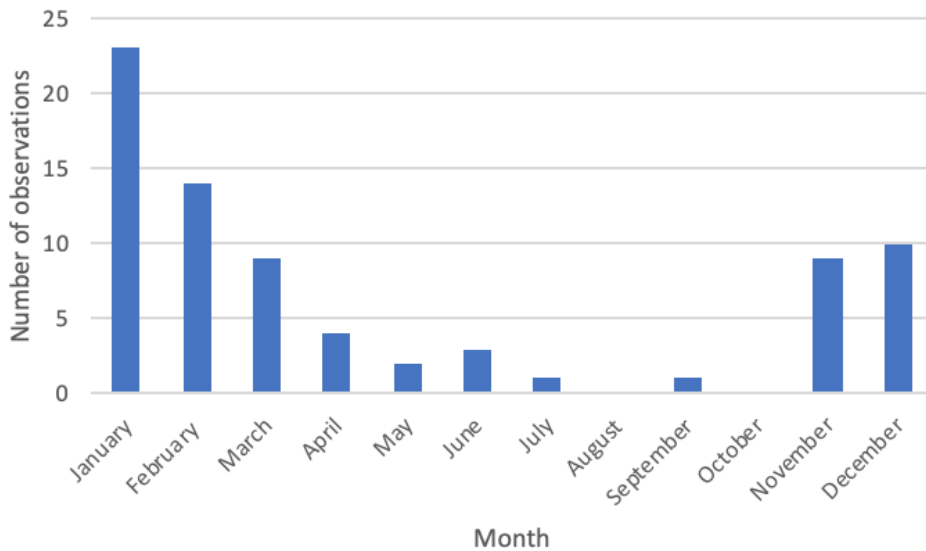


Figure 16: Observations of killer whales from questionnaire in Sognefjorden showed by months.

1/4th of the participants had observed killer whales in the Sognefjord twice. Nine had observed killer whales one time, and eight answered more than 10 times (Figure 17 & A10).

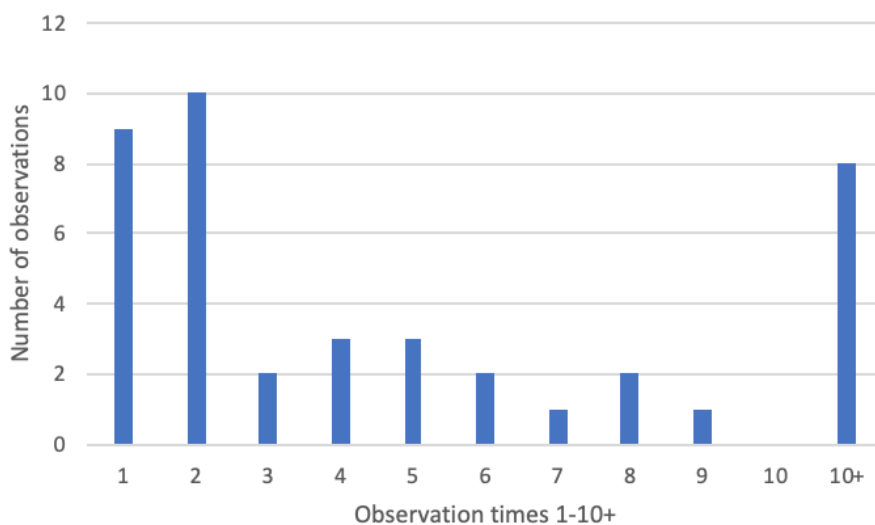


Figure 17: Number of times killer whales were observed in Sognefjord.

Regarding questions concerning killer whale attacks on marine mammals (Figure A11 & A12), 17 out of the 40 participants had observed attacks on porpoises, and 10 had observed attacks on seals.

3.3 MaxEnt model

3.3.1 Observational data

The 4372 observations collected through opportunistically sampled data and citizen science were used in the model as presence data. Before the environmental variables were extrapolated, 1732 observations were lost from falling beyond the confines of the study area or from intersecting with missing environmental values. After extrapolating the environmental spatial layers by replacing missing values with non-missing values, only 851 observations were lost. This approach preserved 881 observations, leaving 3536 observational records to be used in the model as presence data.

3.3.2 Model performance and validation of MaxEnt

Area Under the Curve (AUC) – The AUC was used to test the model performance for the three models. Each model (season 1 = September-January, season 2 = February-March & season 3 = April-August) was able to sufficiently discriminate distribution patterns for killer whales with an AUC > 0.9. The receiving operating characteristics (ROC) curves (Figure 18) showed that AUC for the three models were respectively S1 = 0.909, S2 = 0.907, S3 = 0.901, indicating that the models were able to classify true positives (model predicts where killer whales are present) at a much higher rate than false positives (model falsely predicts killer whales' presence, where they are not present). This indicates a strong performance for all three models in discriminating suitable and unsuitable habitats for killer whales.

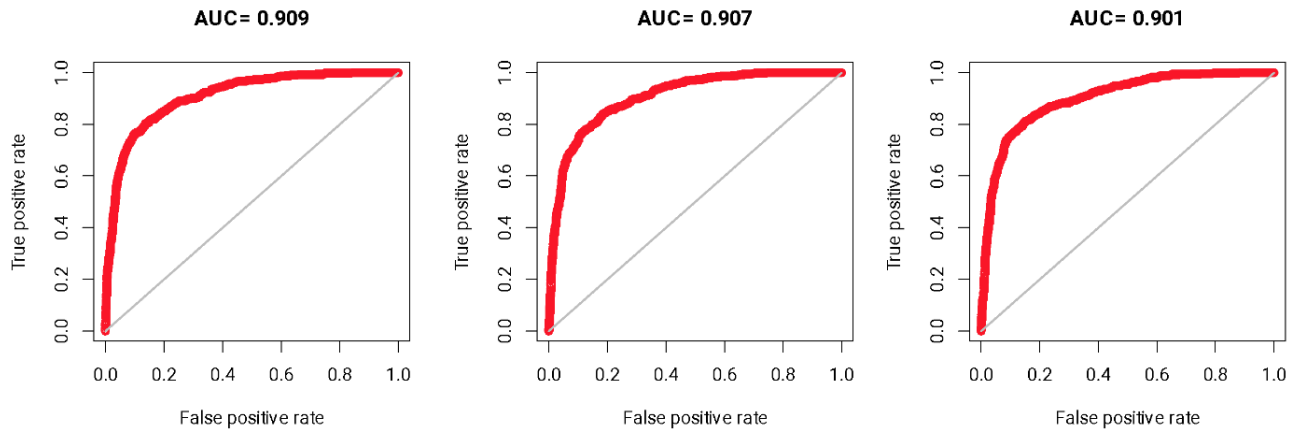


Figure 18: Receiving operating characteristics (ROC) curves for the three MaxEnt models (season 1 to the left; season 2 in the middle & season 3 to the right) with associated AUC demonstrating the performance of the three models with performance of 0.909, 0.907 and 0.901.

True Positive Rate (TRP) - The best performing threshold given by ROC was used to find the true positive rate for each separate model. The TPR curves (Figure 19) for the three seasons were 0.8, 0.84 and 0.81, indicating how well the model correctly identifies true positives. This is opposed to the true negative rate, where the model correctly indicates not suitable environment for killer whales, which is the complement of TPR (20%, 26% and 19%) (Fitzgibbon et al., 2022).

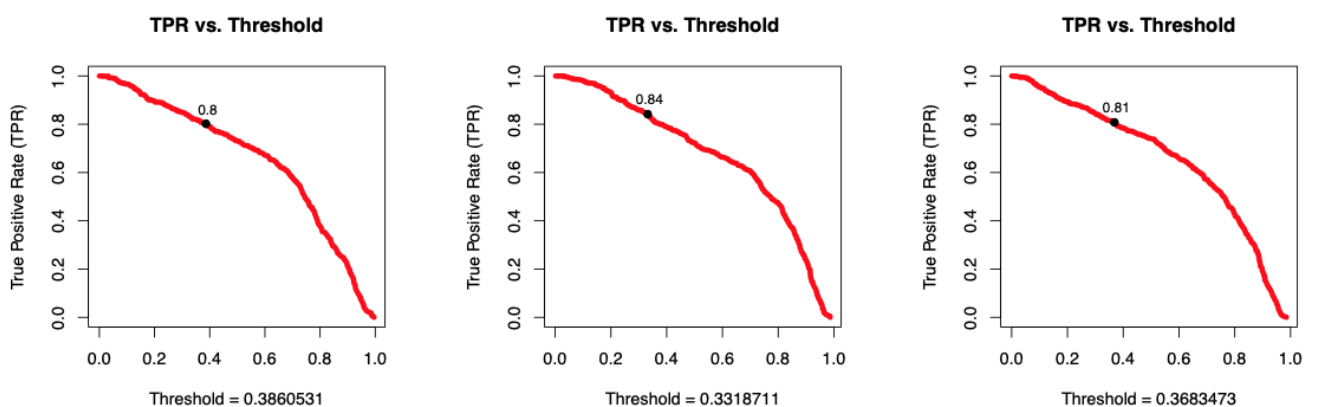


Figure 19: True positive rate curves (TPR) at different threshold levels from the best performing threshold given by ROC, for the three seasons (season 1 to the left; season 2 in the middle & season 3 to the right)

Collinearity and Jackknife test – From Pearson’s collinearity test (Figure 20) rugosity and slope were found to have the highest correlation of 97%, followed by depth and distance to coast with a correlation of 77%, and lastly depth and sea bottom temperature with a correlation of 75%. After assessing the jackknife test for variable importance for regularized training gain, rugosity and depth was found to have little regularized training gain for the three models, neither isolated nor excluded (Figure 21). Consequentially, as the two parameters had high correlation, they were dropped from the model. This left 12 predictor variables to be used in the model: herring, sea surface temperature, sea bottom temperature, salinity, ocean mixed layer thickness, seabed substrate, chlorophyll *a* concentration, vessel density, slope, stratification, stratification roughness (rstrat) and distance to coast.

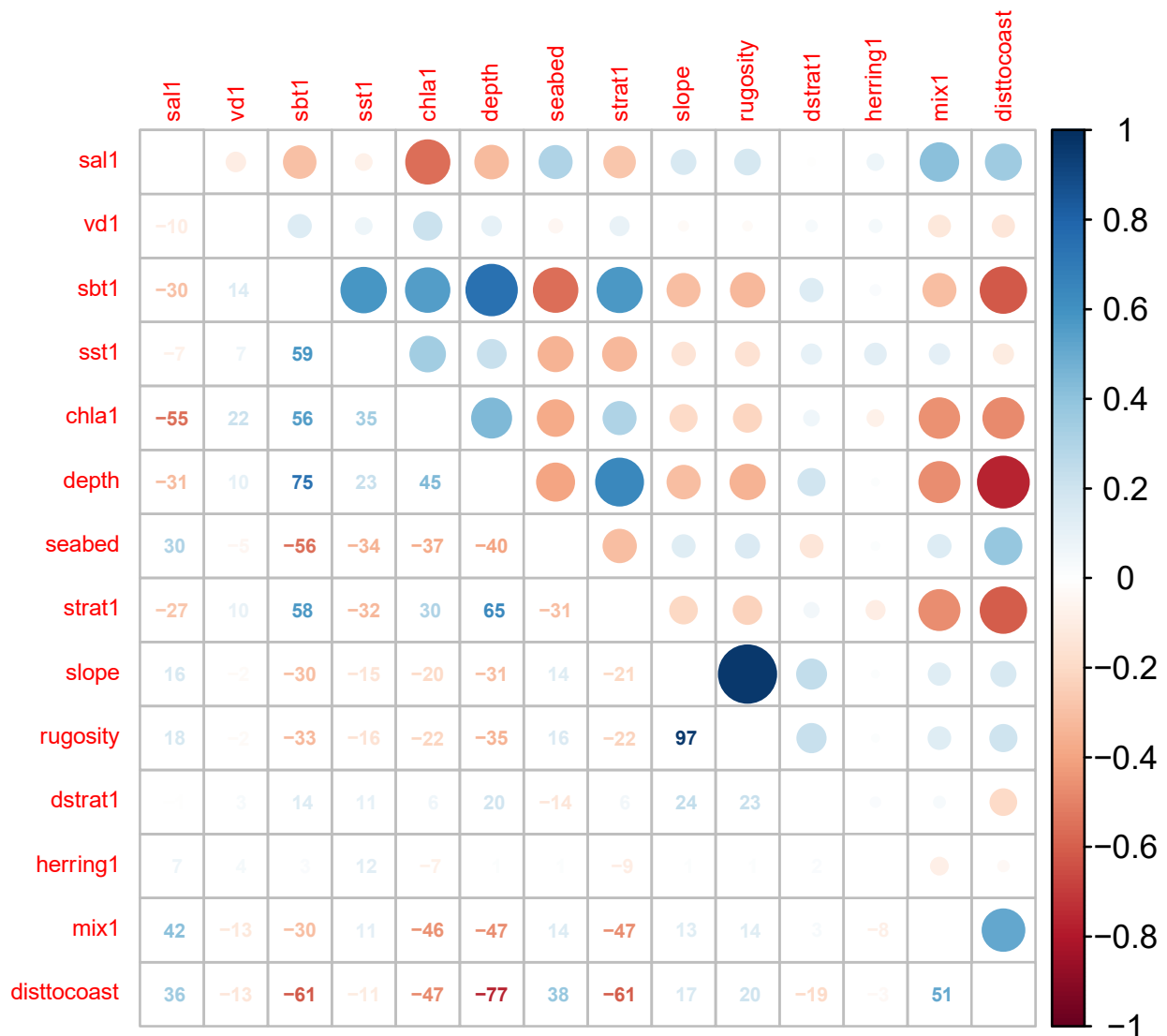


Figure 20: Pearson pairwise correlation matrix of 14 environmental predictor variables illustrated from model of season 1. Correlation coefficient (Pearson's r) is showed on the bottom left, while a graphic presentation of the correlation is showed on the top right. Larger circles and stronger colours represent stronger correlation. Blue coloured circles represent positive correlation and red coloured circles represents negative correlations. Similar outputs were given for all three seasons, where the strongest correlation was seen between rugosity and seabed of 97% and depth and distance to coast with a correlation of 77%, followed by depth and sea bottom temperature with a correlation of 75% (66% for season 2 and 71% for season 3).

Furthermore, the jackknife test (Figure 21) revealed distinct results between the three seasons. Herring exhibited the most significant isolated training gain in season 1 and 2 (September-January & February-March). In season 3 (April – August), the variable with highest isolated training gain was distance to coast, followed by sea surface temperature and sea bottom temperature. This indicates a good fit to the training data.

High isolated training gain indicates that the predictors, when used in isolation, have the most useful information for the model. For season 1 particularly, herring exhibited high training gain in isolation, with levels almost as high as when considering all parameters together. In contrast, slope followed by rugosity showed the least training gain in isolation. In the three models, omitting any of the environmental variables resulted in a similar decrease in model gain. The exclusion of any parameter had a low impact on the models. However, sea surface temperature decreased the gain the most in season 1, chlorophyll *a* concentration, herring and sea surface temperature in season 2, and herring, salinity and sea surface temperature in season 3. Meaning these variables hold important information that is not present in the other variables, making the parameters important factors in the model (Jones et al., 2019).

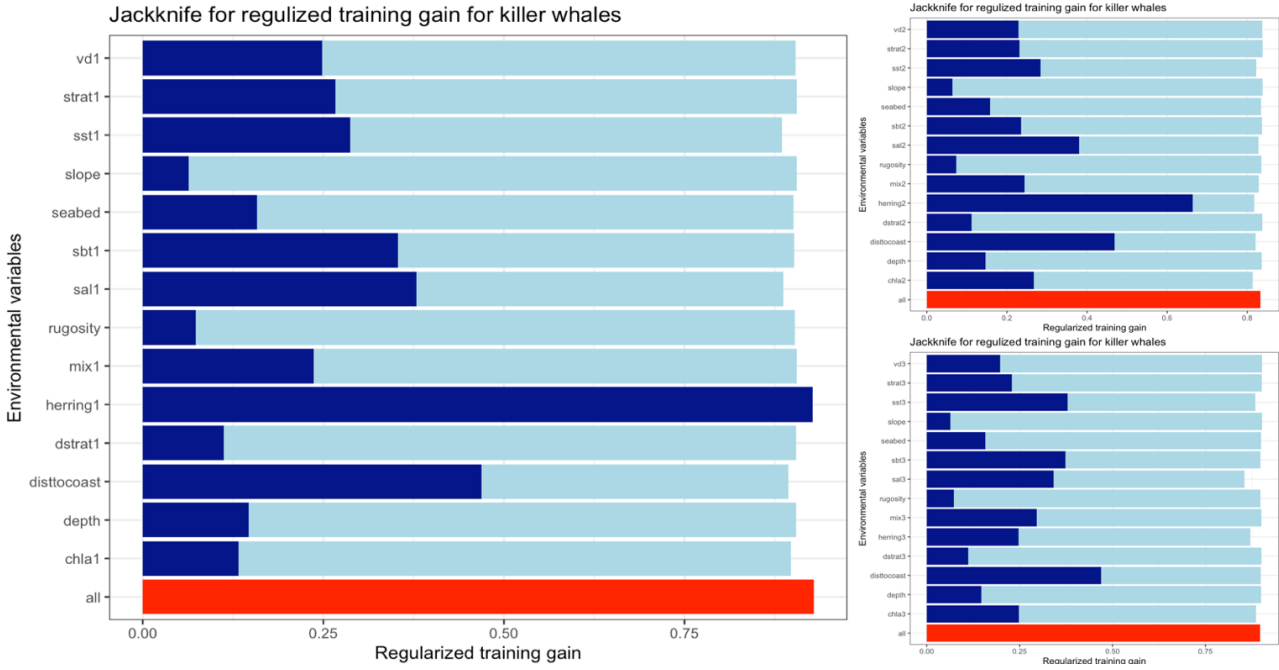


Figure 21: Jackknife output plots from the three different seasons (September- January displayed left, February – March displayed top right and April – August displayed bottom right) assessing the training gain for each 14 parameters for the model. This estimates the importance of each predictor variable in the model. Each variable is excluded in turn when the model is created, illustrated in light blue – without variable. Then each model is created with only one parameter in isolation, illustrated in dark blue – isolated parameter, before a model is created with all the parameters together, illustrated in red – all parameters.

Sensitivity analysis – The sensitivity analysis for the three models did not reveal any observational points with significantly high leverage. The observational points with the highest leverage in the three models (season 1, season 2 and season 3) were 0.0047, 0.0038 and 0.0033 suggesting relatively low impact on the model's predictions. Consequently, all observational points were kept in the model.

Background points – Results from testing the model with 10000, 15000 and 20000 random background points, found the best performing model to be with 20000 random background points. Accordingly, regularized training gain for the three models gave a gain of 0.6-0.63 with 10000 background points, 0.735 – 0.795 with 15000 background points, and 0.862 - 0.929 with 20000 background points.

3.3.3 Environmental variables describing distribution

The variable contribution varied among the three seasons. Contribution was more similar for season 1 and 2, than for season 3 (Figure 22, Table 2). The variable contribution plot (Figure 22) showed that for season 1 and 2, the highest rate of overall relative contribution, from the 12 environmental variables, was from herring with 60% contribution in season 1 and 52% contribution in season 2. The second most influential environmental variable was distance to coast with a relative contribution of 18.6% and 18.2% for seasons 1 and 2, respectively. In season 1, sea surface temperature and sea bottom temperature were the third and fourth most influential environmental variables with relative contribution of 7.1% and 4.9%. In season 2, chlorophyll *a* concentration was the third most influential variable with relative contribution of 9.8%, and thereafter sea surface temperature with 7.6% relative contribution. The most influential environmental variable in season 3 was distance to coast with 28.8% relative contribution. The second most influential variable in season 3 was sea surface temperature with a relative contribution of 25.4%. The third and fourth most influential variables were salinity with 15% relative contribution and herring with 12.3% relative contribution. Recurring parameters with high relative contribution within the three seasons were herring, distance to coast, salinity and sea surface temperature. Additionally, sea bottom temperature had some contribution value in season 1 and 3, and chlorophyll *a* had a significant contribution in season 2. The remaining environmental variables (vessel density, seafloor slope, stratification, stratification

roughness, seabed and ocean mixing layers) were inadequate to significantly contribute in the models.

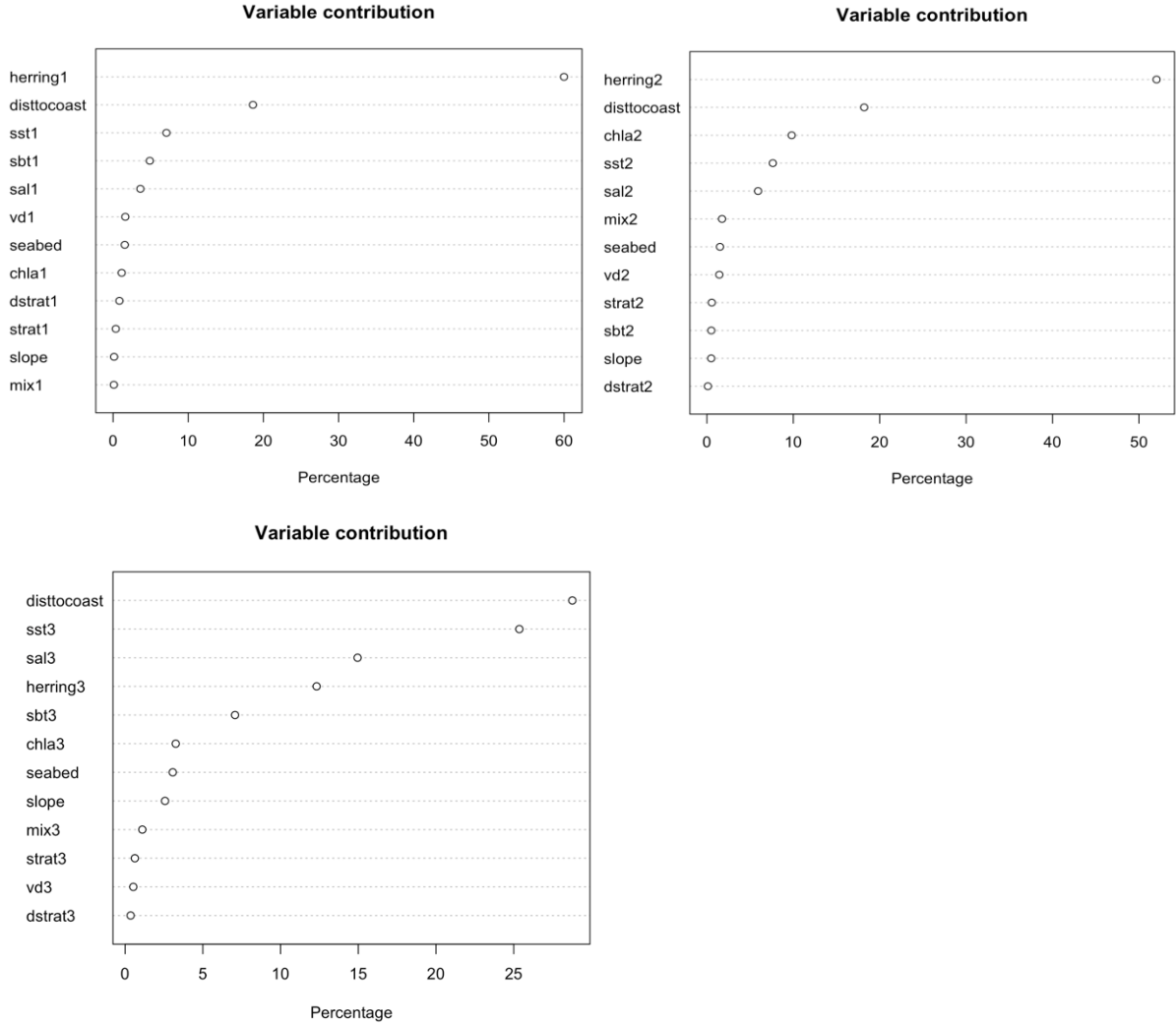


Figure 22: Variable contribution for each environmental parameter for season 1(top left, season 2 (top right) and season 3 (bottom left).

Table 2: Percent contribution and the permutation importance for each 14 parameters, in the three seasons (1 = September – January, 2 = February – March & 3 = April – August) affecting the distribution of killer whales.

Variable	Percent contribution	Permutation importance
Season 1		
<i>Herring</i>	60	22.9
<i>Distance to coast</i>	18.6	11.5
<i>Sea surface temperature</i>	7.1	27.6
<i>Sea bottom temperature</i>	4.9	3.1
<i>Salinity</i>	3.6	20.7
<i>Vessel density</i>	1.6	0.2
<i>Seabed substrate</i>	1.6	2
<i>Chlorophyll a</i>	1.1	6.8
<i>Stratification roughness</i>	0.8	0.5
<i>Stratification</i>	0.4	1.3
<i>Slope</i>	0.1	1
<i>Ocean mixing</i>	1.1	2.4
Season 2		
<i>Herring</i>	52	4
<i>Distance to coast</i>	18.2	9.9
<i>Chlorophyll a</i>	9.8	15.5
<i>Sea surface temperature</i>	7.6	25.5
<i>Salinity</i>	5.9	14.4
<i>Ocean mixing</i>	1.8	21.5
<i>Seabed substrate</i>	1.5	2.3
<i>Vessel density</i>	1.4	0.2
<i>Stratification</i>	0.6	2.3
<i>Sea bottom temperature</i>	0.5	1.9
<i>Slope</i>	0.5	2.3
<i>Stratification roughness</i>	0.1	0.2
Season 3		
<i>Distance to coast</i>	28.8	1.1
<i>Sea surface temperature</i>	25.4	38.83
<i>Salinity</i>	15	38.5
<i>Herring</i>	12.3	6.1
<i>Sea bottom temperature</i>	7.1	3.1
<i>Chlorophyll a</i>	3.3	7.7
<i>Seabed substrate</i>	3.1	1.7
<i>Slope</i>	2.6	1.1
<i>Ocean mixing</i>	1.1	0.5
<i>Vessel density</i>	0.6	0.7
<i>Stratification</i>	0.5	0.3
<i>Stratification roughness</i>	0.4	0.3

3.3.3.1 Response curves

The response curves (Figure 23a, b & c) plot probability of presence (POP) against a series of values within each environmental variable. The probability of presence for recurring environmental parameters contributing in the three models are explained in turn in the next section. Response curves for environmental parameters inadequate to significantly contribute in the models (vessel density, seafloor slope, stratification, stratification roughness, seabed and ocean mixing layers) will not be analysed.

Herring – The response curves for herring (Figure 23a, b & c) showed that greater concentrations gave higher probability of presence in all three seasons, where POP increased relatively with herring catches. POP peaked at herring catches of respectably ca. 518000 kg in season 1, 134300 kg in season 2, and 83830 kg in season 3.

Distance to coast – The probability of presence was higher towards distances of 500 meters and 400 km from the coast in the three seasons, although relatively high levels of POP persisted between 500 meters and 400 km in season 2 and 3. In season 1 and 2, POP was higher towards distances of 500 meter from the coast. For season 1, the response curve (Figure 23a) shows POP decreasing slowly with increasing distances from the coast. In season 2, the response curve (Figure 23b) shows a decrease in POP followed after high POP at 500 meter distance. This was followed by a gentle increase, up to a peak in POP at 400 km from the coast. Similarly, in season 3 (Figure 23c) the POP was slightly higher towards a distance of 400 km from the coast.

Temperature – In terms of temperature suitability, the response curves for POP demonstrated distinct patterns for all three seasons (Figure 23a, b & c). In season 1 (Figure 23a), there was a gradual increase in POP within the range of sea surface temperatures from 0-9°C followed by a steep increase, peaking at approximately 10.37°C. Afterward, a rapid decline followed, resulting in higher temperatures having a probability of zero. A similar trend was found in season 2 (Figure 23b), characterized by a constant increase in POP between the temperatures of 0-6°C, peaking at approximately 6.1°C, followed by a sharp decline to a POP of zero at higher temperatures. In season 3, the response curve (Figure 23b) showed an increase in POP between 3-10°C degrees, with a peak between approximately 8.5 - 9.5°C. This was followed by a decline in POP, although some level of POP persisted at higher

temperatures. Regarding sea bottom temperatures, in season 1, higher POP was found for temperatures between -10 and 9°C, peaking at 9°C, followed by no POP at any higher bottom temperatures. In season 2, optimal conditions for POP were observed (Figure 23b) at higher bottom temperatures, with a peak at 8°C, followed by a decline. However, a persistent level of POP persisted up to 20°C for bottom temperature in season 2. In season 3 the response curve (Figure 23c) demonstrated a contrasting pattern. Here, higher POP was observed at colder temperatures between -10 and -2°C, followed by a decrease in POP as temperatures increased.

Salinity – Concerning optimal salinity conditions for presence, the response curve for season 1 (Figure 23a) showed a gradual increase in POP from 10 PSU (practical salinity units) up to its highest levels within the range of 29-33 PSU, followed by a decline, where no POP was found at any higher salinity levels. Season 2 was characterized by sustained POP at high salinity levels (Figure 23b). Here, an increase in POP was present between 10 PSU up to 32 PSU, followed by a small decrease, but with POP remaining relatively elevated within the range of 40 – 50 PSU. In season 3 (Figure 23c), similar patterns as for season 1 was found. Here, a steep increase in POP was found, with a peak at 26-34 PSU, followed by a steep decline, resulting in no POP at any higher salinity levels.

Chlorophyll a concentration – The optimal chlorophyll *a* concentration varied among the three seasons. In season 1, concentrations of chlorophyll *a* did not affect POP. Here, the response curve (Figure 23a) shows the highest POP at negative chlorophyll *a* concentration, followed by a complete absence of POP at higher concentrations. In season 2 (Figure 23b) chlorophyll *a* had highest POP at 0,2-0,4 mg/m³ concentrations, with no POP at either higher or lower concentrations. In season 3 (Figure 23c) POP increased greatly when chlorophyll *a* concentration exceeded 0 mg/m³.

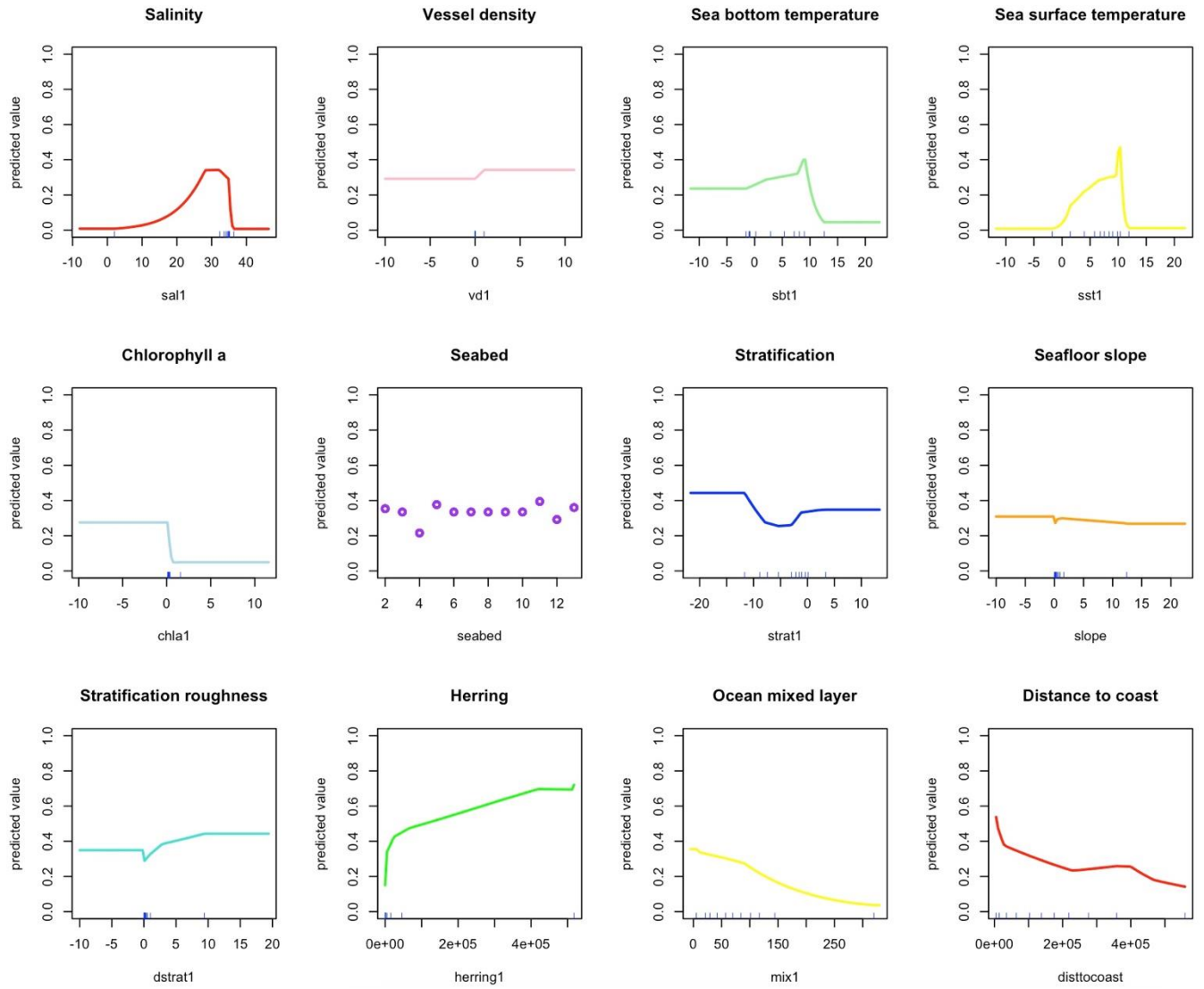


Figure 23a: Response curves for season 1 for 12 environmental parameters, each curve displaying the most suitable ranges and variations for each parameter. The model predicts suitable areas from where most of the parameters have high suitability.

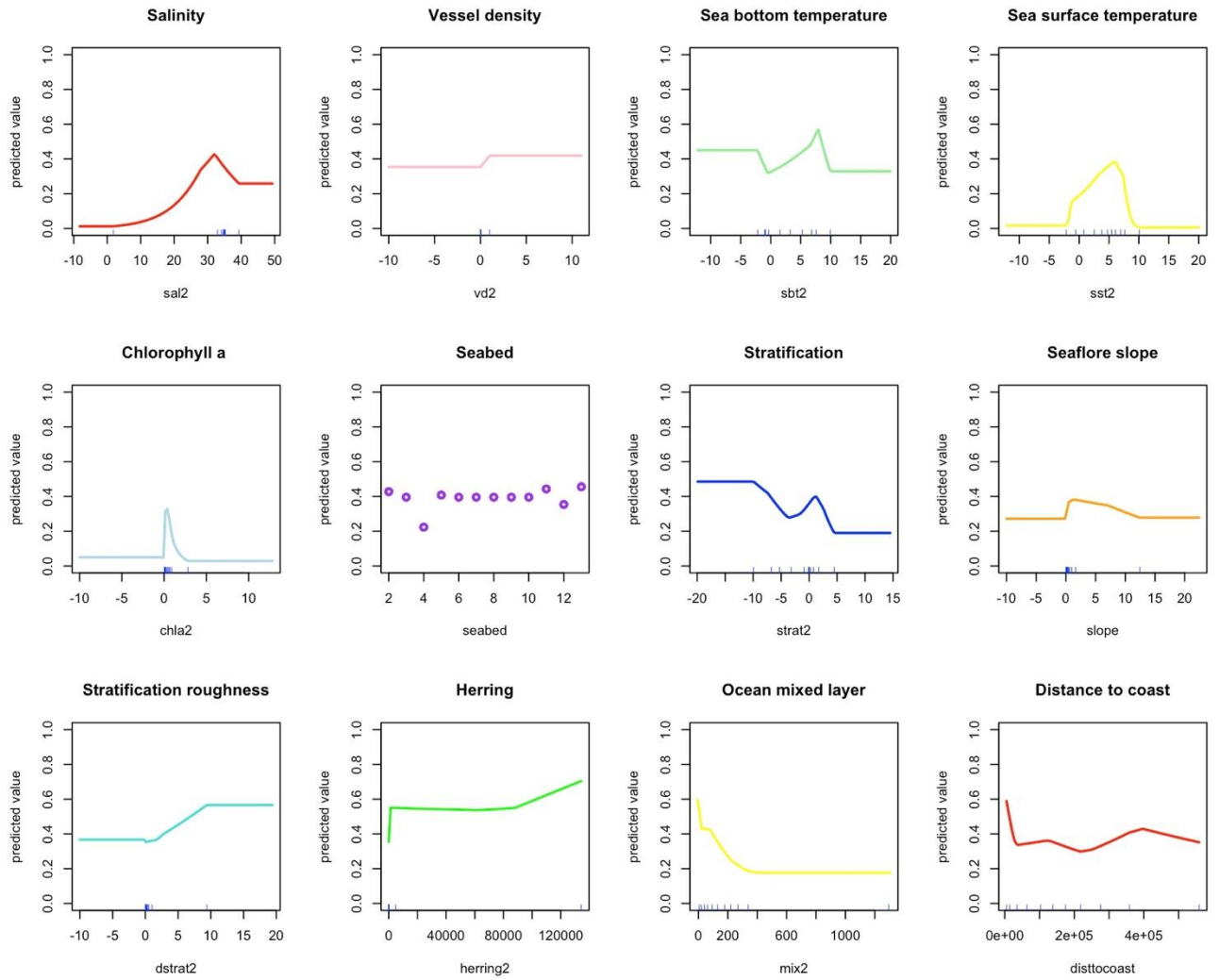


Figure 23b: Response curves for season 2 for 12 environmental parameters, each curve displaying the most suitable ranges and variations for each parameter. The model predicts suitable areas from where most of the parameters have high suitability.

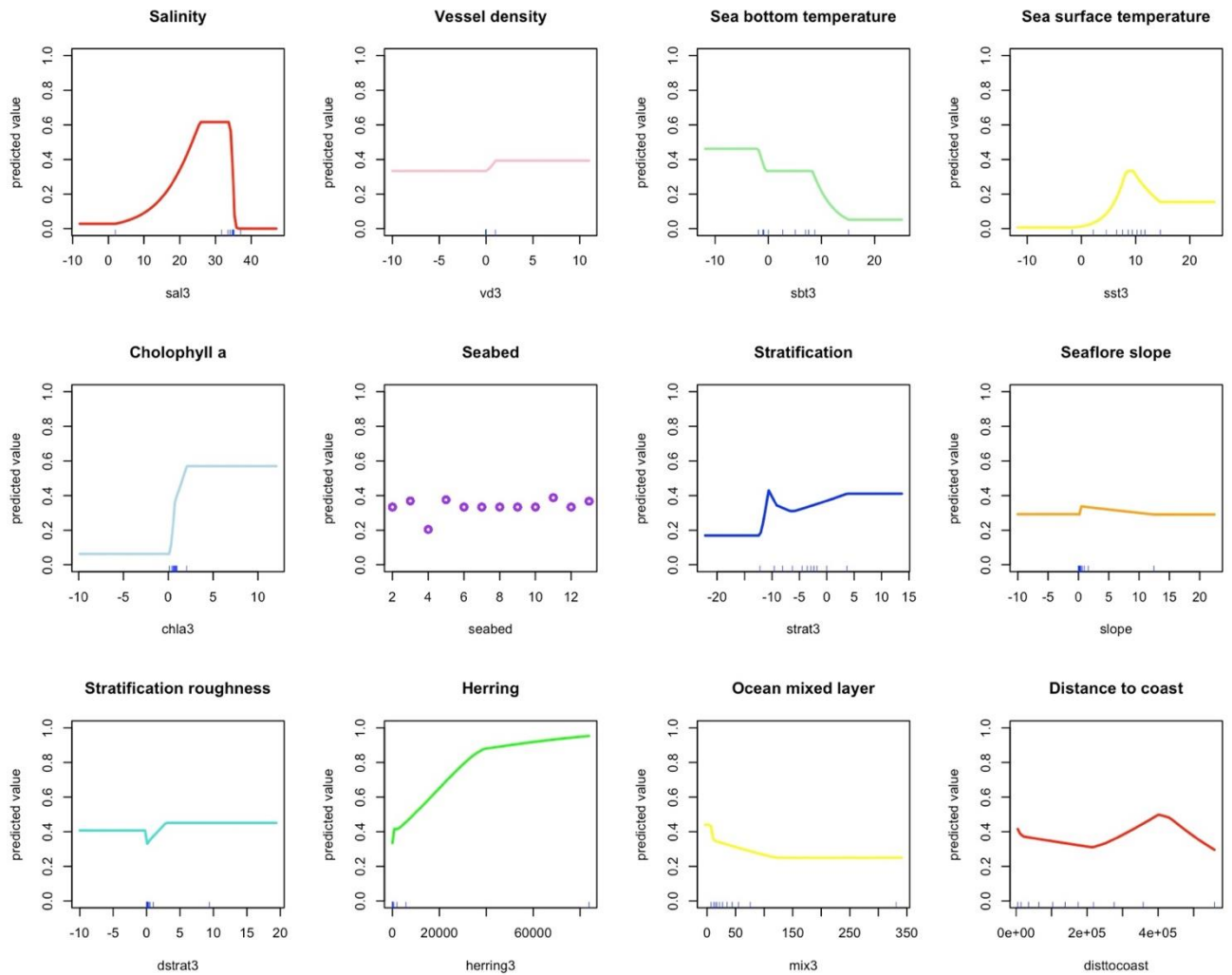


Figure 23c: Response curves for season 3 for 12 environmental parameters, each curve displaying the most suitable ranges and variations for each parameter. The model predicts suitable areas from where most of the parameters have high suitability.

3.3.4 Predicted distribution patterns

Predicted distribution patterns for killer whales were represented by probability maps with the default cloglog output (0 - 1) (Figure 24a, b & c). The maps found areas with higher prediction values predominantly in areas close to the shore, along the entire Norwegian coast, for all three seasons. In season 1, the probability map (Figure 24a) showed that probability of presence was noticeably higher in the north than in the south. For season 2, the highest probability of presence (Figure 24b) moved slightly further south along the coast and outwards into the open waters. Season 3 (Figure 24c), showed the highest probability of presence in both the north and the south, with

less probability in the central coast of Norway. Season 3 has the most probability of presence in the south, out of all three seasons, where probability of presence was found further offshore.

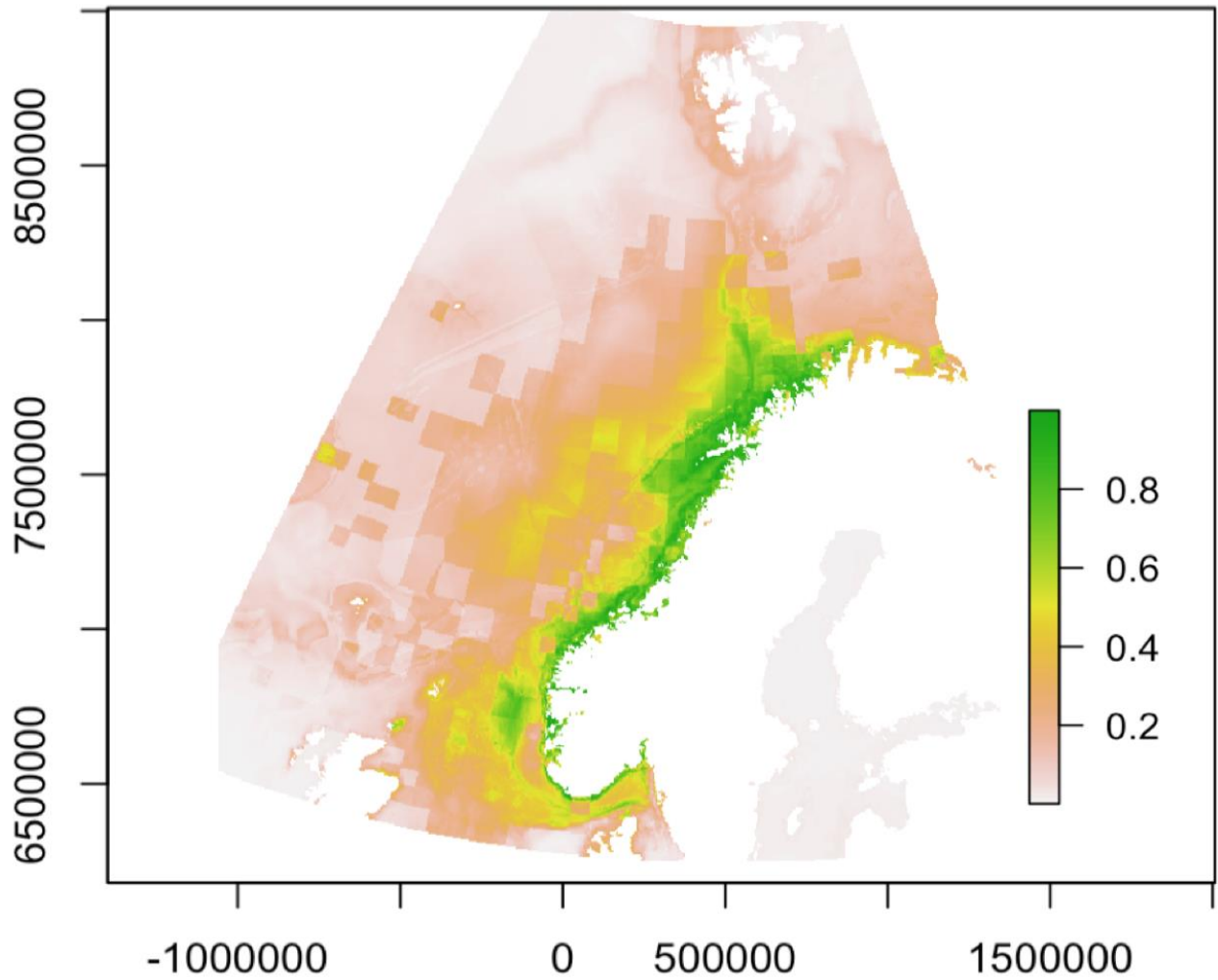


Figure 24a: Map predicting distribution of killer whales in Norway for season 1. Green color indicates areas the model predicted as more suitable for killer whales based on observational points and environmental parameters.

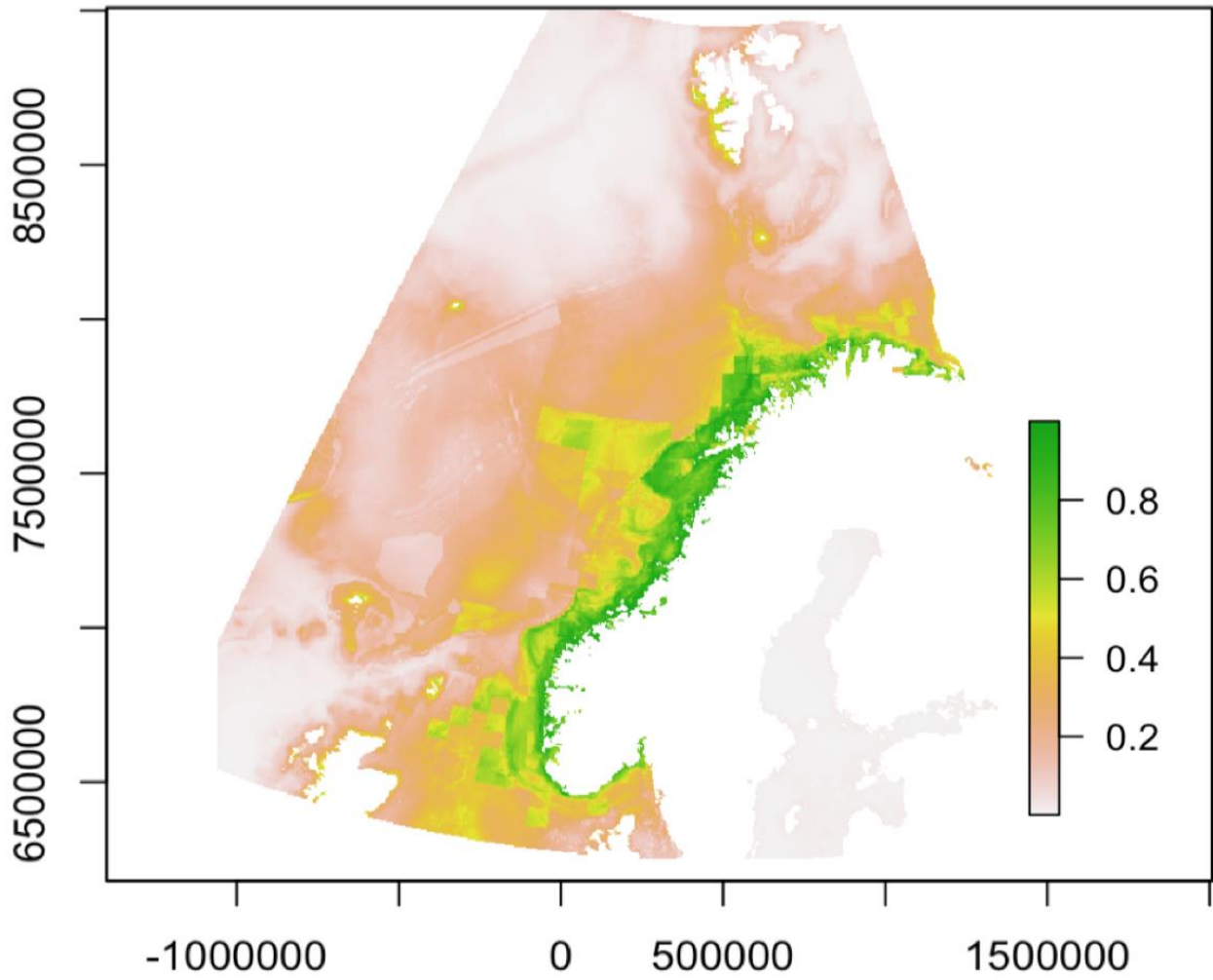


Figure 24b: Map predicting distribution of killer whales in Norway for season 2. Green color indicates areas the model predicted as more suitable for killer whales based on observational points and environmental parameters

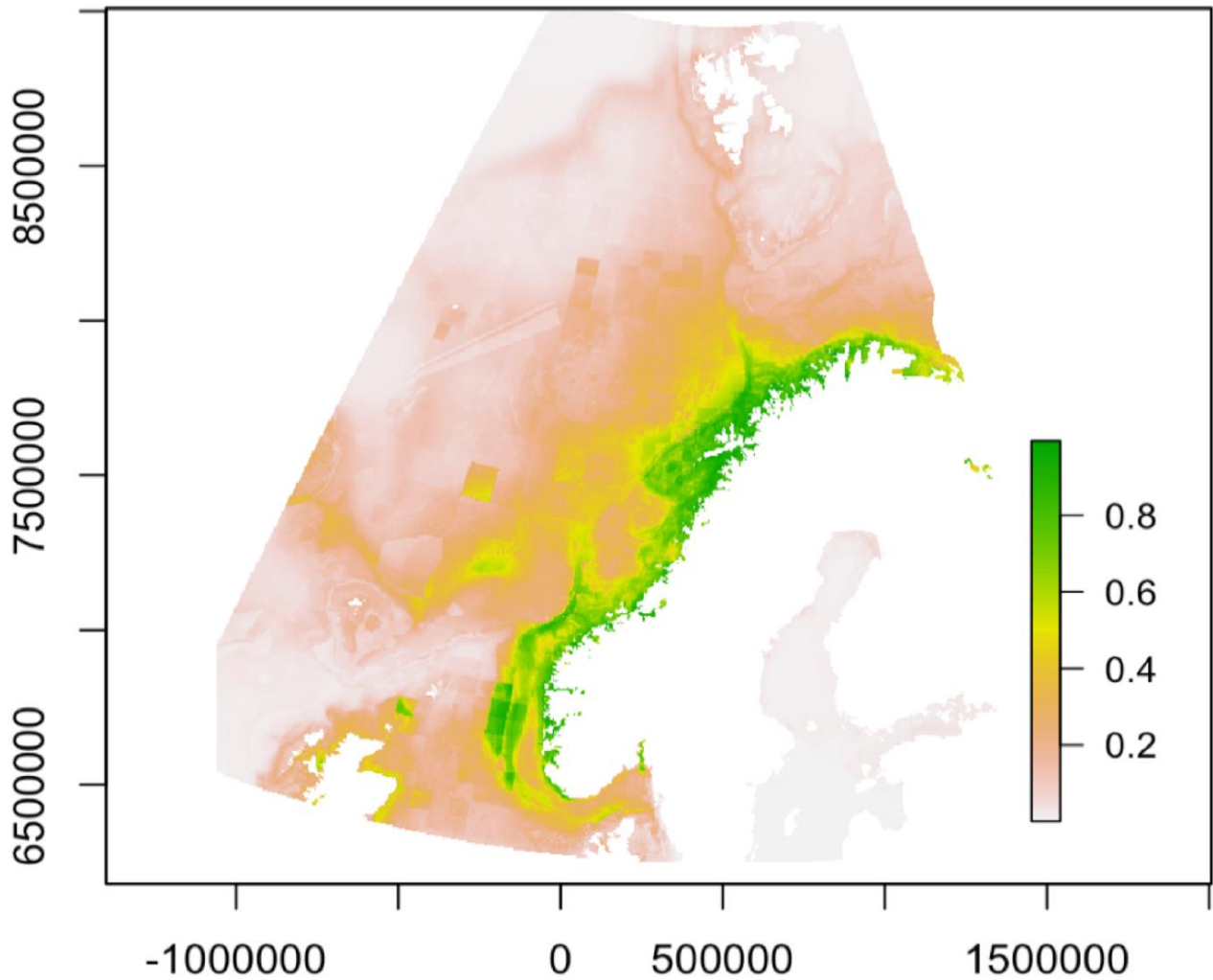


Figure 24c: Map predicting distribution of killer whales in Norway for season 3. Green color indicates areas the model predicted as more suitable for killer whales based on observational points and environmental parameters

3.3.4 Threshold map

The results from the three threshold maps can be found in appendix (Figure A13a, b & c) and show predicted presence of killer whales at the lowest suitable value point for occurrence, for each season. The threshold map illustrates areas suitable for presence above the threshold values for lowest predicted presence (green) and below (white). The three seasons had different values for lowest predicted presence, $S_1 = 0.35$, $S_2 = 0.38$ and $S_3 = 0.44$, respectively. The maps show some variation in the three models. The predicted presence was lowest in season 3 (Figure A13c), compared with the two other seasons. Most predicted presence at the lowest suitable value point was in

season 2 (Figure A13b), with a large area suitable for presence. The threshold map for season 1 (Figure A13a) illustrates a similar pattern in the north as the probability map for season 1.

4. Discussion

This study investigated the use of an alternative approach to model the spatiotemporal distribution of the killer whale, a far-ranging, migrating cetacean species that spends most of its time below the sea surface. This was done by collecting observational data on killer whales through a variety of sources, including citizen science, and thereby avoiding the costs of carrying out regular research surveys. The data collected were used to create a species distribution model that contributes to our understanding of which environmental factors influence the distribution of killer whales in Norwegian waters. Ultimately, this study has synthesized a great amount of data with a broad spatial coverage, covering many geographical regions of Norway.

4.1 The value of citizen science as a tool in research

From the final dataset containing 4372 records, a total of 1716 records came from citizen science observations. The trend in reported observations of killer whales, including observations from all four sources, gradually increased during the study period (Figure 6). This increase in reported observations could possibly reflect distributional shifts and/or changes in killer whale abundance, but it could also indicate increased involvement from the general public (Jourdain et al., 2019). This trend was further investigated by excluding opportunistically sampled data from the Institute of Marine Research, to assess the trend in collected data from citizen science initiatives, as IMR observations are not exclusively gathered from citizen science and the general public. Without the IMR data, a distinct increase in number of reported observations were found for the study period (Figure 8a), and was especially prominent from 2014 to 2021. This was opposed to a gradual decrease in observations collected from IMR (Figure 8b). The IMR dataset consists of a combination of opportunistically sampled data and citizen science data reported from the coast guard, the navy, IMR research vessels, fishermen and the general public. A possible explanation for the increase in observations made by the NBIC, NOS and media analysis could be recognised from larger efforts made by NOS and the NBIC, then of IMR, to gather the public's attention. Another explanation could be that NOS's and NBIC's report systems are more accessible, than the IMR's, making it easier for the general public to report observations of killer whales. This could be attributed to IMR primarily being a research

institute, with observations collected from a variety of sources. Consequently, IMR data does not reflect the increasing trend in citizen science observations. Yet another explanation for the increased reporting's from citizen science may be the Covid19 pandemic, which gave people more time to be outside in nature. Furthermore, a potential explanation describing the decrease in observations collected from IMR could indicate a decrease in killer whale populations in Norway. Although, there is low possibility of this as killer whale numbers appear to be stable, or even increasing, around Norway, despite numerous anthropogenic threats (Jourdain et al., 2019). Lastly, the increased trend in observations collected from citizen science indicates that it has become a more valuable tool. This highlights the use of citizen science as a tool to gather observational data for a larger dataset. Spreading the knowledge of its usefulness, could lead to the enhancement of data quality, as the general public may be more inclined to report observations and contribute to a project. The quality of such observations could also be improved by having established reporting platforms, and not just relying on mass media and social networks.

Over the past decades, there has been a shift in approaches to conservation of wildlife, moving from exploitation to preservation (Reeves and Reijnders, 2002, Reeves, 2009). For cetaceans like the killer whale, a clear change is evident, with a shift from whaling and capturing of killer whales for entertainment purposes, to encountering significant opposition against these practices (Wells et al., 1998, Simon et al., 2009, Kuningas, 2014). This shift, with growing interest in the wildlife, may potentially explain the increased reported killer whale observations through citizen science, evidenced in this study (Figure 6 & 8a). Higher efforts to involve the general public in scientific work, through citizen science, can be a contributing factor to the increase rate of reported observations. Motivating the general public is crucial to ensure the success and sustainability of a project, and poses a challenge to the citizen science approach (Prestopnik and Crowston, 2012, Rotman et al., 2012). However, in this thesis, the study species is a well-known charismatic species that easily captivates the attention of the public. This makes the process of motivating participants to enrol in citizen science initiatives significantly easier. Another way of motivating participants to contribute in a project is by choosing a specific area of interest, or a specific activity (Hyder et al., 2015, Carcia-Soto and van der Meeren, 2017). Such initiatives have been made in the Hardangerfjord region, where NOS has successfully gathered the public's

attention through shared information on two killer whale pods, frequently moving in and out of the fjord, feeding on the harbour porpoise population (Åslein, 2023).

The rise of social media platforms, as well as the use of smartphones, may have contributed to the increased rate of reported killer whale observations (Figure 6 & 8a). These platforms have allowed for information to be shared, and thereby contributed by engaging the general public. Additionally, it has created an accessible platform where observations can easily be reported. Social media platforms can be useful for research purposes, serving as a means to collect information that can be used in more systematic reviews after controlling the quality of the collected data. The Norwegian Orca Survey has made substantial efforts to engage the general public by raising awareness and increasing the knowledge on killer whales, e.g., through social media platforms. The NOS is an example of an organization that has successfully used citizen science as a tool in collecting observational data, where the growing interest in killer whales over the last years, have been extremely beneficial in their research (Jourdain and Karoliussen, 2021). Furthermore, by establishing an online platform, they have made it possible for the general public to access and contribute to research, e.g., by submitting photographs of killer whale encounters for identification.

Results from the questionnaire assessing whether the presence of killer whales in Hardangerfjord and Sognefjord is a new phenomenon gave similar results. This displayed a clear increasing trend in number of observations made the past few years (Figure 11 & 15). There is high awareness of killer whales in the Hardangerfjord, partially due to the efforts of the NOS to involve the general public in citizen science. These initiatives have facilitated the collection of data in this thesis through high response rates in the questionnaire (116 participants). Two killer whale pods have been found frequently moving in and out of the Hardangerfjord the past years, between the months of December and May (Jourdain et al., 2022, Åslein, 2023). This coincides with findings in the questionnaire (Figure 12), and could indicate new distribution patterns. Killer whale distribution patterns are highly associated with the dynamic distribution of prey resources. Potentially, discovering the large harbour porpoise population in Hardangerfjord (Bjørge et al., 2019), could therefore be the reason for this new distribution pattern. Additionally, this coincides with the high percentage (33%) of participants, who have observed attacks on harbour porpoises in the

Hardangerfjord. However, another potential explanation for the increased rate of observed killer whales in the Hardangerfjord could be described by the increased attention on marine mammals. Furthermore, with less efforts made in the past to involve the general public, potential biases in the results may occur, exaggerating the presence of killer whales in the Hardangerfjord.

Accordingly, similar initiatives to involve the general public have been made in the Sognefjord, by the NOS. Here, the response rate of contributing participants (40 participants) was evidently lower than in the Hardangerfjord. An explanation for this lower rate could be posed by lower efforts made to involve the general public. The Sognefjord questionnaire survey showed a similar trend of increased observations the past years. Comparable explanations for the increased rate can be applied as for those discussed regarding the Hardangerfjord. One potential explanation is that fjord systems are nutrient dense ecosystems (Nielsen and Andersen, 2002). This leads to higher abundance of species, including possible prey species for killer whales (Menge, 1992). Another potential explanation for the increased rate of observations in the Sognefjord could, similarly as for the Hardangerfjord, be the high harbour porpoise population inhabiting the fjord (Bjørge et al., 2019) Results from the questionnaire indicate an even higher observational rate of porpoise attacks in the Sognefjord compared to the Hardangerfjord, with 42.5% of the participants having observed an attack. However, more research is needed to find direct potential explanations that relates killer whale presence to the Sognefjord. Additionally, the two questionnaire surveys distributed to citizens in the Hardangerfjord and Sognefjord, identified high rates of observed killer whale attacks on seals. This may indicate that the two killer whale pods, identified as NKW-704s and NKW-280s, entering the fjords are mammal (seals and porpoises) eating killer whales, that consume from a higher trophic level throughout the year (Jourdain, 2020).

All collected data in this study were obtained either directly from citizen science initiatives (i.e., questionnaire, media analysis) or through incidental sightings reported to affiliated institutes working with biodiversity of species, particularly in the case of killer whales (i.e., IMR, Artsdatabanken and NOS). NOS was not able to provide all their collected data from the northern regions, as this study initially intended to only research the west coast of Norway. Later, when the research area expanded to include

the entire Norwegian coast, NOS had insufficient time to organize observational data for the northern region. Subsequently, this could potentially lead to some biases concerning the species distribution model, as observations in the northern region may not be highlighted to the extent it should be. Nevertheless, the other sources, especially IMR, provided enough data to capture the high abundance patterns of killer whales in the north.

4.1.1 Limitations with the citizen science approach

Citizen science as a tool in research has gained a lot of positive attention lately, but is still not fully embraced by the scientific community (Earp and Liconti, 2020b, Burgess et al., 2017). One of the main concerns when utilizing citizen science, is the quality control of collected data (Ellwood et al., 2017), which subsequently was the main concern in this thesis. When collecting data through a media analysis, some biases may occur. Conducting a comprehensive search in newspaper and magazine archives could potentially lead to wrongful inclusions of encounters, from the lack of information on individual encounters. Initially, only encounters with associated photographs were intended to be included in the media analysis. This had to be adjusted as the study period stretches all the way back to 2000, where none of the archived articles included photographs, with the first photograph being included in 2008. Therefore, encounters with enough information, giving specific details, were considered valid and included in the analysis. Another concern, when working with collected opportunistic data from the general public, is duplications of the same encounters, as numerous of newspaper articles frequently depicted the same killer whale encounter.

Another limitation associated with data collected through citizen science, is a lack of systematic structure, where it can fail to provide equal probability of coverage of killer whale presence (Viddi et al., 2010). This leads to geographical biases, where the amount of collected observations adjusts with its surrounding environment. There are substantial differences in the number of inhabitants throughout the coast of Norway, where some areas are geographically harder to access. Additionally, some areas are more visited than others, as they are more aesthetically or biologically interesting, making probability of observations considerably greater. This can lead to reported

encounters being biased towards reachable and inhabited areas, e.g. coastal areas with more inhabitants.

Additional challenges arise when setting up systematic surveys for migrating cetaceans. As cetaceans exploit the environment disproportionately, clear distribution patterns are lacking to setup surveys, which make them inherently challenging (Viddi et al., 2010). This includes logistical challenges, which plays a significant role in the lack of studies conducted south of Lofoten. As an example, the waters outside of Møre are considered the most dangerous area along the Norwegian coast, where many ships have been wrecked (Riksringkasting, 2003, Aftenposten, 2018, Ariansen, 2018). These kinds of issues may have made it very difficult to conduct systematic surveys in this region, of which killer whales have been known to frequently visit, feeding on the spawning herring (Similä et al., 1996). These challenges have made it considerably important to create good SDMs that can predict occurrences, while studying species distribution in a safe environment.

4.2 Predicting presence of killer whales

The MaxEnt model identified the highest predicted presence of killer whales for the north region, during season 1 (September – January), compared to the rest of the coast (Figure 24a). This finding supports previous literature, indicating killer whale abundance in the north during the winter months, for feeding on the overwintering herring (Bisther and Vongraven, 1995). This may suggest strong model performance, as the model successfully reflects the importance of herring in the north during the winter. Furthermore, this in turn may indicate accurate model predictions in the southern regions.

In season 2 (February – March), the probability map predicted distribution of killer whales towards the open waters, and slightly towards the south, compared to season 1. This predicted southward movement coincides with the migration of herring towards spawning grounds between Lofoten and Lista (69°N - 58°N) (Slotte, 1999). Additionally, a more evident predicted presence was found along the central- and south coast of Norway in season 2, compared to season 1. For season 3 (April – August), the probability map predicted presence along the north and south coast of Norway,

with less predicted presence on the central coast. Contrary to the herring's migration patterns, the killer whales were predicted to occur in close proximity to the coastline during season 3. During this period, herring is found in large parts of the Norwegian Sea (Slotte, 1999). Furthermore, the probability map predicted presence in the south of Norway slightly towards the open waters of the Northern Sea. This may be explained by other available prey resources, indirectly affecting the presence of killer whales through other environmental variables. This includes environmental variables that may have contributed to warmer water temperatures (sea surface temperature & sea bottom temperature) and higher nutrient levels (chl-*a*) impacting the ecosystem by bottom up control (Frederiksen et al., 2006).

Little is known about the eastern North Atlantic killer whale's migration and foraging patterns, especially during the summer months (Dietz et al., 2020). Nonetheless, previous studies have suggested that killer whales may have highly variable summer distribution patterns (Leonard and Øien, 2019). Additionally, as they are strongly associated with prey dynamic resources, they are susceptible toward year to year variations (Nøttestad et al., 2015). This was evident when the Atlantic mackerel population increased between the years 2007-2014. During this period the killer whales were found feeding on mackerel even while herring was present (Nøttestad et al., 2015). A study using the citizen science approach, investigated movement and abundance of killer whales in Norway using opportunistic data collected through questionnaire surveys, found results consistent with those discussed here. It identified the presence of killer whales along the entire Norwegian coast, throughout the years of 1982-1987 (Christensen, 1988). Additionally, it found remarkably high concentrations of killer whales in Lofoten and Møre, which corresponds with herrings overwintering and main spawning ground, respectively (Slotte, 1999). Furthermore, seasonality in distribution was found in decreasing numbers in March, in Lofoten (1987), corresponding with herring being present at spawning grounds further south during this period (Christensen, 1988, Slotte, 1999). These findings coincide with findings in this thesis, of killer whales moving south in the months of February – March (season 2). The study additionally found killer whales to occur in the offshore banks and over the continental slope during summer months (Christensen, 1988). However, this is not reflected in the findings in this thesis, where predicted distribution in season 3 was in close proximity to the coastline (figure 24c). Reasons for predicted distribution

along the coast in season 3 may reflect other environmental variables contributing in the model, or the relative importance of herring as prey, during this season.

A novel study by Dietz et al. (2020) assessed the migration of 15 killer whales in northern Norway and found that the majority of killer whales follow the NSS herring after the winter aggregation in northern Norway down south to their spawning grounds. However, three of the individuals migrated north to the Barents Sea. The study suggested that all killer whales aggregate in the north of Norway to feed on the overwintering herring, but once it ends, the foraging and migratory behaviour may differ among different pods. Some pods may choose to follow the herring south; others may move to regions with other prey species; some may still remain in the area and feed on other available prey species. Factors like abundance of prey and suitability of the remaining prey may influence these choices. The presented probability map provides some indications on where the killer whales are present during the different seasons of herring migration, and can be used to further investigate movement patterns of killer whales. However, it is important to note that the findings here are results from an innovative study. Naturally this comes with a degree of associated uncertainty, and one should exercise caution when interpreting the result.

4.2.1 Environmental variables associated with killer whale distribution

Investigating which environmental parameters to use is very important when building a MaxEnt model, as it assumes that species distribution is not random, but influenced by specific environmental parameters (Esteban et al., 2014). 12 environmental parameters influencing killer whale distribution along the Norwegian coast were used in the model to illustrate the climatic environment of the study area (Table 1).

The MaxEnt model performed well in demonstrating complex interactions between environmental parameters that describe killer whale distribution. The variable contribution plots (Figure 22) found herring and distance to coast to be most influential parameters, in season 1 and 2. In season 3, distance to coast and sea surface temperature (SST) were the most influential variables. Additional important variables were salinity, sea bottom temperature (SBT) and chlorophyll a concentration, recurring in the three seasons. In season 1 and 2, herring was the most influential variable, with

52% and 60% of contribution, providing significant information to the model. Predicted presence was highest with greater densities of herring catch, in all three seasons (Figure 23a, b & c). This coincides with prey resources being the most direct driver for determining movement patterns for killer whales, and herring being its main prey (Similä et al., 1996). In season 1, the jackknife test found herring to have almost as high isolated training gain alone, as all environmental parameters together (Figure 21). This underlines that the distribution of killer whales seems to be highly dependent on their main prey species in these months, a fact which coincides with previous studies (Similä et al., 1996, Dietz et al., 2020). Herring is also the most important parameter in season 2, which corresponds to killer whales preying on herring assembled at spawning grounds (Christensen, 1988). The slightly lower contribution value in season 2 (52%) may indicate potential shifts in killer whale migratory and foraging behaviour towards becoming less dependent on herring exclusively, after feeding on the overwintering herring in season 1 (Dietz et al., 2020). Still, herring remains the most influential parameter for distribution in season 2. Another reason for the slightly lower contribution value in season 2 than in season 1, is that there is lower herring catch densities indicating lower herring abundance. This can explain the lower contribution value in season 2, compared to season 1. In season 3, herring was found to have lower valuable contribution than in the other two seasons, with only 12.3%. Consequently, this result may indicate a strong model performance, as it correlates with migration patterns of herring during their feeding period. Herring migrate out to the open waters of the Norwegian Sea, (Slotte, 1999) where they are not found in large aggregations, making it more challenging for killer whales to feed on them. However, another possible explanation for the lower contribution value could simply be reflected by the reduced densities of herring catch data, as it decreases for each season. Further, there is still a need for more research on environmental parameters as potential drivers for killer whale distribution in Norway.

Predicted distribution of killer whales, regarding distances to the coast, was found to be most similar in season 2 and 3. In these two seasons, the highest probability of presence was found around 500 meters, and 400 km from the coast. Although, relatively high probability of presence persisted between these distances. In season 3, the probability of presence was found to be slightly more towards distance of 400 km from the coast, than in season 2. For season 1, predicted distances for killer whale

presence were approximately 500 meters from the coast, where POP decreased with increasing distances to the coast. Distance from coast was the second most important variable in season 1 and 2, and the most important variable in season 3. A possible explanation for predicted presence in close proximity to the coast (500 meters), may be described by killer whales particularly being found in coastal areas of higher latitudes, potentially as a result of higher ocean productivity (Forney et al., 2006). Alternatively, high probability of presence predicted near the coast could be described by sampling biases in observational records (Figure 4 & 5). These biases include uneven efforts across the study area due to geographical biases. This bias was expected, given that the majority of observations collected from the general public were encounters made from, or in close proximity to, the coastline. Consequently, this bias can lead to model errors as presence-data is insufficiently spread throughout the study area. Another study on killer whale distribution in Australia, by Jones et al. (2019), found predicted distances to shelf breaks, to be at approximately 5000 meters. Reasons for the contrary findings are unknown, but could be described by very different environments or different datasets in the two studies.

While oceanographic parameters may not impact killer whale presence directly, it can affect killer whales indirectly by affecting its prey (Mayer and Piepenburg, 1996, Majewski et al., 2013). Sea surface temperature was an important parameter, recurring in all three seasons. The sea surface temperature that predicted highest probability of presence for killer whales was 10.37°C in season 1, 6.1°C in season 2 and between approximately 8.5 and 9.5°C in season 3. Higher temperature in the seasons 1 and 2 gave no probability of presence, while temperatures above 9.5 °C in season 3, gave lower probability of presence. Killer whales are known to be abundant in temperate to cold waters with high productivity, which can explain the preferred temperatures found in this study (Forney et al., 2006). Since biological seasons were added to the model to investigate the temporal distribution, sea surface temperature and chlorophyll *a* was used as an indicator for the amount of phytoplankton near water surface, indicating the availability of nutrients (Murphy et al., 2001, Sumner et al., 2003). Chlorophyll *a* is often used as an index to determine phytoplankton production, which, in turn, supports higher abundance of zooplankton, fish, seabirds and cetaceans (Moors-Murphy, 2014). Chlorophyll *a* was most important during season 2 (9.8% contribution), which covers the early spring months. In season 2, higher concentrations of chl-*a* affected

higher probability of killer whale presence. The importance of chl-*a* concentrations in season 2 corresponds to high chl-*a* levels associated with phytoplankton blooms in early spring months, providing validation to the model. This observation is consistent with previous studies (Bagøien et al., 2012, Broms and Melle, 2007). This finding highlights the role of phytoplankton at the base of the food chain, supporting nutrient and energy to the entire ecosystem, all the way up to apex predators like the killer whale. During the summer months (season 3), phytoplankton can become nutrient limited, as limited amounts of nutrients are being mixed up from the deep to the water surface (Wafar et al., 1983). However, chl-*a* had a degree of importance during the summer (season 3) with 3.3% contribution. During the winter months (season 1), chl-*a* had no significant impact on the model with 1.1% contribution. This finding may validate the model performance by accurately describing seasonal patterns for phytoplankton occurrence in temperate waters.

Sea bottom temperature and salinity were expected to indirectly impact killer whale distribution as factors conditioning the growth of fish species (Bœuf and Payan, 2001). Salinity is a crucial factor in marine ecosystems, impacting metabolic and physiologic processes in marine animals. Consequently, affecting the development, growth rate and metabolic costs of adult and juvenile fish (Bœuf and Payan, 2001). Additionally, sea bottom temperature and salinity affects prey abundance, through community composition and species distribution (Mayer and Piepenburg, 1996, Stransky and Svavarsson, 2010). Sea bottom temperature had lower variable contribution in the three models than expected. In season 1 and 3, a small contribution for POP were found, with respectively 4.9% and 7.1%. The response curves (Figure 23a & c) predicted higher POP for killer whales with lower sea bottom temperatures. This was especially seen in season 3, which describes the summer months of April to August. In season 2, the response curve (Figure 23b) unexpectedly predicted presence at higher sea bottom temperatures. However, sea bottom temperature contributed with little information to the model (0.8%) in season 2. This indicates low variable importance for sea bottom temperature, possibly as a result from the unexpectedly high bottom temperatures. Salinity was an influential variable recurring in all three seasons (Table 2). The results showed similar patterns in optimal salinity levels for predicted presence in all three seasons. Here, the POP increased to a threshold of $S_1 = 29-33$ PSU, $S_2 = 32$ PSU and $S_3 = 26-34$ PSU in the three seasons respectively,

followed by a steep decline. The salinity levels found to influence killer whale presence may offer valuable insight to how salinity effects killer whale distribution. Correspondingly, other studies have found salinity to be of high importance to cetacean distribution (Stalder et al., 2020, van Beest et al., 2018). A study by van Beest et al. (2018) suggests salinity to be a good indicator to find suitable feeding areas for harbour porpoises. This could in turn explain the high relative importance for salinity in the three models. However, there are still need for research to link salinity more directly to killer whale distribution.

Other relevant parameters, like depth, seafloor slope, rugosity and sea bottom substrate, contributed with relatively little information to the models. This was contrary to a study conducted in Australia finding depth to be the most influential environmental variable for killer whale presence (Jones et al., 2019). In this thesis, depth and rugosity had to be removed from the model due to collinearity problems. This decision was made after accounting for their variable contribution, which was found to be low from the jackknife test (Figure 21). Seabed substrate and seafloor slope were expected to impact prey abundance, but this was not reflected in the models, as both contributed with relatively little information. Seabed substrate and seafloor slope contributed the most to the models in season 3, where seabed substrate had a variable contribution of 3.1% and seafloor slope of 2.6%. Additionally, vessels had little contribution to the three models, illustrating that the models were unable to pick up possible altered foraging and diving behaviour triggered by physiological stress that vessels pose on killer whales (Lusseau et al., 2009). In Norway, recent studies have emphasised the importance of sound production for killer whales, when feeding on herring (Samarra and Miller, 2015). Noise pollution from sonars and other anthropogenic sources impact feeding and diving behaviour by source avoidance for killer whales, which can possibly lead to group separation and reduced foraging success (Samarra and Miller, 2016). These effects of noise pollution have been verified in the Pacific Ocean (Lusseau et al., 2009), but not yet assessed in the North Atlantic Ocean (Jourdain et al., 2019). This thesis was not able to verify the effects of noise pollution in the North Atlantic Ocean. Stratification, stratification roughness and ocean mixing were expected to indirectly impact the phytoplankton growth by supplying nutrients from the deep, while keeping phytoplankton in the photic zone. This, in turn, sustains higher abundance of marine species up the food chain. (Wafar et al., 1983, Bristow et al., 2017, Murphy,

1998). However, the three parameters exhibited low impact on the seasonal models, indicating higher importance from other environmental variables included in the model.

4.2.2 Limitations to the MaxEnt model

Environmental data obtained from Copernicus marine service and EMODnet did not include data for the entire study area. This first led to some limitations in the model, where observational points were lost from missing values in the environmental raster layer. This limitation was resolved by replacing missing values with the nearest non-missing value within the study area. This approach aimed to preserve data from as many observational points as possible. However, it could potentially introduce some biases to the model, as locations were regarded more similar than they actually are. Additionally, this contradicts the requirements for data points to be independent, emphasized by Renner and Warton (2013), which may lead to the misrepresentation of a location due to the inclusion of altered values for a specific data point. Several factors contribute to the extent of this limitation, including the size of the missing data location. This could lead to the misallocation of patterns in the data, potentially resulting in incorrect values that, in turn, can affect variable contribution. Nonetheless, this approach was considered the most optimal solution, as opposed to losing numerous of valuable observational points.

Another limitation in the model includes herring data being downloaded as catch data instead of obtaining herring population measures. This was used in the model, as no other available data for herring was found for the study area. Herring catch data were used as an indicator, in the model, for herring abundance. As a consequence, this could lead to an incorrect representation of the population size, potentially affecting the models' evaluation of herring's importance. Moreover, herring could create a bias in the models, as killer whale seasonality is based on herring migration. A consequence of this includes that herring as a variable predictor may exceed its actual importance in the model. Nonetheless, herring was considered important for distribution, as main prey for the North Atlantic killer whale population. Despite these weaknesses, it was therefore included in the model.

4.3 Future studies

The lack of research in the central and south coast of Norway became evident, by reviewing previous studies on killer whale distribution. This thesis highlights the need for future studies regarding killer whale's movement and abundance in Norwegian waters south of Lofoten. The MaxEnt model is a good tool to research environmental variables affecting killer whale distribution, and future studies should utilize this approach to investigate smaller areas along the Norwegian coast to gain further knowledge on distribution. This could then be compared with environmental variables found to be important in this study, to get a better understanding of local environmental contribution. Additionally, surveys conducted on extensive offshore areas could be a potential option to get a better understanding of spatial distribution, and to avoid biases towards the coast.

Furthermore, two separate models should be generated, excluding and including herring data, to investigate whether the herring can create bias on the models. Excluding herring as a parameter could potentially generate more information on other environmental variables influencing killer whale distribution in Norway. Additionally, more exact data on herring is needed since only catch data was available for the use in the model.

Finally, the study failed to include other specific prey species, then herring, related to killer whale distribution. This should be taken into consideration for future studies, to improve the MaxEnt model. A platform for downloading data on different prey resources, namely Global Biodiversity Information Facility (GBIF), was discovered too late during the modelling process. Therefore, future studies should include additional prey when investigating the distribution of killer whales.

5. Conclusion

First, the use of citizen science as a tool in complementing observational data made it possible to synthesize a unique dataset containing 4372 killer whale observations, of which 1716 came from citizen science initiatives. This dataset was collected from a variety of sources, covering many geographical regions in Norway over a span of 22 years. Findings from citizen science initiatives demonstrated a clear increase from 2014, highlighting its increased value as a tool in recent years. By using the collected observational data to fit a species distribution model using the MaxEnt method, it was possible to explore the distribution patterns of killer whales and examine environmental factors contributing to their distribution. The MaxEnt model used 3536 observations from the unique dataset and was able to successfully discriminate distribution patterns for killer whales in Norway with AUC levels > 0.9 (season 1 = 0.909, season 2 = 0.907, season 3 = 0.901). The model predicted killer whale presence along the entire coastline, with a clearly higher prediction rate near the coast. Further, the predicted presence of killer whales was found to coincide with herring migration in season 1 (Sept – Jan) and 2 (Feb – March), but not in season 3 (April – Aug), indicating higher reliance on other available prey species, during season 3, which describes herrings feeding period, when they are found in the open waters of the Norwegian Sea. Additionally, the model found herring to be the main contributing factor determining killer whale presence in season 1 and 2, and distance to coast to be the main contributing factor in season 3. This was followed by salinity and sea surface temperature in all three seasons. These findings provide insight into species distribution patterns for killer whales south of Lofoten. Additionally, the environmental factors found to influence killer whale presence could be useful for further investigating killer whale distribution south of Lofoten. However, more research is still needed to definitely conclude presence in the south and central regions.

Secondly, the questionnaire surveys in both Hardangerfjord and Sognefjord clearly indicated that the presence of killer whales in the fjords was a new phenomenon, that could possibly be explained from the killer whales' discovery of the harbour porpoise populations in the two fjords. This finding supports the theory of prey availability being the main driver behind killer whale distribution. However, further research is still

required to identify the exact cause of their altered distribution patterns, of frequently inhabiting the two fjords in the Vestland region.

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Appendix

Questionnaire survey distributed to the citizen in Hardangerfjord

1. Har du noen gang observert spekkhoggere i Hardangerfjorden?

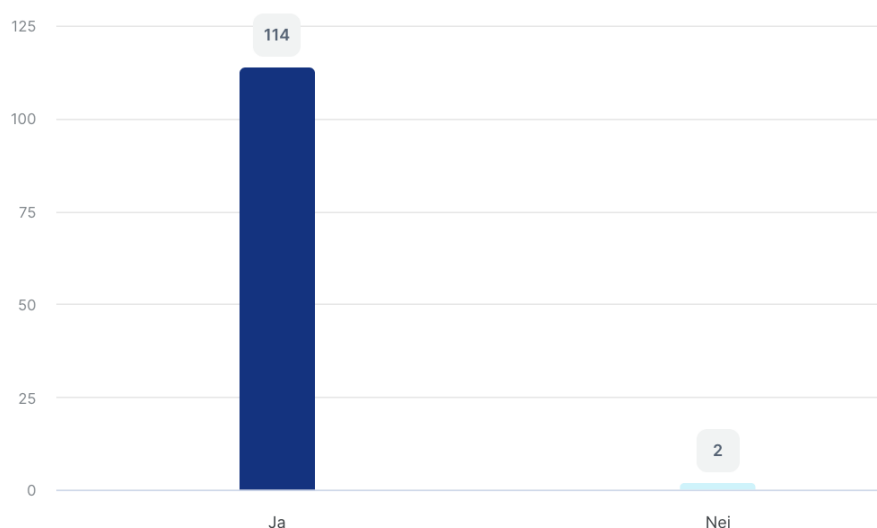


Figure A1: First question in survey on Killer whale presence in Hardangerfjord.

2. Hvis ja, hvilket år observerte du først spekkhoggere i Hardangerfjorden?

SVAR	ANTALL	ANDEL
2 021	16	13.8%
2 019	16	13.8%
2 020	13	11.2%
2 018	13	11.2%
2 022	12	10.3%
2 016	4	3.4%
2 017	3	2.6%
2 015	3	2.6%
Usikker	3	2.6%

Figure A2: Second question in survey on Killer whale presence in Hardangerfjord.

3. Hvis ja, hvilken tid på året observerte du spekkhoggeren/spekkhoggerne?

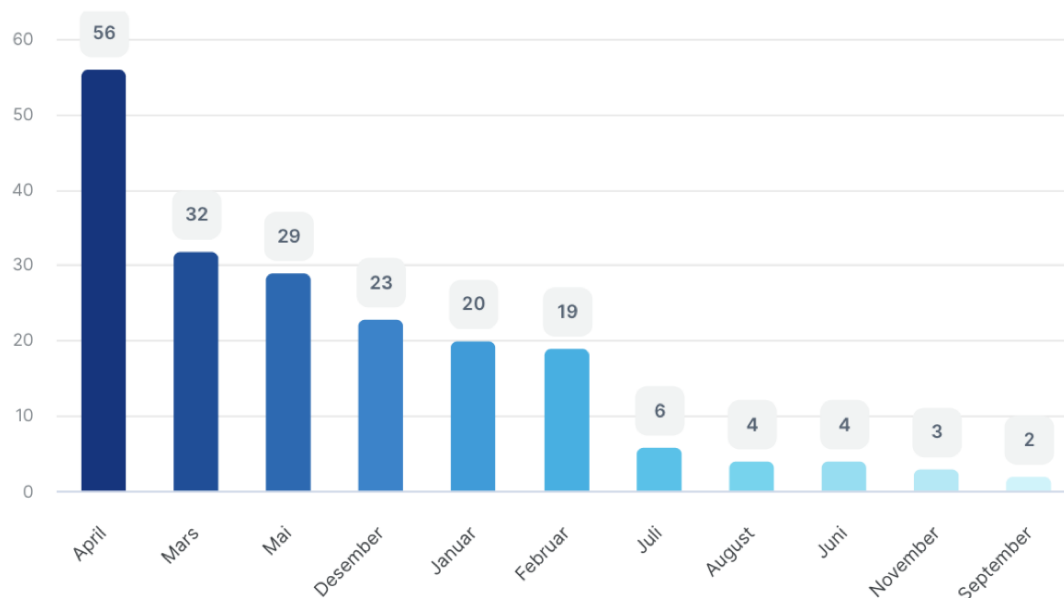


Figure A3: Third question in survey on Killer whale presence in Hardangerfjord.

4. Hvor mange ganger har du sett spekkhoggere i Hardangerfjorden?

SVAR	ANTALL	ANDEL
10+	24	20.7%
2	20	17.2%
5	16	13.8%
3	15	12.9%
1	15	12.9%
4	14	12.1%
6	7	6%
8	3	2.6%
7	2	1.7%

Figure A4: Fourth question in survey on Killer whale presence in Hardangerfjord.

5. Har du noen gang observert spekkhoggere angripe niser i Hardangerfjorden?

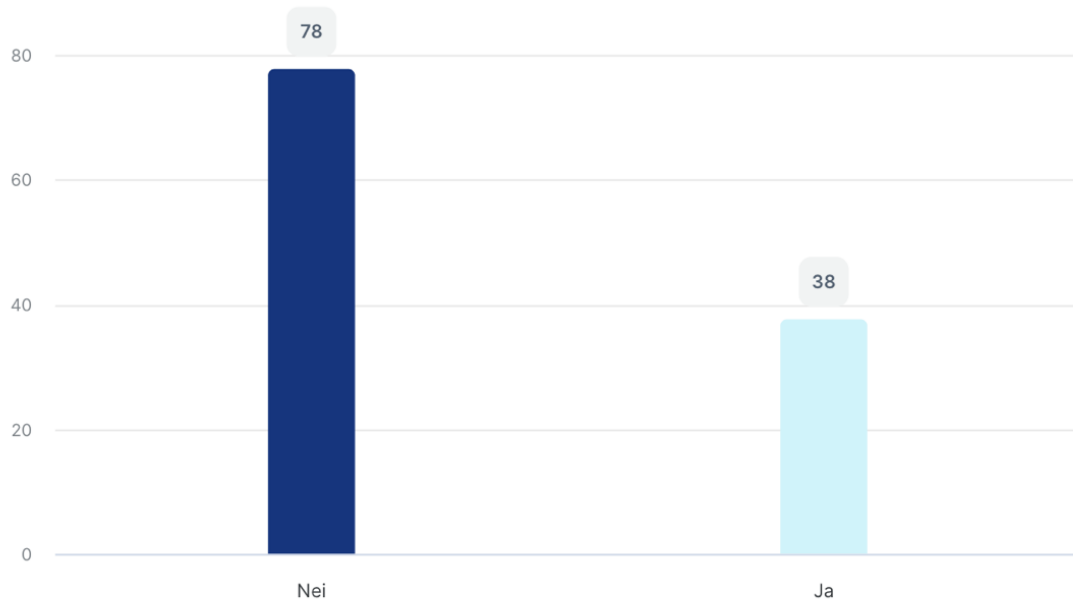


Figure A5: Fifth question in survey on Killer whale presence in Hardangerfjord.

6. Har du noen gang observert spekkhoggere angripe sel i Hardangerfjorden?

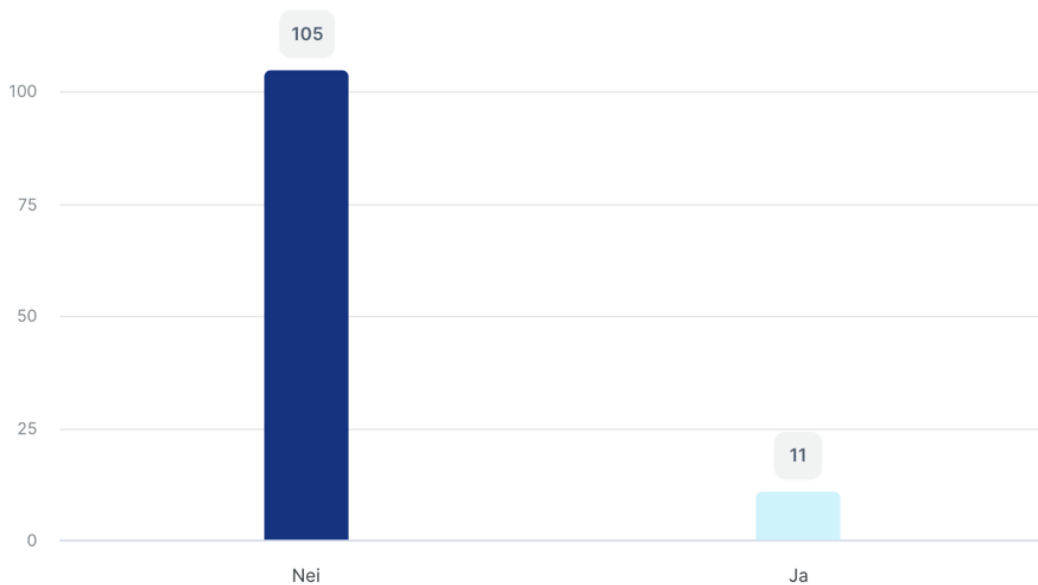


Figure A6: Sixth question in survey on Killer whale presence in Hardangerfjord.

Questionnaire survey distributed to the citizen in Sognefjord

1. Har du noen gang observert spekkhoggere i Sognefjorden?

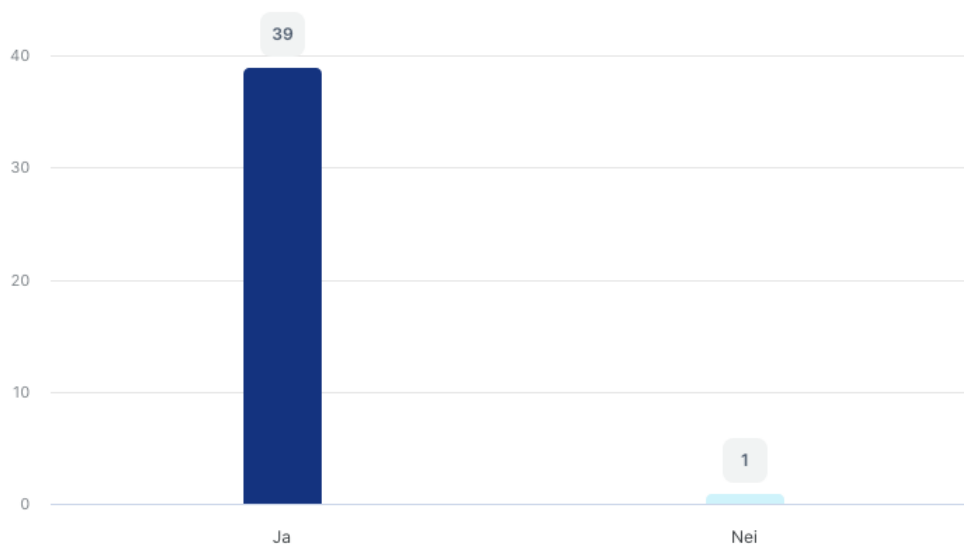


Figure A7: First question in survey on Killer whale presence in Sognefjord.

2. Hvis ja, hvilket år observerte du spekkhoggere i Sognefjorden?

SVAR	ANTALL	ANDEL
2 023	8	20%
2 022	4	10%
2 021	4	10%
2 017	3	7.5%
Siste 5 år. Fleire ganger i året 😊	2	5%
2022, 20023	1	2.5%
2022 og 2023	1	2.5%
2022, høst, var på tur til Bergen	1	2.5%
2021, 2022 og 2023	1	2.5%
.....

Figure A8: Second question in survey on Killer whale presence in Sognefjord.

3. Hvis ja, hvilken tid på året observerte du spekkhoggere?

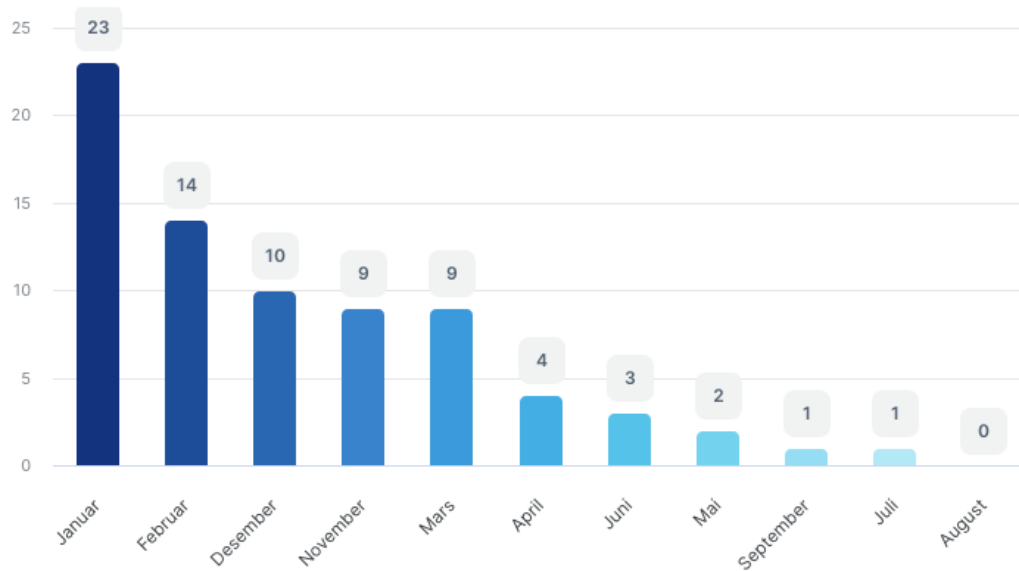


Figure A9: Third question in survey on Killer whale presence in Sognefjord.

4. Hvor mange ganger har du sett spekkhoggere i Sognefjorden?

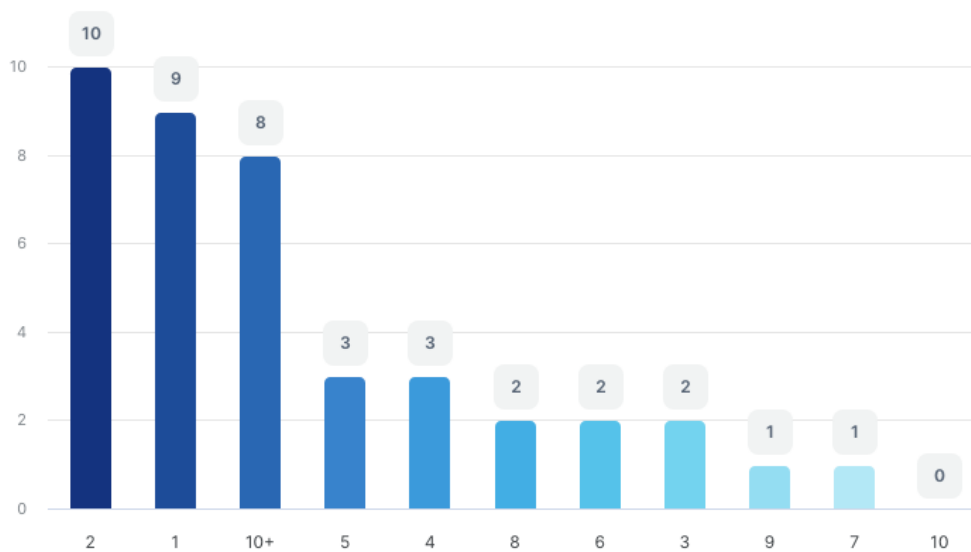


Figure A10: Fourth question in survey on Killer whale presence in Sognefjord.

5. Har du noen gang observert spekkhoggere angripe niser?

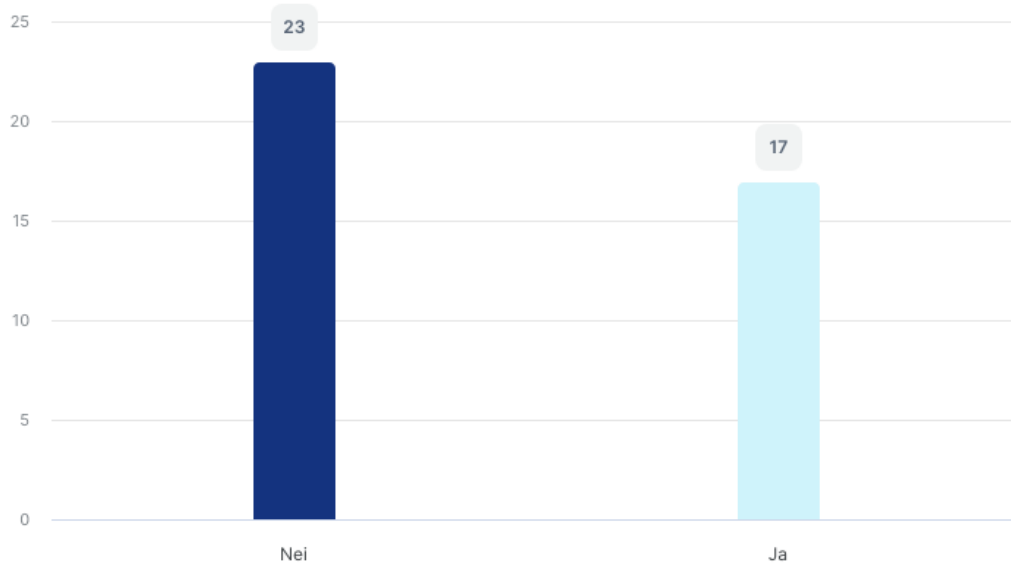


Figure A11: Fifth question in survey on Killer whale presence in Sognefjord.

6. Har du noen gang observert spekkhoggere angripe sel?

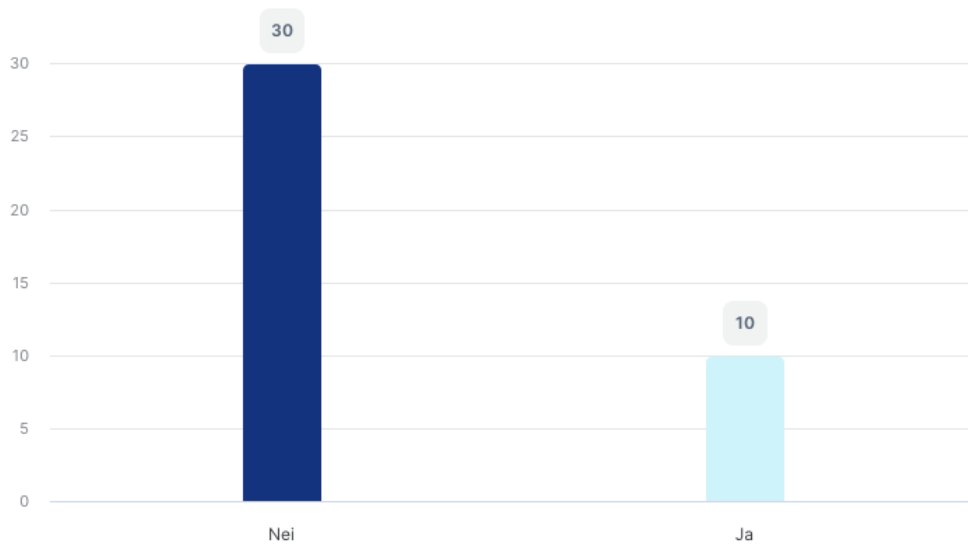


Figure A12: Sixth question in survey on Killer whale presence in Sognefjord.

Threshold map showing predicted presence for killer whale distribution at lowest suitable value

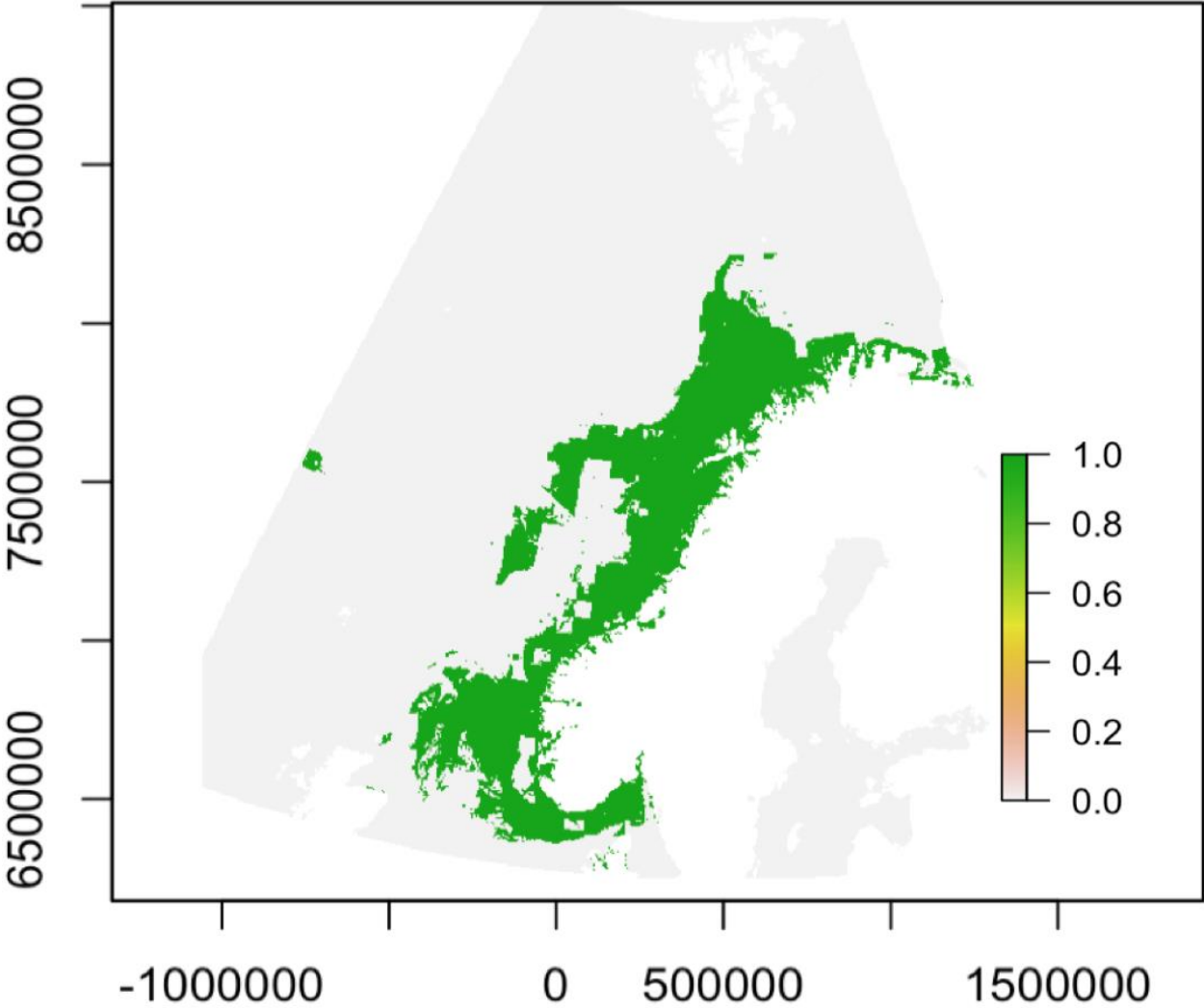


Figure A13a: Threshold map for season 1 showing predicted area of presence where killer whales can occur above the threshold of 0.39

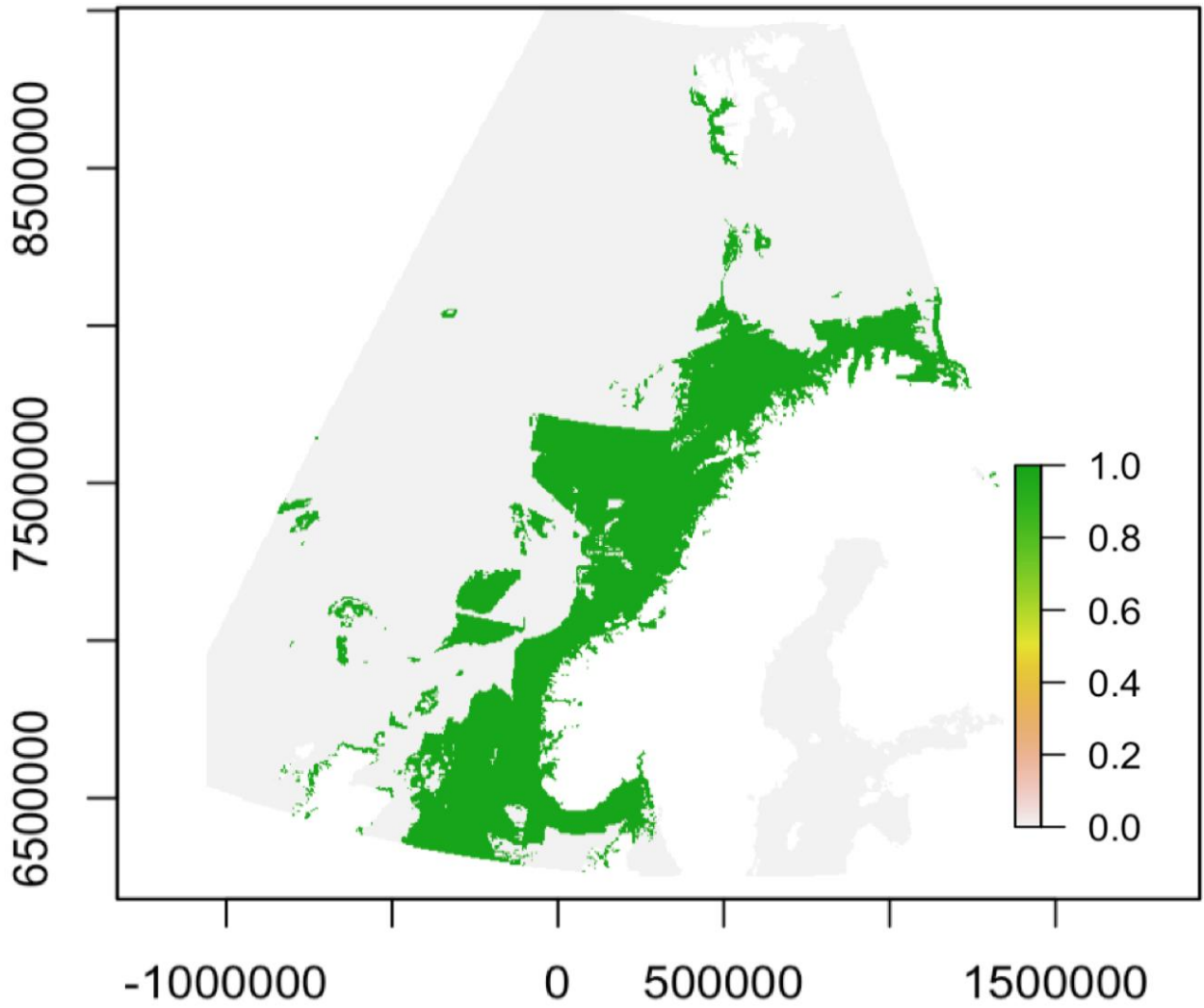


Figure A13b: Threshold map for season 2 showing predicted area of presence where killer whales can occur above the threshold of 0.33

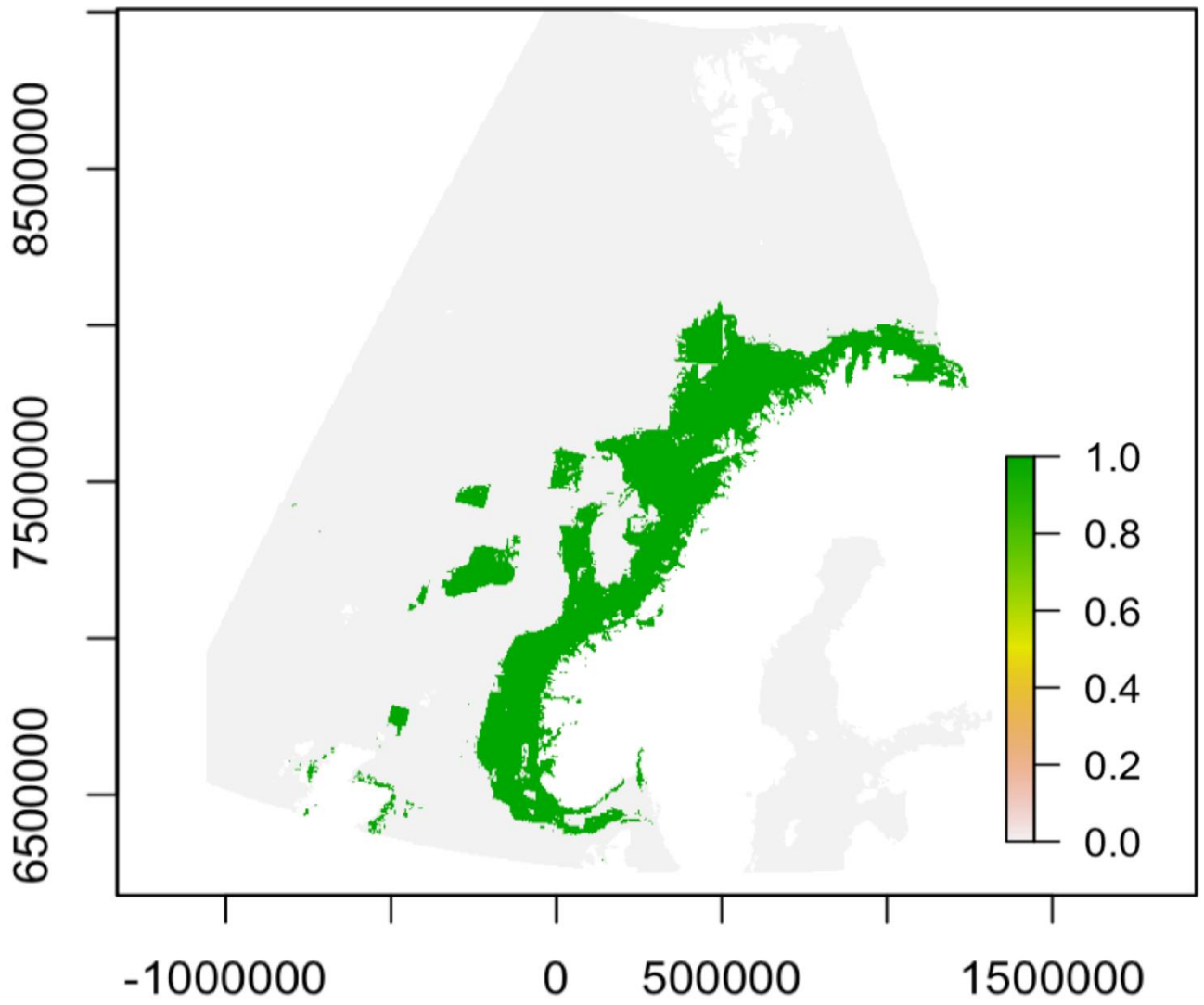


Figure A13c: Threshold map for season 3 showing predicted area of presence where killer whales can occur above the threshold of 0.39