

Killer whale (*Orcinus orca*) predation on harbour  
porpoise (*Phocoena phocoena*) in Hardangerfjord,  
Western Norway

Emma Høgh Åslein



Thesis submitted for the degree of  
Master of Science in Marine Biology and Limnology  
60 credits

Department of Bioscience  
Faculty of Mathematics and Natural Sciences

UNIVERSITY OF OSLO

May 2023

# Killer whale (*Orcinus orca*) predation on harbour porpoise (*Phocoena phocoena*) in Hardangerfjord, Western Norway



## Supervisors:

Eve Jourdain<sup>1</sup>

Øystein Ole Gahr Langangen<sup>2</sup>

André Moan<sup>3</sup>

Arne Bjørge<sup>3</sup>

<sup>1</sup>Norwegian Orca Survey

<sup>2</sup>Department of Biosciences, University of Oslo

<sup>3</sup>Department of Marine Mammals, Institute of Marine Research



© Emma Høgh Åslein

Killer whale (*Orcinus orca*) predation on harbour porpoise (*Phocoena phocoena*) in Hardangerfjord, Western Norway

Author: Emma Høgh Åslein

<http://www.duo.uio.no/>

Print: Reprosentralen, University of Oslo

# Abstract

The Hardangerfjord has a high density of harbour porpoises, making it stand out among Norwegian fjords as a particularly important habitat. A new predator-prey relationship emerged in 2017, with killer whales entering the fjord in an intermittent pattern and preying on the residing harbour porpoise population. Killer whales, as top predators, have the potential to significantly influence marine communities through their impact on the abundance, behavior, and distribution of their prey. It is important to understand the predator-prey dynamics in an area to maintain the ecological integrity of aquatic ecosystems.

This thesis aimed to investigate the population-level impact of killer whale predation on the harbour porpoise population in Hardangerfjord. The killer whale's predation rates were successfully estimated by integrating bioenergetics and predators' presence estimates, followed by an implementation of the predation rate into an individual-based model. Multiple scenarios with predation rates ranging from 0.12-0.28 had to be run in the model, to account for uncertainties in the parameters used. When the highest predation rate ( $p = 0.28$ ) occurred over a 20-year period, the killer whales reduced the harbour porpoise population by 90 %. In this scenario, the porpoise population would be classified as 'endangered' on the IUCN red list, and they would be at risk of going extinct.

This research has provided a deeper understanding of the predator-prey dynamics between killer whales and harbour porpoises, giving valuable insight into the conservation and management efforts in this region. The harbour porpoise is a species of conservation concern globally due to high bycatch levels. Thus, this investigation will establish baseline data for future research, which can help develop strategies to further protect the harbour porpoise species. Further understanding of the killer whales' and porpoises' distribution, diet, and movement patterns within Hardangerfjord, will be an important step towards ensuring their conservation.

# Acknowledgements

First and foremost, I want to thank my four supervisors that have guided me through the seemingly never-ending process of writing a master thesis. Arne Bjørge, you introduced me to the wonderful world of marine mammals, and I am grateful for the efforts you put in for making this thesis possible. I also want to thank you for introducing me to some great people across Scandinavian borders and making it possible for me to attend and present my thesis at multiple conferences. Next, I wish to thank Andre Moan for the countless hours he helped me with my coding, especially with understanding and altering the codes in NetLogo. I do not think I would've ever gotten through those endless NetLogo codes if it wasn't for his help. Thank you for all the time you put into proofreading my thesis, and for all the constructive feedback, you have truly been the best supervisor a student could wish for.

I also want to thank Øystein Langangen, for his contributions to the modeling aspects of my thesis, and for always keeping me on my toes and pushing me to continue with the hard work. Lastly, I want to thank my fourth supervisor, Eve Jourdain, who made it possible for me to write about my absolute favorite species, the killer whale. You have taught me so much about these amazing animals, and particularly what makes them unique in Norwegian regions. Most importantly, you have inspired me to follow my dreams, regardless of the obstacles I may face, and for that, I will be forever grateful.

Furthermore, I want to thank Olve Erdal, for providing me with great photographic evidence of the killer whale predation in Hardangerfjord, among them the cover photo. I also want to thank Nick Tregenza for helping me decipher the acoustic data on the CPODs, and at last Nabe-Nielsen for letting me use his harbour porpoise code and alter it for my study system. Moreover, thank you to the girls in my study room: Emma, Amanda, Lone, Celina, and Pernille, for making the writing of this thesis a fun process with a lot of laughter during the frustrating times.

Finally, I want to give a special thanks to my boyfriend, Jonas, for always encouraging and helping me with coding at times when I wanted to give up, and my twin sister, Maren, for listening to my frustration or excitement at bad and good times. They both deserve special thanks for being my ultimate cheerleaders during this process.

Emma Høgh Åslein

Oslo, May 2023

## TABLE OF CONTENTS

<b>1 INTRODUCTION</b> .....	- 1 -
<b>1.1. PREDATION AND PREDATORS</b> .....	- 1 -
<b>1.2. THE KILLER WHALE (<i>Orcinus orca</i>)</b> .....	- 2 -
<b>1.3. THE HARBOUR PORPOISE (<i>Phocoena phocoena</i>)</b> .....	- 4 -
<b>1.4. ACCOUSTICS AND RECORDINGS</b> .....	- 6 -
<b>1.5. INDIVIDUAL-BASED MODELS IN ECOLOGY</b> .....	- 7 -
<b>1.6 AIMS AND HYPOTHESIS</b> .....	- 8 -
<b>2 MATERIALS AND METHODS</b> .....	- 9 -
<b>2.1. THE STUDY AREA</b> .....	- 9 -
<b>2.2. ESTIMATING THE TEMPORAL PRESENCE OF KILLER WHALES</b> .....	- 9 -
2.2.1. Mark-recapture data.....	- 10 -
2.2.2. Acoustic monitoring.....	- 10 -
<b>2.3. ESTIMATING KILLER WHALE PREDATION RATE ON HARBOUR PORPOISE</b> .....	- 11 -
2.3.1. Killer whale’s energetic requirements.....	- 12 -
2.3.2. Energetic content of harbour porpoise.....	- 13 -
2.3.3. Estimating predation rate.....	- 13 -
<b>2.4. INDIVIDUAL-BASED MODEL TO STUDY THE EFFECT OF PREDATION</b> .....	- 15 -
2.4.1. Introduction.....	- 15 -
2.4.2. Model description.....	- 16 -
2.4.3. Calibration.....	- 19 -
2.4.4. Software used.....	- 20 -
<b>3 RESULTS</b> .....	- 21 -
<b>3.1. TEMPORAL PRESENCE OF KILLER WHALES</b> .....	- 21 -
3.1.1. Mark-recapture data.....	- 21 -
3.1.2. Killer whales’ identity.....	- 22 -
3.1.3. Acoustic monitoring.....	- 23 -
<b>3.2. THE KILLER WHALE’S PREDATION RATE</b> .....	- 24 -
<b>3.3. THE INDIVIDUAL-BASED MODEL</b> .....	- 25 -
3.3.1. Dynamics of the porpoise population.....	- 25 -
3.3.2 Effect of predation on the porpoise population.....	- 27 -
<b>4 DISCUSSION</b> .....	- 31 -
<b>4.1. TEMPORAL PRESENCE ESTIMATE OF KILLER WHALES</b> .....	- 31 -
Mark recapture data.....	- 31 -

Acoustic monitoring .....	- 32 -
Limitations .....	- 33 -
<b>4.2. THE KILLER WHALE’S PREDATION RATES .....</b>	<b>- 34 -</b>
Main findings .....	- 34 -
The driving force behind .....	- 36 -
Limitations .....	- 37 -
<b>4.3. THE POPULATION-LEVEL IMPACT OF KILLER WHALE PREDATION ON THE PORPOISE POPULATION IN HARDANGERFJORD .....</b>	<b>- 37 -</b>
Main findings .....	- 37 -
Suitability of method .....	- 39 -
Causes of death .....	- 40 -
Limitations .....	- 41 -
<b>4.4. FUTURE IMPROVEMENTS AND APPLICATIONS .....</b>	<b>- 43 -</b>
The killer whales’ temporal presence .....	- 43 -
The killer whales’ predation rates .....	- 44 -
The individual-based harbour porpoise model .....	- 44 -
<b>5 CONCLUSIONS .....</b>	<b>- 46 -</b>
<b>REFERENCES .....</b>	<b>- 48 -</b>
<b>APPENDIX .....</b>	<b>- 61 -</b>

# 1 INTRODUCTION

## 1.1. PREDATION AND PREDATORS

The ecosystems of the world's oceans consist of producers and consumers interacting in complex food webs (Denny, 2008). All trophic levels in the food web are linked through different mechanisms as organisms consume and predate on others for their resources (Power, 1992). Predation is a natural feeding behavior where an organism, *the predator*, uses energy to search for and locate another organism, *the prey*, which is then consumed for its energy (Curio, 2012, Stevens, 2012). At the top of the aquatic food web, you find the *top predators*. In most cases, they remain immune to predation and consist of large, toothed whales, sharks, and birds (Denny, 2008).

The predator-prey interaction affects life-history parameters such as survival, growth, behaviour, size, and distribution, along with biodiversity and community structure of a system (Brooks and Dodson, 1965, Carpenter et al., 1985). Predation can have a significant impact on prey populations through various mechanisms, such as direct – and indirect predation, trophic cascades, and evolutionary responses. The direct – and indirect effects can manifest at two ecological levels; individually, as the prey gets a sudden reduction in fitness, and at the community level, as predators can control the prey population dynamics (Williams et al., 2004, Stevens, 2012). Prey may experience reduced predation pressure and increase in numbers when predators are scarce. This relationship has the ecological terms of top-down control, often causing a trophic cascade where the predator effect can propagate downwards through the food webs. This can alter the biomass of adjacent and lower trophic levels, affecting the ecosystem structure (Baum and Worm, 2009).

However, the cascading effects following a predator's top-down control have rarely been demonstrated with compelling evidence in marine case studies (Williams et al., 2004, Baum and Worm, 2009). Multiple hypotheses explain the lack of empirical evidence for this pattern. First, it has been suggested that marine ecosystems are mainly structured by bottom-up processes, such as resource limitation, making top-down control truly rare (Cushing, 1975, Aebischer et al., 1990, Verity and Smetacek, 1996). Furthermore, the effect of top-down control might be reduced by high connectance among species, ontogenetic dietary shifts, and a prevalence of omnivory and complex food web interactions in marine systems (Jennings and Kaiser, 1998, Steele, 1998, Link, 2002, Casey et al., 2017). An alternative and simpler explanation is that top-down control does occur in marine systems, but it has not been studied



sufficiently (Baum and Worm, 2009). This can be explained by the methodological challenges connected to the direct experimental analysis, as predators often have large migration ranges, deep foraging depths, rapid movements, and sparseness (Davis et al., 1999, Williams et al., 2004). Thus, there are obvious challenges in collecting the data needed to demonstrate the top-down effects of such large, migratory predators. Baum and Worm (2009) presented evidence of top-down control in marine systems. However, they emphasized that it is not uniformly strong, and depends largely on the strength and nature of disturbances to predator abundance.

Even though predation has the potential to control prey dynamics and reduce prey population size, the consequences are not all negative. Terrestrial studies have shown that top predators can contribute to sustaining or increasing the biodiversity in an ecosystem (Schmitz, 2003, Ripple and Beschta, 2012, Letnic et al., 2012). A famous example of top-down control in marine systems, is the case of sea otters having a keystone role in Alaskan kelp forests by preying on urchins (Estes and Duggins, 1995). Moreover, the predisposition of predators to target substandard individuals, such as the young, sick, or old in a population, contributes to an important selective force in evolution. This mechanism can keep the prey population strong and healthy (Dawkins and Krebs, 1979, Darwin, 2004, Genovart et al., 2010). The substandard individuals are easier targets to predators as they tend to be slower, weaker, and less capable of escaping predators compared to healthy adults (Errington, 1946, Jefferson et al., 1991, Curio, 2012).

## 1.2. THE KILLER WHALE (*Orcinus orca*)

Killer whales (*Orcinus orca*) are carnivorous top predators with patchy distributions ranging across all temperatures and depths of the Earth's oceans (Forney et al., 2006). Nonetheless, the highest abundance has been recorded along cold, temperate and polar coastal waters (Forney et al., 2006). Killer whales have been known to hunt and consume a wide variety of prey, ranging from fish, birds and cephalopods (squid), to marine mammals like pinnipeds (seals) and cetaceans (whales) (Ford, 2009). Notwithstanding such a broad diet, some local populations adapt feeding strategies based on prey type and availability (Nichol and Shackleton, 1996, Ford et al., 1998, de Bruyn et al., 2013, Jourdain et al., 2020). The killer whales tend to structure in stable, social groups that hunt cooperatively (Brault and Caswell, 1993). A general killer whale group consists of a mature female as the leader, a varied number of male and post-reproductive females, and the offspring of the females in the group (Brault and Caswell, 1993). Males and females can reach a maximum age of 50-60 and 80-90 years, respectively (Olesiuk et al., 1990).

Killer whales in North Pacific have been divided into distinct ecotypes based on behaviour, habitat - and feeding preferences. These ecotypes typically differ in acoustic behaviour, morphological – and genetic traits, social organization, and diet (Dalheim et al., 2008, Foote et al., 2009, de Bruyn et al., 2013). Three ecotypes have been described for the North Pacific Killer whales; the ‘resident’ nearshore piscivore (fish-eater), the ‘transient’ marine mammal eaters, and the ‘offshore’ type, which is believed to be piscivorous also feeding on higher trophic level fish prey (e.g. sharks) (Ford et al., 1998, Herman et al., 2005, Dalheim et al., 2008). The transient killer whales prey on threatened marine mammal populations like harbour seal (*Phoca vitulina*), stellar sea lion (*Eumetopias jubatus*), sea otter (*Enhydra lutris*), and northern fur seal (*Callorhinus ursinus*) in the North Pacific (Estes et al., 1998, Springer et al., 2003).

In Norwegian waters, killer whales are found along the entire coastline with peaks in abundance off the coast of Lofoten and Møre (Similä et al., 1996). Their abundance has been estimated to 15 056 individuals (CV=0.29, 95% CI: 8,423-26,914) (Leonard and Øien, 2020). The killer whales populating the Norwegian coast have been known to mainly predate on the overwintering spring-spawning herring (*Clupea harengus*) (Similä et al., 1996, Jourdain, 2020). In recent years, observational studies found evidence of the Norwegian killer whales’ also preying on marine mammals such as harbour porpoise (*Phocoena phocoena*) (Cosentino, 2015), harbour seal (*Phoca vitulina*) and grey seal (*Halichoerus grypus*) (Vongraven and Bisther, 2014, Jourdain et al., 2017). The Norwegian killer whales preying on seals have a mean group size of five individuals (Similä et al., 1996, Jourdain et al., 2017).

Foote et al. (2009) have described two morphologically distinct ecotypes of North Atlantic killer whales. Type 1; a generalist believed to be feeding mainly on fish and potentially seals. Type 2; a larger specialist believed to be feeding solely on other cetaceans. This was further investigated in a dietary variation study on 38 killer whales in Northern Norway (Jourdain et al., 2020). Three differentiated clusters based on diet were described: Cluster 1 individuals were seal-eaters, whilst Cluster 2 and 3 individuals seasonally specialized on herring and lumpfish, respectively. The elevated nitrogen ( $\delta^{15}\text{N}$ ) values in seal-eaters indicated a prey specialization on higher trophic levels throughout the year. However, these were lower than expected for killer whales solely preying on seals, suggesting that predation occurred on other marine mammals and fish as well. Thus, the study supported other studies suggesting that killer whales populating the Norwegian coast have a multi-prey feeding type where they may switch between prey types in response to seasonal changes in availability (Vester and Hammerschmidt, 2013, Nøttestad et al., 2014, Jourdain et al., 2017, Jourdain, 2020, Jourdain et al., 2020).

The killer whales' ecological role as top predators in Norwegian marine ecosystems has not been investigated to date. But as long-term datasets on individuals' counts, movement and feeding preferences becomes available (Norwegian Orca Survey, unpublished data), there are emerging opportunities to investigate this. Two killer whale groups have been observed in the inner Western fjords of Norway, among them Hardangerfjord, where they reside for variable periods each year (Jourdain et al., 2022, Norwegian Orca Survey, 2021). When in Hardangerfjord, these killer whales have been observed feeding on harbour porpoise (Jourdain, pers. comm). The killer whales' presence in the Vestland region has been monitored through citizen science as initiated by Norwegian Orca Survey in 2017. The photographic records of their whereabouts (i.e., which whales seen when and where) are part of the ongoing long-term photo identification project of killer whales in Norway (Jourdain et al., 2021).

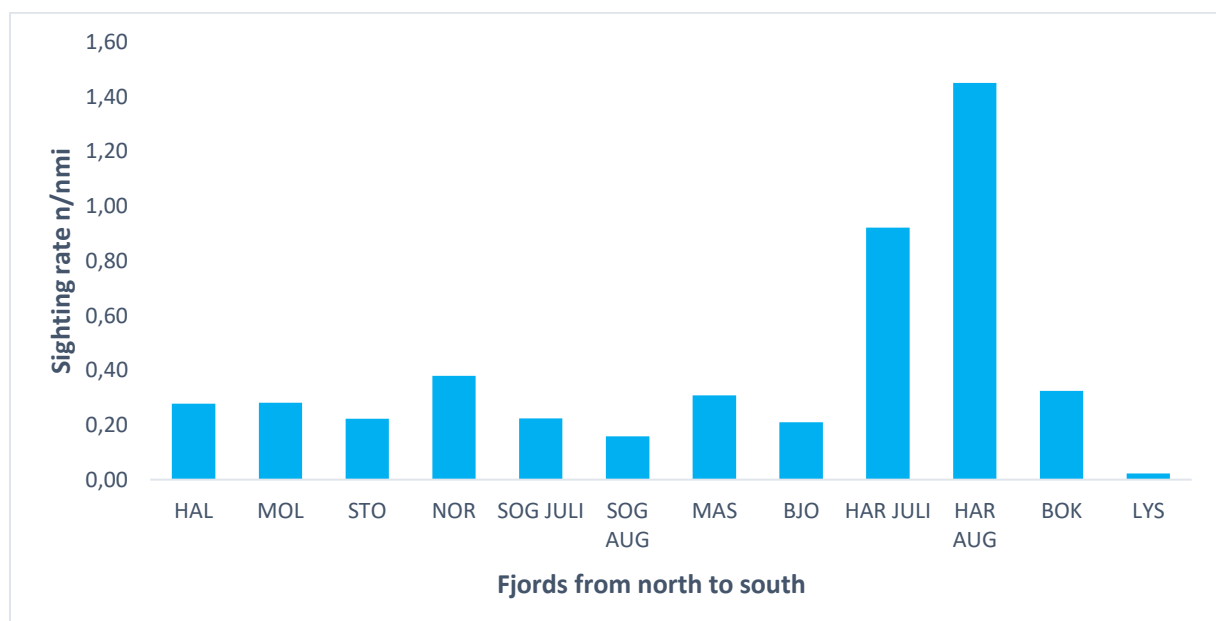
### 1.3. THE HARBOUR PORPOISE (*Phocoena phocoena*)

Harbour porpoises are small cetaceans populating coastal - and continental shelf waters of the northern hemisphere. They are among the most widespread porpoise species, and a minimum of 700 000 individuals are estimated globally (Carwardine, 2019). As opportunistic piscivore predators, the harbour porpoises feed on a wide variety of fish based on availability, region, and specific season (Aarefjord et al., 1996, Bjørge, 2003, Carwardine, 2019). Their pelagic prey consists of small schooling fish like sprat, mackerel, and herring, whilst the benthic prey consists of demersal fish and crustaceans (Santos and Pierce, 2003, IAMMWG and Siemensma, 2015, Carwardine, 2019). They typically live as solitary individuals or may travel in loose groups of three individuals or less (Bjørge et al., 1991, Hammond et al., 2002).

They can be affected by numerous intrinsic (e.g. density dependence) and extrinsic (e.g. predation, competition, anthropogenic disturbances) mechanisms, which can impact their population dynamics by altering population structure and vital rates (Juliano, 2007, Koons et al., 2016). Fishery remains the biggest threat against cetaceans today (Read et al., 2006, Young and Ludicello, 2007). Fishing and unintentional catches in fishing gear, termed bycatch, selectively removes piscine predators and key prey species (Beauchamp et al., 2007). Therefore, it can severely threaten the populations that get bycaught, by reducing their numbers. The shared fish resource between porpoises and commercial fishing vessels can cause an overlap between fisheries and harbour porpoises, and the porpoises in Norwegian waters are particularly vulnerable to bycatch in gillnet fisheries (Roche et al., 2007, Goetz et al., 2015, Moan et al., 2020).

The harbour porpoises populating the Norwegian waters belong to the North Atlantic sub-species *P. p. phocoena*. This is one of five sub-species characterized and distinguished by their morphological and genetic differences (Fontaine et al., 2007, Carwardine, 2019, Quintela et al., 2020). The average lifespan for porpoises in North Atlantic waters is estimated to lie between 8-12 years (IMR and NAMMCO, 2019). Previous studies have indicated that approximately 7.5 % survive the age of 12, and a maximum life expectancy of 24 years has been recorded (Lockyer, 1996, Learmonth et al., 2014). The harbour porpoise is a typical ‘fast living’ marine mammal relative to other cetaceans, with life history traits like early maturation, higher reproduction rates, and shorter lactation periods (Kanwisher, 1965, Read, 1990, Read and Hohn, 1995).

Estimations of harbour porpoise abundance in Norwegian fjords have been limited due to their elusive behaviour and the logistical difficulties when studying marine environments (IMR and NAMMCO, 2019). However, the Norwegian line-transect cetacean abundance surveys from June 2020 indicated a high abundance of harbour porpoise in Hardangerfjord compared to other Norwegian fjords (Fig. 1) (Bjørge et al., 2019). More specifically, the population size was estimate to 1 339 individuals with a 95 % CI ranging between 992-1808 (Institute of Marine Research, unpublished data). A predator-prey dynamic emerged in the fjord in 2017, when killer whales were first observed predated on the residing porpoise population (Jourdain, pers. comm).



**Figure 1:** Sighting rates (sightings/n. mile) of harbour porpoises in some Western Norway fjords made from ship-borne surveys in 2018. HAR is Hardangerfjord (Bjørge et al., 2019).

#### 1.4. ACCOUSTICS AND RECORDINGS

In general, odontocetes (toothed whales) can produce two types of sounds: clicks and tonal sounds like whistles and calls (Au, 1993, Simon et al., 2007b). Clicks are used in echolocation: a process where an organism sends out high-frequency sounds in search of prey, navigation, communication, or in avoidance of predators (Carwardine, 2019). The harbour porpoises use echolocation but can be distinguished from other odontocetes by their lack of tonal sounds (Møhl and Andersen, 1973, Verfuß et al., 2009, Miller and Wahlberg, 2013). Instead, they only emit echolocation clicks with specific narrow-band high frequencies, and listen for echoes projected from prey (Miller and Wahlberg, 2013). The click sounds have a wavelength of 12 mm and a frequency ranging between 100-160 kHz, mainly centred around 130 kHz (Miller and Wahlberg, 2013, Cosentino et al., 2019).

The killer whales have complex vocalisations with group-specific dialects (Ford, 1989, Ford, 1991). Studies have shown that killer whales use a broader band of frequencies when echolocating, ranging between 20 – 120 kHz dependent on location and prey type (Barrett-Lennard et al., 1996, Au et al., 2004, Simon et al., 2007a, Wellard et al., 2015). The tonal sounds of killer whales consist of whistling and pulsed calls (Filatova et al., 2007). Whistles are vocal signals that occur in social settings and short-range communication (Ford, 1989), with a dominant frequency range between 2 – 18 kHz (Thomsen et al., 2001, Thomsen et al., 2002, Riesch et al., 2006).

Killer whales have evolved specific vocal behavioural strategies in response to their prey's evasive behaviour and hearing ability (Baird et al., 1992, Deecke et al., 2002). Marine-mammal eaters are typically less vocal than the piscivores, and they remain silent except from sporadic trains of echolocation clicks (Barrett-Lennard et al., 1996, Deecke et al., 2005, Deecke et al., 2011). Likewise, current literature indicates that Norwegian killer whales remain silent while foraging on mammals (Jourdain et al., 2017). Hypothetically, this could be to prevent mammal-prey from detecting the vocal calls and responding with avoidance behaviour. Killer whales prey species, such as harbour porpoises and harbour seals, have a good underwater hearing at the killer whale frequencies, and can easily respond with evasive behaviour during the predator's vocal communication (Deecke et al., 2002).

The Chelonia CPOD is an acoustic recorder that can monitor the activity and presence of odontocetes. It captures probable cetacean clicks by recording the duration (10 ms resolution), intensity, bandwidth, centre frequency, and frequency trend of clicks. The recordings are taken

with an omni-directional hydrophone with a detection range of 20-160 kHz, which is optimal for recording porpoise clicks (Chleonia Limited, 2016). Although it is theoretically possible for odontocetes producing clicks between 20-160 kHz to be captured on the CPODs, it is not yet known whether they are good devices to monitor killer whale acoustic.

## 1.5. INDIVIDUAL-BASED MODELS IN ECOLOGY

Individual-Based Models (IBM), are widely used to study how environmental factors like resource availability, pollution, disturbance, and predation may impact populations (Hall et al., 2006, Boyles and Brack, 2009, Weise et al., 2010, Grimm and Railsback, 2013, Schmitt et al., 2016). IBMs are distinguished from other ecological models by their ability to model a spatially, explicit area based on a collection of unique individuals and their behaviour (Grimm and Railsback, 2013, Nabe-Nielsen et al., 2018). The individual's behavior and interaction with the study area and each other, give rise to emergent patterns in the population (e.g. age structure and spatial distribution) that can be compared to real-life systems (Grimm et al., 2005). Moreover, it enables the detailed capture of an individual's traits (e.g. age, energy use, position), and the possibility for individuals to adapt and learn from their environment (Jørgensen and Fath, 2011).

When the mechanisms that create the pattern of interest are included in ecological models, the predictions they generate tend to be more realistic than other ecological models (Grimm and Railsback, 2012). The movement of mobile animals is a fundamental element of their behaviour, hence an important concept when using IBMs. Understanding the drivers of individual movement is a key concept in population ecology, and a prerequisite when developing movement-based models with the aim of conserving and managing threatened species (Nathan et al., 2008). IBM simulations can be used to explore possible population trajectories under several scenarios, such as predation. Prior data are needed to determine and set up the initial state of the population. This consists of key variables such as age, age at maturity, movement characteristics, energy level, and pregnancy – and lactating status.

Despite the many advantageous sides of IBM, they have been subject to critique. Since they are based on the behaviour of individual agents and their interaction with the environment, they face challenges related to maintaining detail and accuracy in the parameterizing and validation. This also gives the model a high level of complexity, which requires sufficient coding skills and computing power.

## 1.6 AIMS AND HYPOTHESIS

The overall aim of this thesis was to investigate the population-level impact of killer whale predation on the harbour porpoise population in Hardangerfjord. The analysis was conducted using a multi-step approach.

Firstly, the killer whale's presence in Hardangerfjord must be quantified, i.e., residence time, number of individuals using the fjord, and specific group composition. The following hypotheses were made:

- 1 Mark-recapture data from NOS, collected with use of citizen science, and acoustic recordings could be used to quantify killer whale presence in Hardangerfjord.
- 2 The occurrence of killer whales in Hardangerfjord is a relatively new phenomenon.

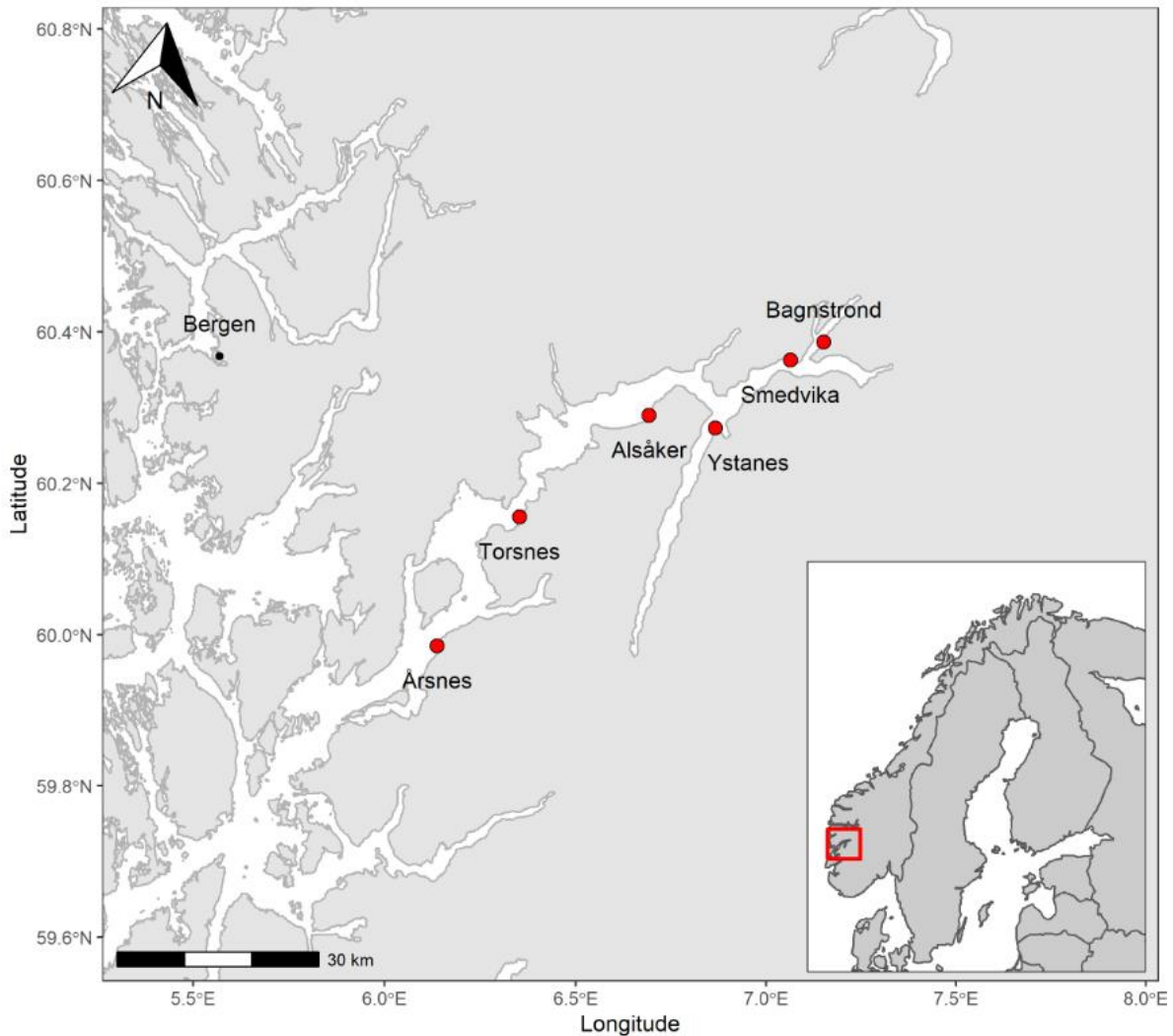
Secondly, the expected predation rates for the total killer whale population must be estimated by combining estimates of harbour porpoise energy content, energy requirements per killer whale, and the killer whale's age – and group structure. Lastly, the killer whale's predation rates must be implemented in an individual-based model for the porpoise population in Hardangerfjord. The following hypothesis was made:

- 3 Killer whale predation will reduce the porpoise population in Hardangerfjord to an extent that puts the population at risk of going extinct.

## 2 MATERIALS AND METHODS

### 2.1. THE STUDY AREA

Hardangerfjord is located in Vestland County and is the second largest fjord in Norway, stretching 179 km inland (Thorsnæs, 2021). The fjord ranges from 1-10 km in width with many branching side fjords, and has a maximum depth of 860 meters (Fig. 2) (Thorsnæs, 2021).



**Figure 2:** Map of the study area located along the coast in Western Norway: Hardangerfjord. The red dots represent five acoustic devices (CPODs) deployed in Hardangerfjord from September 2020 to October 2021.

### 2.2. ESTIMATING THE TEMPORAL PRESENCE OF KILLER WHALES

A combination of mark-recapture and acoustic data was used to quantify killer whale presence in Hardangerfjord. Microsoft Excel and R (Version 4.1.2) were used to analyze and graph the mark-recapture – and CPOD data. The two next sections will explain these in turn.



### 2.2.1. Mark-recapture data

Killer whale photographs, along with metadata on date and location, have been collected from the public in Hardangerfjord since 2017. For each encounter (defined as a sighting of a group of killer whales at a given time and location), the best photograph for each killer whale was selected and individuals were identified using the method proposed by Bigg (1982), i.e. using natural markings on the dorsal fin and adjacent grey saddle patch and other persistent markings. Each individual received a unique numeric ID code and was added to an existing catalogue of killer whales in Norway (Jourdain and Karoliussen, 2021). For each new observation, individuals received a new record in a database of sighting histories of killer whales in Norway (Norwegian Orca Survey, unpublished data).

Citizen science observational data i.e., photographs and reports from local photographers and wildlife enthusiasts were obtained from NOS, which established an online platform for this purpose in 2017 (Norwegian Orca Survey, 2021). Additional data were obtained by requesting info/photographs from people who had reported killer whale observations on social media (e.g., Facebook, Instagram, YouTube). To avoid false positives, only killer whale reports with associated photographs were included in the analysis.

The mark-recapture and photo identification data were also used to identify the killer whales' group – and age structure. The group structure was determined based on observed patterns of association, specifically identifying which individuals were consistently observed together during their presence in the fjord. The whales were aged by investigating their body – and fin size (Olesiuk et al., 1990), the appearance of saddle patches, the presence of fetal folds, and age of maturity.

### 2.2.2. Acoustic monitoring

#### *Data recordings*

To investigate whether the killer whale photo identification data could be supported by acoustic data, recordings collected with CPODs were explored. Five CPODs were deployed five meters below the surface at approximately 25 meters depth in Hardangerfjord, in the period September 2020 to October 2021 (Fig. 2). Data were downloaded and batteries changed about every 7-14 weeks, giving five data collection periods (Table 1). The CPODs successfully recorded data over a one-year period. Period 5 has two different retrieval dates as the CPOD in Årsnes were retrieved later due to lack of detection on the first date.

**Table 1.** The five data collection periods from the five CPODS over a total of 374 days.

<b>Data collection</b>	<b>Date (days)</b>
<b>Period 1</b>	27.09.2020–03.12.2020 (67 days)
<b>Period 2</b>	03.12.2020–04.03.2021 (91 days)
<b>Period 3</b>	04.03.2021–10.06.2021 (91 days)
<b>Period 4</b>	10.06.2021–26.08.2021 (77 days)
<b>Period 5</b>	26.08.2021–06.10.2021/28.10.2021 (41/63 days)

#### *Analysis of CPOD data*

The data were analysed using proprietary software designed just for this purpose (CPOD.exe). This software classifies the sounds recorded into one of four categories: ‘NBHF’ (Narrow Band High Frequency, e.g., harbour porpoise), ‘other cetacean’ (toothed whales), ‘sonar’ (click with regular patterns coming from vessels), ‘unclassified’ (train identified but the source is unknown, e.g., sediment transport, crustaceans). The porpoise’s echolocation clicks fall within the ‘NBHF’ category, as they consist of narrow-band-high-frequency sounds between 120-160 kHz. The classifier has been proven to have good detection rates for porpoises, but its ability to log clicks from 20-160 kHz enables it to detect all cetaceans except the sperm whale (*Physeter macrocephalus*) (Chleonia Limited, 2016). This allows the program to distinguish porpoises and other narrow-band high frequency species from broadband species like killer whales.

CPOD recordings from the 5 stations were scanned for killer whale acoustic signals to generate complementary data on killer whale presence. Two approaches were used: first, the sound files were analyzed to identify echolocation click-trains potentially belonging to killer whales, which would fall under the ‘other cetacean’ category. If no significant findings were made with the first approach, a novel approach was applied. This consisted of identifying the killer whale’s lower frequency vocal sounds not recognized by the classifier, like their communicational whistles. To do this, a filter of maximum 30 kHz was applied to acoustic trains of high and moderate quality. Further, the number of clicks in the data were exported and plotted over time.

### **2.3. ESTIMATING KILLER WHALE PREDATION RATE ON HARBOUR PORPOISE**

The number of porpoises taken by killer whales annually was estimated using the estimates of killer whale residence time and group composition, their energetic requirements and the energy content of an individual porpoise taken from scientific literature. The estimated number of porpoises killed was divided by the harbour porpoise population size in Hardangerfjord to

obtain the killer whale’s annual predation rates. The three next sections will elaborate on these estimations.

### 2.3.1. Killer whale’s energetic requirements

Daily prey energy requirements (DPERs) for adult males and females, juveniles, and immature killer whale individuals in the eastern Pacific Ocean were estimated in a study conducted by Noren (2011) (Table 2). These values closely resembled previously reported energetic requirements for killer whales in other locations (Kriete, 1994, Baird and Dill, 1996, Williams et al., 2004, Lefort et al., 2020, Matika et al., 2022). Matika et al. (2022) studied herring-feeding killer whales in northern Norway and estimated an average DPER of 227 859 calories for adult, male killer whales. Since this estimate only included adult males, and closely resembled the one presented by Noren (2001), the DPER values estimated by Noren (2011) were used in this study. They were combined with the killer whale age structure data, to estimate the age-specific energetic requirements for the killer whales’ occurring in Hardangerfjord. This was necessary because the DPERs for individual killer whales depend largely on their age and gender, increasing from juveniles to adult males (Noren, 2011).

The DPERs were calculated from the field metabolic rate (FMR), which accounts for the metabolic costs tied to an individual’s activity and physiological processes. Individual FMRs were estimated from the body mass of the different killer whale ages and sex classes, where it was assumed that the daily metabolism ranges from five to six times Kleibers predicted basal metabolic rates (Kleiber, 1975). The DPER ranges cover all potential killer whale individuals in a population, except for calves less than one-year-old (Table 2). The calves depend largely on nourishment from their mother’s milk up to one year of age, even though they have been observed nursing up to the age of three (Noren and Edwards, 2007). In the present study, for simplicity, the two- and three-year-old calves were assumed to have a diet based on 100 % prey consumption. A digestive efficiency of 84.7 % was assumed when estimating the DPER range, which is in line with the scientific literature (Williams et al., 2004, Noren, 2011).

**Table 2.** *The DPER range of individual killer whales. The range values were calculated from the body mass of killer whales with specific ages and gender.*

<b>Age and sex class</b>	<b>DPER range (calories/d)</b>	<b>Average DPER (calories/d)</b>
Immature (1-6)	41 376 – 130 246	85 811
Juvenile (7-12)	118 019 – 174 380	146 200
Adult female >12	149 972 – 217 775	183 874
Adult male >12	155 885 - 269 458	212 672

### 2.3.2. Energetic content of harbour porpoise

The exact energy content of a harbour porpoise remains unknown. It is assumed in the present study that the energy content of the harbour porpoise closely resembles similar marine species. In general, when calculating the total energy content of a marine mammal, solely blubber, muscle, and viscera are included, as the rest consists of bones and the cranium, which is indigestible (Table 3). The porpoises can be roughly divided into three age and gender classes: 60 kg for males, 75 kg for females, and 5 kg for calves of either sex (Lockyer, 2003, Bjørge and Tolley, 2009). A weighted average of 43.75 kg was utilized when estimating the harbour porpoise energy content (Table 3). This value was based on the weights for the three different age classes and the age distribution data from Lockyer and Kinze (2003) 0-1 year: 38 %, 2-24 years (females): 31 % and 2-24 (males): 31 % of the population.

**Table 3.** Rounded average values based on different cetacean and pinniped species to estimate the total energy content (kcal) of an average harbour porpoise (43.75 kg).

Tissue	% of body mass	Kcal. /100g	Kcal. per kg porpoise	Kcal. per porpoise
<b>Blubber</b>	30	810	2430	145 800
<b>Muscle</b>	23	110	253	15 180
<b>Viscera</b>	11	100	110	6 600
<b>Total</b>	64	-	2793	122 194

### 2.3.3. Estimating predation rate

Lefort et al. (2020) estimated killer whale predation rates on narwhales when investigating the impact of killer whale predation on the residing narwhale population. A similar method was used to estimate the killer whales' predation rates, and by extension; the number of porpoises killed by the killer whales when they reside in Hardangerfjord (Eqn. 1).

$$\# \text{ Porpoise killed} = \frac{DPER_{total} \times N \times t \times pDiet}{U_p \times m_p \times pConsumed}$$

Eqn. 1

Here,  $DPER_{total}$  is the DPER of the killer whales (weighted by age and sex),  $N$  is the total killer whale population size,  $t$  is the number of days killer whales reside in the study area, and  $pDiet$  is the proportion of the killer whale's diet that comprise of porpoise.  $U_p$  is the porpoises' energy content per kg,  $m_p$  is the porpoises' mass (kg) and  $pConsumed$  is the proportion of porpoises consumed during one predation event (Lefort et al., 2020). The equation gives the number of



event can vary depending on various factors like the type of prey and location (Ferguson et al., 2012, Willoughby et al., 2020). Since harbour porpoises are relatively small-sized animals compared to many of the other known prey organisms for killer whales, and as no specific body parts have been observed after the predation events, values of 0.75 and 1.00 was chosen for the *pConsumed* variable (Table 4) (Dahlheim and Matkin, 1994, Estes et al., 1998).

To address the uncertainties in the harbour porpoise population size for Hardangerfjord, different simulations were run based on the 2.5%, 50%, and 97.5% quantiles of the abundance estimate (mid-range: 1339, 95 % CL = 992-1808) (Table 4). Moreover, to explore the effect of killer whales potentially only entering the fjord and eating porpoises when the porpoises exceed some critical abundance or density, a threshold parameter *min-pop-size-for-predation* was also added to the model. Killer whale predation was only applied when the porpoise population was above this threshold. In total, 10 different simulations were investigated with different *pDiet*, *pConsumed*, *min-size-for-predation*, and porpoise population size values (Table 4).

**Table 4.** Overview of the different scenarios explored with regards to differences in the parameters used when estimating the killer whale predation rates. The *pDiet* and *pConsumed* values from Scenario 4 were used for scenarios 7-10 as this was one of the mid-range predations estimates from the six scenarios run on differences in *pDiet* and *pConsumed*.

<b>Scenario</b>	<b>pDiet</b>	<b>pConsumed</b>	<b>Population size</b>	<b>Min-pop-size-for-predation</b>
<b>1</b>	1.00	1.00	1339	0
<b>2</b>	1.00	0.75	1339	0
<b>3</b>	0.75	1.00	1339	0
<b>4</b>	0.75	0.75	1339	0
<b>5</b>	0.50	1.00	1339	0
<b>6</b>	0.50	0.75	1339	0
<b>7</b>	0.75	0.75	992	0
<b>8</b>	0.75	0.75	1808	0
<b>9</b>	0.75	0.75	1339	0.50
<b>10</b>	0.75	0.75	1339	0.75

## 2.4. INDIVIDUAL-BASED MODEL TO STUDY THE EFFECT OF PREDATION

### 2.4.1. Introduction

The individual-based model (IBM) was based on a harbour porpoise model developed for inner Danish waters, and the original model is described in detail in Nabe-Nielsen et al. (2014). In this thesis, the original model has been altered and set up with oceanographic data, as explained

below, to represent Hardangerfjord. The next section includes a general summary of the model and a detailed description of the changes that were made to add killer whale predation. This includes a detailed description of the input data, alterations made, and how the model was set up for Hardangerfjord. The description of the model closely follows the ODD (Overview, Design concept, Details) protocol used by Nabe-Nielsen et al. (2014) and recommended by Grimm et al. (2010).

#### 2.4.2. Model description

##### *Purpose*

Killer whale predation on harbour porpoises was implemented in an IBM to study its effect on the population dynamics of harbour porpoises in Hardangerfjord.

##### *Structure*

The structure of the model used was the same as the original (Nabe-Nielsen et al., 2014), except for a few changes made to accommodate the unique geographical features of Hardangerfjord. The model system includes only one type of agent: female harbour porpoises. The model keeps track of state variables that describe the structure of the system: the state of the individual porpoises, their behaviour, and the environment they occur in. The porpoise agents are characterized by the state variables age, age at maturity, energy level, location, movement direction, speed, and pregnancy and lactation status (Nabe-Nielsen et al., 2014). Environmental state variables of importance to the model are food patch distribution and the time of year.

Adjustments to Nabe-Nilsen's code were made to fit Hardangerfjord. Simulations were based on a 120 x 100 km non-wrapped landscape covering the 799 km<sup>2</sup> large Hardangerfjord and mid-land areas (Fig. 2). The landscape was divided into 300 x 250 grid cells, each cell covering 400 x 400 meters, projected in UTM33N (EPSG code 32633). Each cell had the following properties: distance from land, water depth, and current food level. Food was placed in randomly distributed food patches in Hardangerfjord and was governed by several parameters. This included the number of food patches, the maximum amount of food in a patch,  $U_{max}$ , and how fast food was replenished,  $r_U$ . Porpoises could only move into cells where the water depth exceeded four meters. Furthermore, the landscape was divided into 12 20 x 20 km blocks, and the average food level was calculated for each of these blocks. Quality was defined as the average food content in a block during the current season, divided by the distance to that block from the current position.

## Processes

The processes in this model follow many of the same assumptions presented in the original model by Nabe-Nielsen et al. (2014) However, ships and wind turbines have been removed. The descriptions of how the processes were modelled and the equations used, can be viewed in Table A1 '*Process overview and scheduling*' in Appendix A.

The model used the same parameters for energy level, mortality, and movement as the original model. In short, the porpoise's energy level ranged from 0 to 20 and depended on the food eaten and the energy used for metabolism, lactation, and movement (Nabe-Nielsen et al., 2014). Once a food patch was reached, the porpoise consumed an amount of food related to its energy level. If the energy level decreased for a consecutive three days, they would start to disperse towards one of five target blocks at least 45 km away from the current location. If the porpoises were stuck (i.e., the distance to their target block does not decrease, or decreases too slowly), they altered their dispersal pattern by dispersing along the coast until a better area was located.

The porpoise's energy expenditure each time step, *Euse*, remained fixed in the model as studies on captive porpoises show a constant energy expenditure rate (Lockyer, 2003). However, the original model included an increase of 15 % in October and April and 30 % from November - March, to compensate for increased energy expenditure in colder waters (Lockyer, 2003), and an increase of 40 % for lactating individuals due to increased energy expenditure (Williams et al., 2007, Srinivasan et al., 2018). An additional energy expenditure was added to the current model for immature individuals (age < 3.44), by increasing their energy use with 50 % (Innes et al., 1987). Studies have shown that juvenile marine mammals have higher growth rates before reaching maturity (Perez et al., 1990).

The individuals faced a risk of dying once every day. They died if their energy level was too low, if reaching the maximum age of 24 years (Lockyer, 1996, Learmonth et al., 2014), or from killer whale predation. Additionally, they could become pregnant, give birth, wean a calf, or mate with a certain probability, dependent on the time of year (Appendix A, Fig. A1). If an individual had a calf, they could lose it at low energy levels. If the calf survived past the first 8 months, a new individual entered the population (if the calf was female; males were discarded). The porpoises had fine-scaled movements that depended on a correlated random walk behaviour developed by Nabe-Nielsen et al. (2013) and memory of previously found food locations.



The effect of predation in the model was parameterized based on yearly predation probabilities,  $p$ , which included several steps of calculations, described in ‘*Estimating killer whale predation rate*’. In short, the number of porpoises killed annually was estimated with Equation 1. This number was then divided by the porpoise population size estimate to get the percentage of porpoises killed yearly. Monthly predation rates,  $p_m$ , for each month,  $m$ , were calculated based on the killer whale’s presence estimates and the annual predation probability,  $p$ .  $p_m$  was implemented in the IBM by setting a daily survival probability,  $s_m$ , with the equation:

$$S_m = e^{\ln \frac{(1-p_m)}{30}}$$

Eqn. 2

Killer whale predation was applied in daily steps. If the porpoise individual being predated on had a calf, the calf would die instead of the mother. The predation was added to the model when the population had stabilized.

#### *Design concept*

The model assumed that porpoises were food limited in the absence of anthropogenic factors, and the survival probability increased with increasing energy levels. Killer whale predation could have a direct effect on the population, by removing multiple individuals from the population.

#### *Initialization*

The model was initialized by randomly placing 90 super individuals (one represents many, identical individuals) into the landscape (Fig. 4). 68 % of the adults in the model were set to be pregnant (adults include every individual with an age > 3.44). The starting age class distribution matched the one presented in the original model (Nabe-Nielsen et al., 2014). As most mating’s occurred in August, the mating day was picked at random from a normal distribution with a mean of 225 and a standard deviation of 20 based on Lockyer (2003). Similarly, the porpoises were given an initial energy level based on a random normal variable with a mean of 10 and a standard deviation of one. The model started running on the 1<sup>st</sup> of January.

#### *Input data*

The input data included food patches with a set growth rate and a maximum level that varied seasonally. The seasonal food level for each food patch (termed “mean maxent values”) was based on a maximum entropy (maxent) habitat suitability model which in turn was based on porpoise tracking data in inner Danish water (Edrén et al., 2010). There were no telemetry data

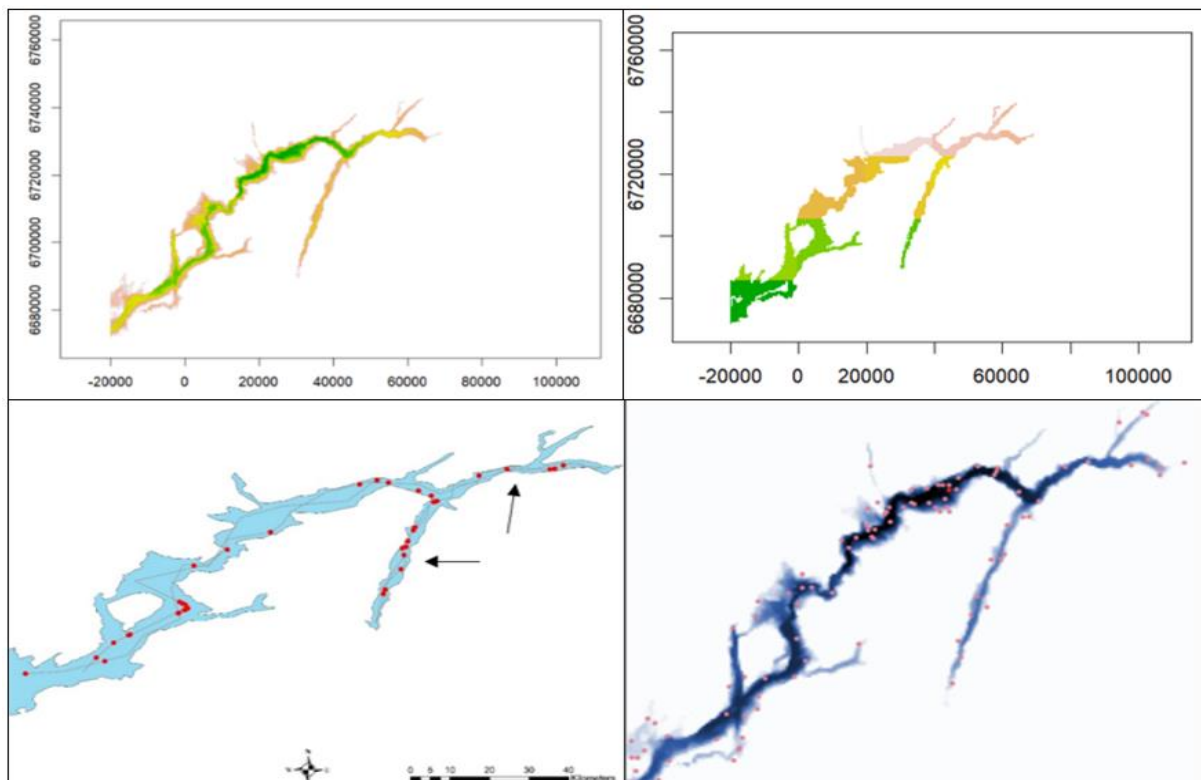
or similar information on porpoise incidence and/or their prey concentration in Hardangerfjord, so in the current model, the seasonal maxent levels for all food patches were generated by resampling the quarterly maxent levels with replacement from Nabe-Nielsen et al. (2014).

### Submodels

A description of the submodels for each process is specified in ‘*Process Overview*’ in Appendix A. In short, the submodels are related to the processes describing the system’s food levels, and the porpoise’s mortality, energy level, and movement.

#### 2.4.3. Calibration

The porpoises had a realistic movement pattern in the fjord when they were able to move up to 50 meters (2000 m in the original model) close to land before trying to turn away, and a minimum of 50 meters (500 m in the original model) from land when dispersing along the coast. These alterations were made to ensure that the porpoises dispersed out to the narrowest fjord arms (Fig. 4). Since mortality depended on energy level, it was linked to variation in food availability and the porpoise’s ability to move around in the landscape in search of food. Recent surveys indicate that the porpoises are distributed along the entire length of the fjord, including the inner fjord arms (Fig. 4) (Institute of Marine Research, unpublished data). The movement patterns of the porpoises were inspected visually in Netlogo to ensure that they obtained a realistic distribution in the fjord and its narrow arms (Fig. 4).



**Figure 4:** Bathymetric map (upper left) and block map (upper right) of Hardangerfjord. The porpoise distribution map in Hardangerfjord (Institute of Marine Research, 2021), the arrows point to the narrowest fjord arms and the red dots are porpoises (lower left). Bathymetry map of Hardangerfjord generated in Netlogo (6.2.2) where the pink dots are super individuals randomly positioned (lower right).

To ensure that the model could maintain a stable population of porpoises over time, and a realistic movement - and distribution pattern, relevant model parameters had to be calibrated. These parameters were originally calibrated by Nabe-Nielsen et al. (2014) to fit the inner Danish waters. They had to be re-calibrated in the current model since both the landscape and the number of super-individuals were different from the original (Appendix A, Table A2, and Fig. A2). The parameters included the porpoise's energy use per time interval,  $E_{use}$ , the number of food patches, and their food growth rate,  $r_U$ .

The Hardangerfjord model was run with re-calibrated parameters and killer whale predation disabled to represent the reference scenario. Sensitivity analysis for the selection of simulation time and model parameters has been described in Appendix A. The reference scenario was used as a baseline of comparison when investigating the potential effects of the different scenarios (Table 4) on the porpoise population size.

#### 2.4.4. Software used

NetLogo is a free software that was used in this thesis to implement the individual-based harbour porpoise model for Hardangerfjord. The model code and data files are available upon request.

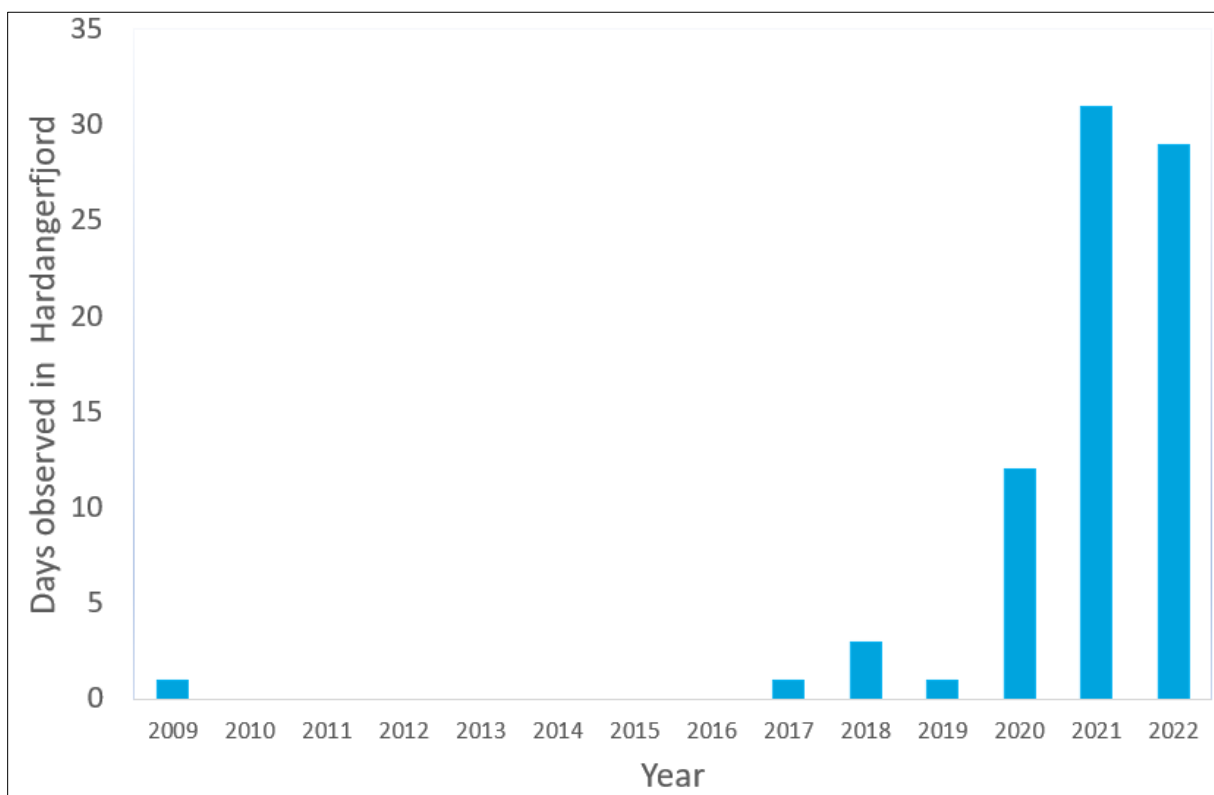
R (4.1.1) was used to prepare model input files for the spatial data, analyze the model output and visualize the simulation result in figures and plots. To make the model input files for the spatial data, multiple raster files had to be generated. They represented different aspects of the landscape, like water dept (bathymetry), food patches, and 12 dispersal blocks defined by their food quality (Fig. 4). The *raster* (Hijmans, 2021), and *sf* (Pebesma E, 2018 ) packages were used to generate the raster data. The bathymetric depth of Hardangerfjord was downloaded from the European Marine Observation and Data Network (EMODnet, 2020) and projected onto the specific study area. The map had to be slightly altered, most importantly a strip of land was added to the fjord mouth opening, and some problematic, very narrow areas were manually widened for technical-performance reasons. The strip of land was added to model the population as a closed population where no migration in and out of the fjord occurred, which is thought to be the case for the Hardangerfjord harbour porpoise population (Bjørge, pers.comm.). See 'Generating spatial data' in Appendix A for a more detailed description of how the raster files were generated.

## 3 RESULTS

### 3.1. TEMPORAL PRESENCE OF KILLER WHALES

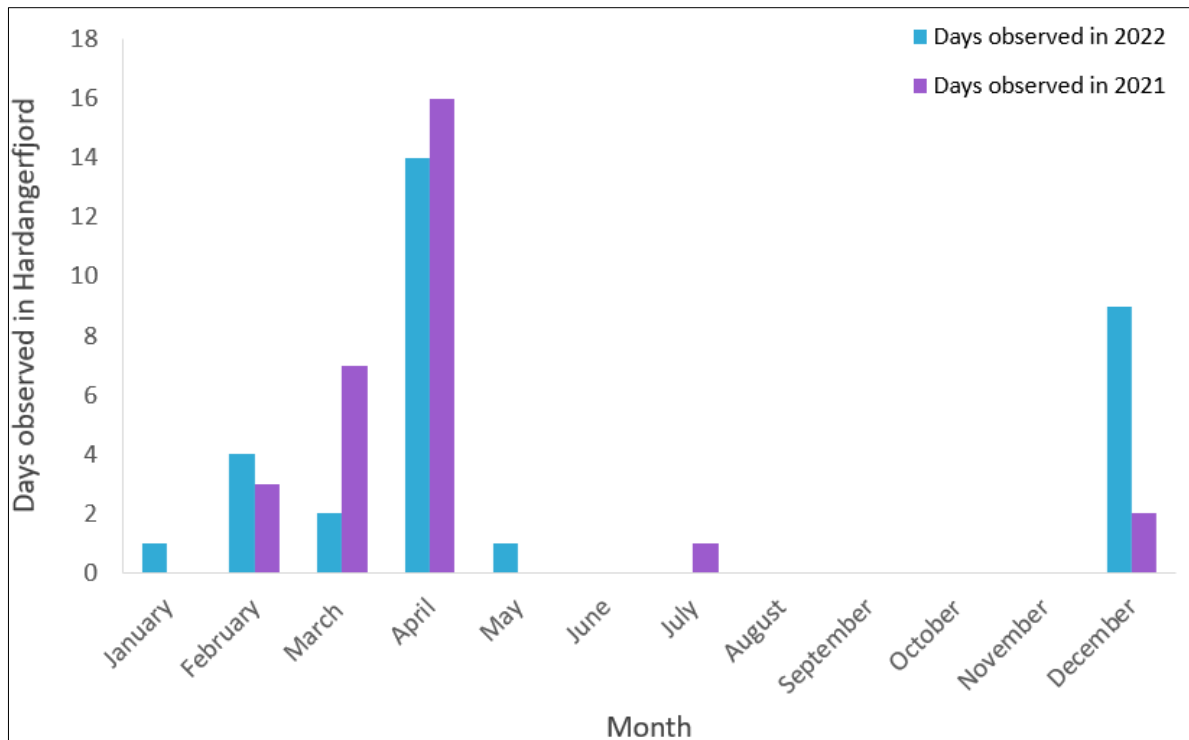
#### 3.1.1. Mark-recapture data

78 records of the two killer whale groups in Hardangerfjord covering the period April 2009 to December 2022 were compiled. After the one observation in 2009, the whales were not recorded again until March 2017. From 2017, a steep increase in the number of observations was noted (Fig. 6). Mark-recapture data from 2021 and 2022 were utilized in the presence estimates, as the whales were not widely recognized until the end of 2020, ensuring a more reliable data source for the analysis.



**Figure 6:** Days killer whales were recorded in Hardangerfjord during the period 2009-2022, based on citizen science data collected by NOS (Norwegian Orca Survey, unpublished data).

The two killer whale groups occurred in Hardangerfjord mainly between December and May in an intermittent migratory pattern. In 2021 and 2022 the two groups were observed for 29 and 31 days, respectively (Fig. 7) (Norwegian Orca Survey, unpublished data). This gave an average value of 30 days in the fjord annually, which is the value that was used when calculating predation rates (parameter  $t$  in Eqn. 1).



**Figure 7:** Number of days killer whales were observed in Hardangerfjord every month during 2021 (purple) and 2022 (blue), based on citizen science data collected by NOS (Norwegian Orca Survey, unpublished data).

### 3.1.2. Killer whales' identity

The photo identification data collected by NOS made it possible to identify the group composition (i.e., count of individuals) every time they were observed in the fjord, and further their age composition (Table 5). The IDs of the individuals and their assigned group start with the prefix NKW (Norwegian Killer Whale), followed by three to four numeric digits that represent the order in which they were first identified. The letters a and b indicate the first and second presumed offspring of the whale with the same ID code. Group 1 entering the fjord has been termed “NKW-280s” and group 2 has been termed “NKW-704s” (Table 5) (Jourdain et al., 2022). The two killer whale groups are frequently observed in Hardangerfjord between December and May, though rarely at the same time. The individuals in the same group tend to stick together. However, there is one exception for group NKW-280s, as individual NKW-1215 and her calf 1215a tend to separate from the rest of the group (Table 5) (Norwegian Orca Survey, unpublished data).

**Table 5.** Group composition of the two killer whale groups that occur seasonally in Hardangerfjord, with their gender and age as estimated at the time of writing (Norwegian Orca Survey, unpublished data).

Group	ID	Gender	Age (years)
NKW-280s	NKW-280	Female	30 +

	NKW-1215	Female	20
	NKW-565	Male	21
	NKW-269	Male	24
	NKW-281	Male	28
	NKW-280a	Unknown	7
	NKW-280b	Unknown	< 1
	NKW-1215a	Unknown	7
<b>NKW-704s</b>	NKW-704	Female	20+
	NKW-366	Female	21+
	NKW-877	Female	23+
	NKW-878	Female	19
	NKW-704a	Unknown	7
	NKW-366a	Unknown	8
	NKW-877a	Unknown	10
	NKW-877b	Unknown	4
	NKW-878a	Unknown	5

### 3.1.3. Acoustic monitoring

The acoustic data recorded with the CPODs did not give sufficient findings for assessing the temporal occurrence of killer whales based on echolocation clicks or whistles. Thus, it was not possible to conduct analyses to determine whether they correlated with the citizen-science-based data.

The echolocation clicks classified by the CPOD program as ‘other cetaceans’ were few and only partly overlapped the killer whale presence estimated with the photo identification mark-recapture data. Only the Torsnes, Årsnes, and Bagnstrond CPOD sites held such echolocation clicks. The ‘other cetacean’ detection in the Torsnes station on 21.07.2021 was likely sonar noise misidentified as cetacean noises (Appendix A, Fig A6). These detections did not match the characteristics of a cetacean click train, as explained by Tregenza (2013). Short pulses at 72–80 kHz with uniform lengths and intervals indicated that the noise was not of biological origin, but rather artificial.

The Bagnstrond site held the most ‘other cetacean’ detections with a count of 27 detections. 9 of these detections were made in the data period 1-3 (27.09.2020-10.06.2021). While periods 4-5 (10.06.2021-28.10.2021) had more ‘other cetacean’ detections with a count of 16. The Årsnes station had one ‘other cetacean’ detection on 16.10.2021. Most of these identified click trains resembled the characteristics of other cetacean acoustics as explained by Tregenza (2013). They were in a broad frequency range of 40–140 kHz, had low durations (<15 cycles),

and continuously changing click rates characteristic of cetacean vocalizations (Appendix A, Fig. A7-A8).

The second approach was similar in its lack of sufficient findings. As the low-frequency sounds were extracted from the acoustic data, they clustered at random intervals throughout the year. The illustration of the low-frequency sounds over time for the five CPOD locations has been given in the supplementary data (Appendix A, Fig. A9-A13).

### 3.2. THE KILLER WHALE'S PREDATION RATE

Citizen-science imagery material documented six events of killer whale killing and feeding on harbour porpoises between 2017 and 2022 (Fig. 8) (Norwegian Orca Survey, unpublished data). These were considered indicative of these killer whales' feeding habits, at least when present in the Hardangerfjord.



**Figure 8:** Footage of three events where killer whales were observed preying on/consuming harbour porpoises in Hardangerfjord. The photo (left) was taken by Olve Erdal, and the two to the right were drone footage taken by Leif Kåre Havås.

The 17 individual killer whales entering the fjord were divided into two distinct groups (Table 5). Every time a killer whale individual within a specific group was observed, it was assumed that the entire group was present and the group's total DPER was accounted for in the predation rate estimate. There was one exception for NKW-1215 and her calf, as they were included only

at times they were specifically observed. The adult female NKW-1215 and her calf had a summarized DPER of 330 000 calories, whilst the remaining five individuals in group NKW-280s had a summarized DPER of 968 000 calories (Tables 2 and 5). NKW-704s group consisted of nine individuals and had a summarized DPER of 1 345 700 (Tables 2 and 5). The estimated energy content was 122 200 calories for one average porpoise (43.75 kg) (Table 4).

Different scenarios had to be run to account for uncertainties in several of the parameters used when estimating the killer whale’s predation rates (Table 5). In the worst-case scenario (scenario 2), the two killer whale groups had to consume 399 porpoises in total annually to cover their energy needs during their stay. This means that they on average consumed 12.5 porpoises every day they were present in the fjord. Table 6 is an extended version of Table 5 as it includes an overview of the scenarios investigated and their calculated predation rates, that were implemented in the IBM.

**Table 6.** Overview of the different predation scenarios explored concerning changes in the parameters used when estimating predation rates.

<b>Scenario</b>	<b>pDiet</b>	<b>pConsumed</b>	<b>Population size</b>	<b>Predation probability</b>	<b>Min-pop-size-for-predation</b>
<b>1</b>	1.00	1.00	1339	0.24	0
<b>2</b>	1.00	0.75	1339	0.28	0
<b>3</b>	0.75	1.00	1339	0.18	0
<b>4</b>	0.75	0.75	1339	0.21	0
<b>5</b>	0.50	1.00	1339	0.12	0
<b>6</b>	0.50	0.75	1339	0.14	0
<b>7</b>	0.75	0.75	992	0.28	0
<b>8</b>	0.75	0.75	1808	0.16	0
<b>9</b>	0.75	0.75	1339	0.21	0.50
<b>10</b>	0.75	0.75	1339	0.21	0.75

### 3.3. THE INDIVIDUAL-BASED MODEL

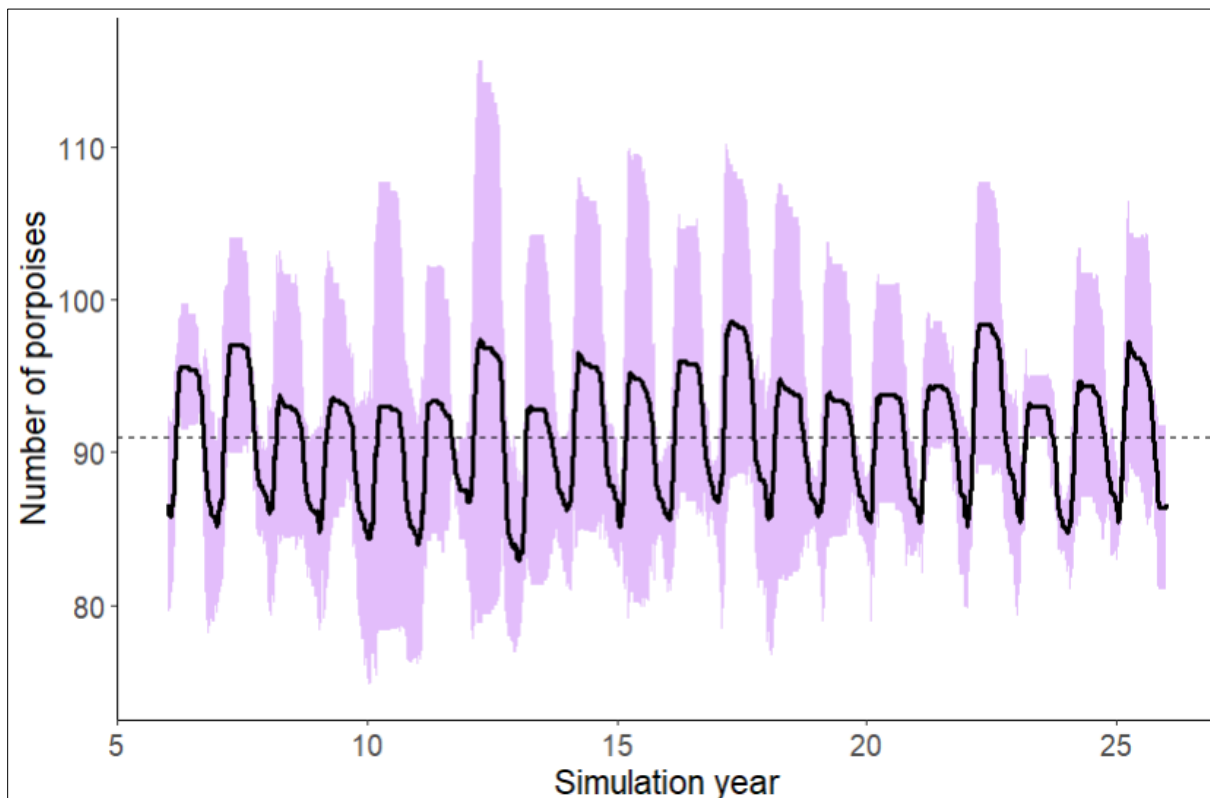
#### 3.3.1. Dynamics of the porpoise population

The food level and population stabilized within five years when the model was run with  $p = 0.05$  (Fig. A2, Appendix A). Thus, the predation process was added in year six when the population had stabilized. The population size (measured every day) for the scenarios run was based on simulation years 6-26 to look at the effect of predation over 20 years. Five replicates



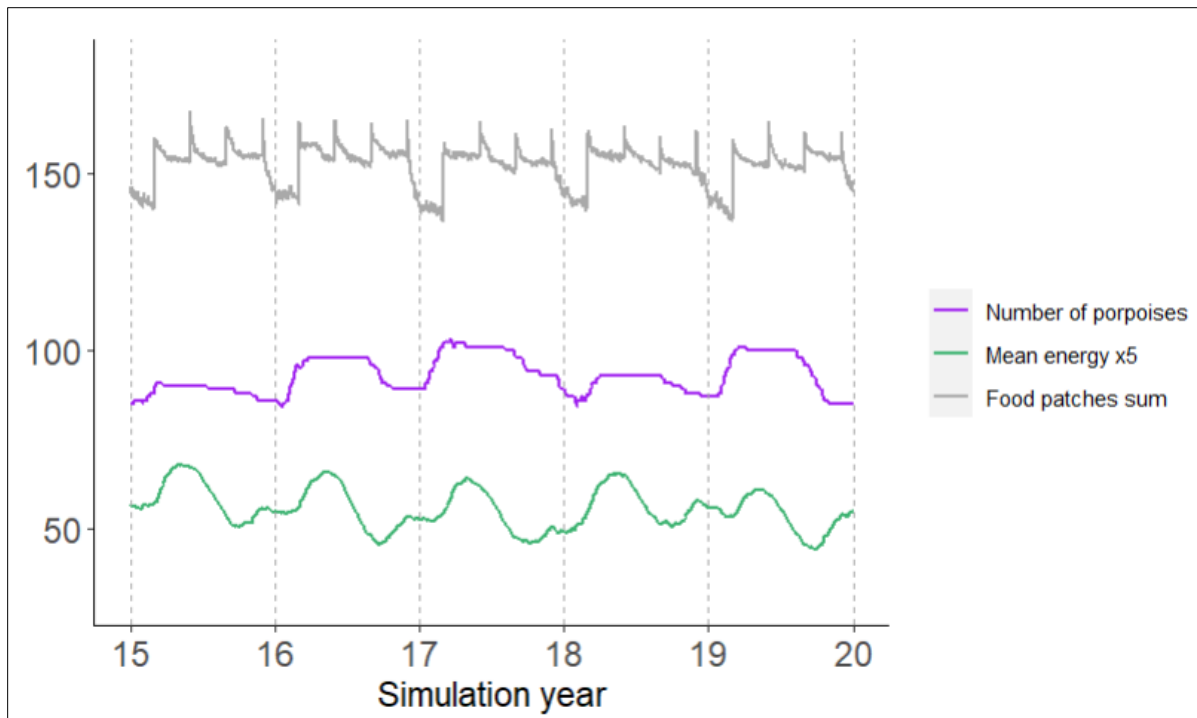
were run, as it was found to be sufficient in the model's initial experiments conducted by Nabe-Nielsen et al. (2014) to offer a reliable estimate of the population dynamics' fluctuations.

The reference scenario was able to maintain a stable population size of 90 super-individuals over time, while simultaneously producing realistic movement patterns for the individuals (Fig. 9). The equilibrium population size was kept stable over time with 275 food patches (food probability of 0.367%), and parameter value of  $E_{use} = 5.0$ ,  $r_U = 0.11$  and  $\beta = 0.4$  (Fig. A1 in Appendix A). Sensitivity analysis for this model showed that it was most sensitive to lower food replenishment rates,  $r_U$  (Fig. A4, Appendix A).



**Figure 9:** Average number of porpoises simulated daily over 20 years (year 6-26) in five replicates of the reference scenario ( $E_{use} = 5.0$ ,  $R_U = 0.11$ ,  $B = 0.4$ ) in a landscape without predation, plotted by year. The purple, shaded band shows  $\pm 1$  SD, and the dashed horizontal line represents the average population size from years 6-26.

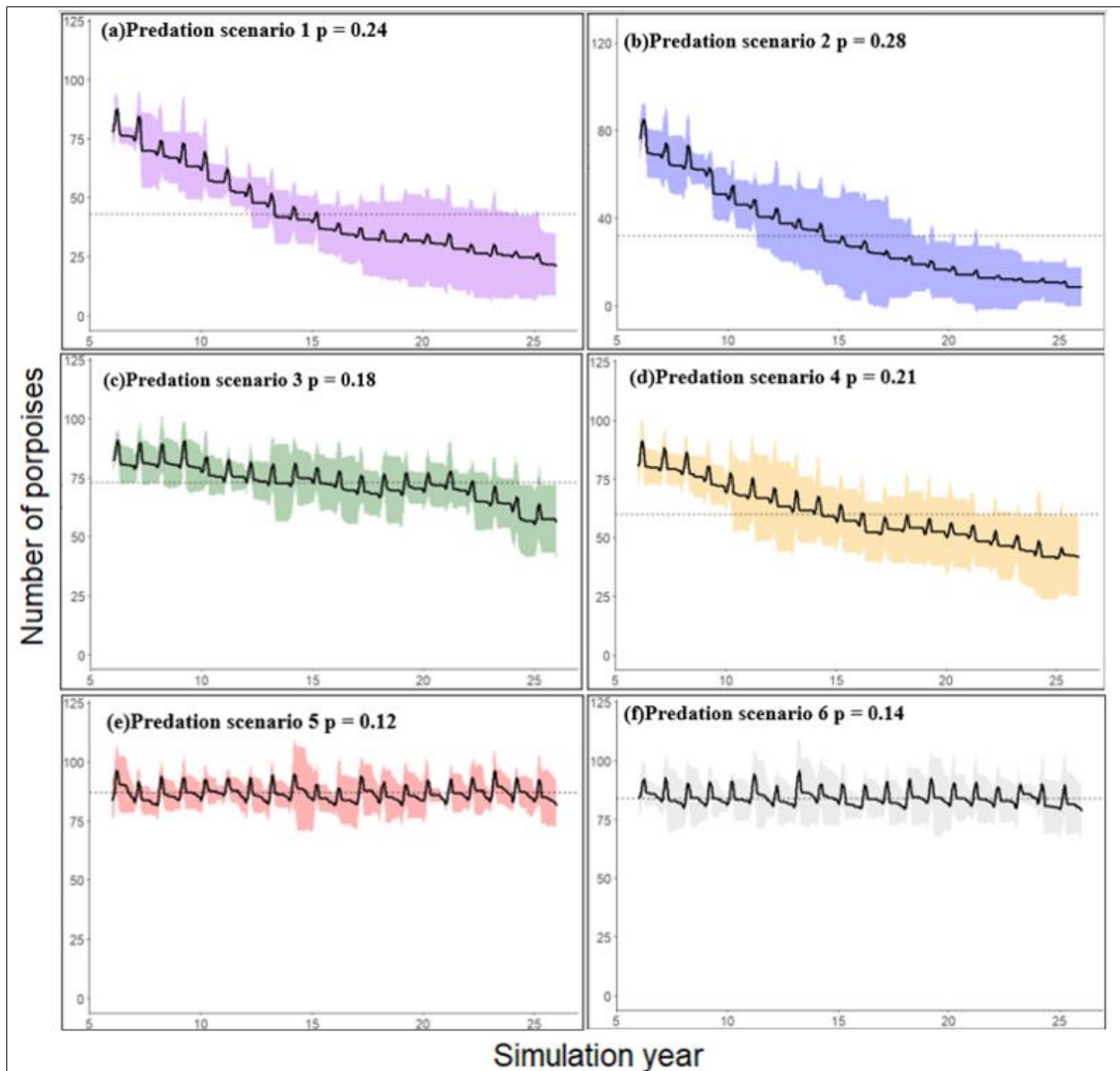
The model followed the same dynamics as the model calibrated for inner Danish waters: the population size increased at the start of the year when calves became independent individuals 8 months after they were born (Fig. 10). As the population grew, the amount of food available in the system decreased and thus also the energy level of the porpoises. The increased competition for food caused a decrease in population size towards the end of the year.



**Figure 10:** Simulated population dynamics based on the reference scenario ( $E_{use} = 5.0$ ,  $r_U = 0.11$ ,  $B = 0.4$ ) in a landscape without predation. The green line shows the mean energy level  $\times 5$  of the porpoises, the purple line shows the porpoise population size, and the grey line shows the summarized amount of food in the landscape. This is plotted against simulated time, in this case, years 15 to 20. Each individual is a super individual and only female porpoises are represented.

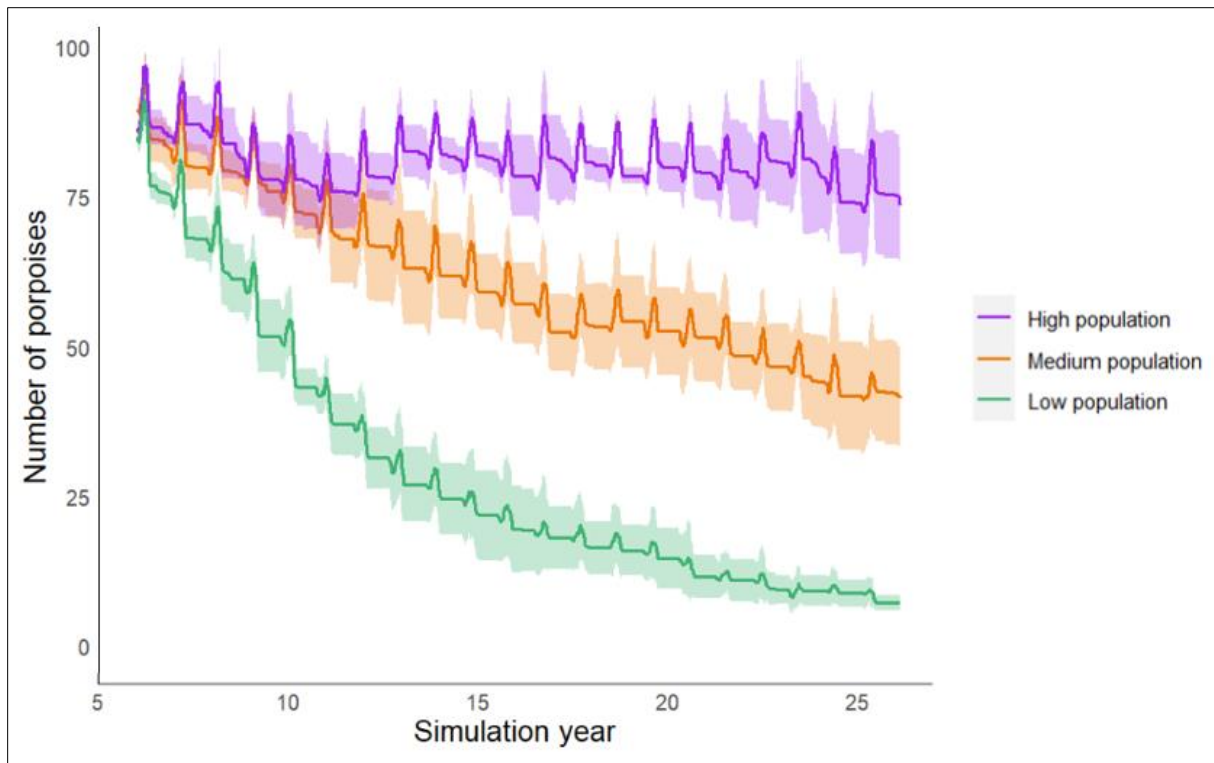
### 3.3.2 Effect of predation on the porpoise population

The simulated population trajectories (years 6-26) were graphed for each of the 10 scenarios investigated (Fig. 11-13). Both the variation in  $pDiet$  and  $pConsumed$  gave a distinguishable difference in predation probabilities (Table 6). The difference was most noticeable when the  $pDiet$  varied from 1.00 (Scenario 1-2) to 0.75 (Scenario 3-4) and 0.50 (Scenario 5-6) (Fig. 11). Scenario 2 had the highest predation probability ( $p = 0.28$ ), and the population was reduced to approximately 10 % of its initial abundance after 20 years of being subject to this predation rate (Fig. 11). The populations were able to stabilize at 95 % and 92 % of their initial abundance when being subject to a predation rate of respectively 0.12 and 0.14 (Scenario 5-6) (Fig. 11). In scenario 4, one of the two median predation probabilities, the population size gradually decreased and kept on decreasing towards the end of the simulation time. The population was reduced to 45 % of its initial size after 20 years (Fig. 11).



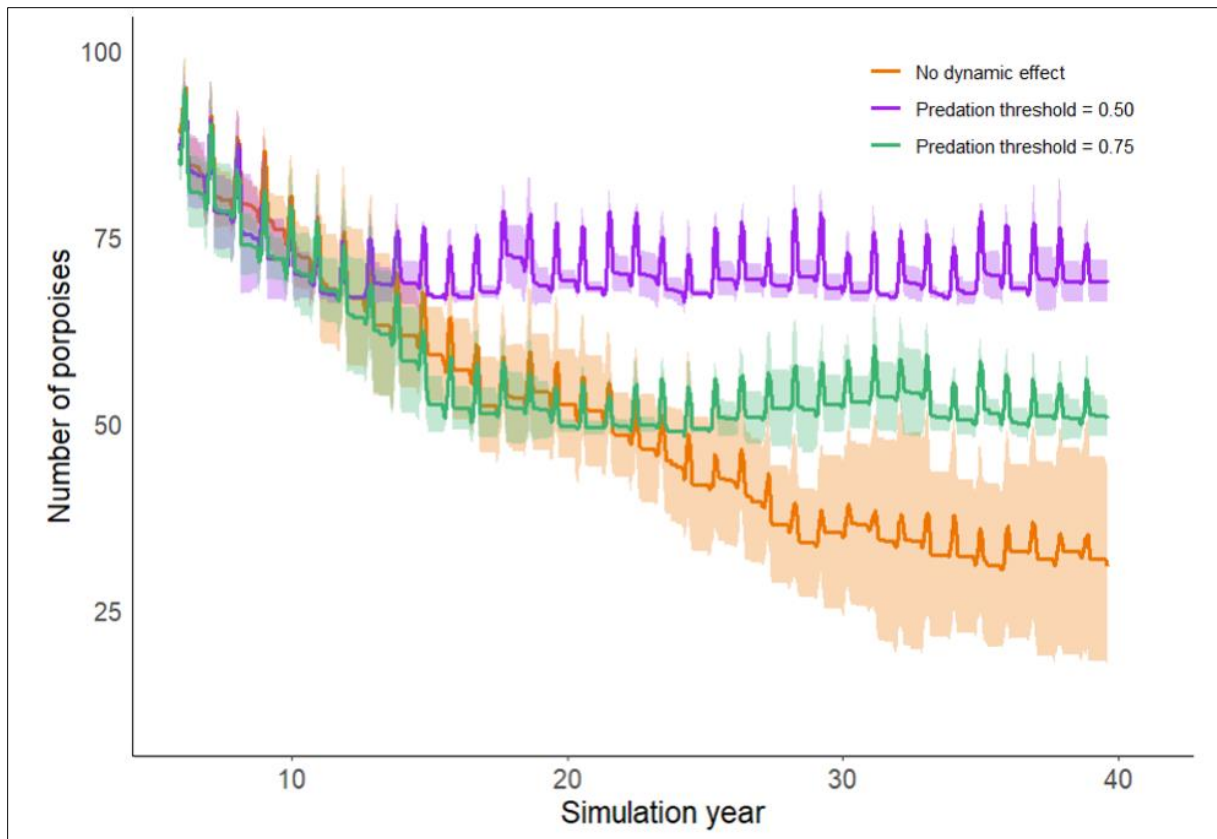
**Figure 11:** Comparison of the variation in porpoise population size when predation probability varied due to differences in  $p_{Diet}$  and  $p_{Consumed}$  values, giving six scenarios (a-f) (each run in five replicates). The dashed horizontal line is the mean population size during the simulation time (among replicates). The colored, shaded ribbons indicate the mean  $\pm$  1 SD from the five replicates.

The use of low, mid-range, and upper values for the porpoise abundance estimates (mid-range: 1339, 95 % CL = 992-1808) gave a pronounced difference in the population size outcome (Scenario 4 & 7-8) (Fig. 12). The population size was reduced to respectively 10, 67 and 89 % of its initial abundance. Both the low- and mid-range population scenarios had a decreasing trend, whereas the high-population scenario stabilized at a size of 89 % of the initial population size within simulation year 13, and maintained stability after this.



**Figure 12:** Comparison of the variation in porpoise population size when predation probability varied due to differences in the high (1808 individuals), medium (1339 individuals), and low (992 individuals) population estimates (Institute of Marine Research, unpublished data). A predation rate of 0.21 was used in all three scenarios (scenario 4). The colored, shaded ribbons indicate the mean  $\pm$  1 SD from the five replicates.

Running the model with a dynamic effect gave a distinct difference in population size over time (Fig. 13). The simulation was run for 40 years to fully illustrate the difference in population size between the scenarios. When predation only occurred when the porpoise population size was above 75 % of its initial size, the population size decreased by 23 % within 5 years of predation and stabilized at this level for the rest of the simulation time. Whilst for the case of predation occurring above 50 % of the initial size, the population had decreased by 50 % within 20 years of predation (year 26). In the non-dynamic scenario where the predation rate was kept constant at 0.21 throughout the simulation time, the population continuously decreased and by year 40 the population was reduced to 67 % of the initial size.



**Figure 13:** Comparison of the variation in porpoise population size when the predation probability varied due to different dynamic scenarios. The purple and orange line represent the scenarios where predation occurred only at times when the population size was above 75 and 50 % of its initial size, respectively. The green line represents the scenario where predation continuously occurred throughout the simulation time. A predation rate of 0.21 was used in all three scenarios (Scenario 4). The scenarios were run for 40 years to observe the difference between them. The colored, shaded ribbons indicate the mean  $\pm$  1 SD from the five replicates of each scenario.

## 4 DISCUSSION

This study investigated the population-level impact of killer whale predation on the harbour porpoise population in Hardangerfjord. This was done by quantifying killer whale presence, estimating predation rates, and implementing them in an individual-based model, ultimately examining the risk of porpoise population extinction. Multiple scenarios with different predation rates were investigated in the IBM, and there were large variations in the effect they had on the porpoise population size (Fig. 11-13).

### 4.1. TEMPORAL PRESENCE ESTIMATE OF KILLER WHALES

It was hypothesized that both citizen science and acoustic recorders could be used to quantify the killer whale's temporal presence in the fjord. However, only the multi-year recapture approach, collected with the use of citizen science, had sufficient findings. The next subsections will focus on the main findings and limitations of these two methods.

#### Mark recapture data

Norwegian Orca Survey has used citizen-science-based initiatives to photo-identify and document the occurrence of killer whales in Hardangerfjord with mark-recapture techniques since 2017. Observational data from 2021 and 2022 indicate that the killer whales had an average residence time of 30 days annually. The multi-year data confirm a seasonal trend in the two killer whale groups' movement patterns in and out of the fjord (Fig. 7). In general, killer whales occur in an intermittent pattern between the months of December to May every year, some months having higher presence estimates than others. April was the most frequently visited month, where approximately 50 % of the observations were made (Fig. 7).

The citizens-science-based data was considered successful in estimating the temporal presence of the killer whales in the Hardangerfjord. This study emphasizes the importance and accuracy of citizen-science-based programs when investigating rare and migrating species, like the Norwegian killer whales (Garcia-Soto et al., 2021). The topography of Hardangerfjord (i.e., mostly narrow with settlements in multiple places) and the characteristic look of killer whales in the region have facilitated their observations. In this regard, Hardangerfjord represents a unique study area for which precise data on killer whales' residence time and group composition (number of individuals present, individuals' age, and expected energy requirements) are available to investigate killer whales' role as predators.

The estimated days present might be an underestimation of their temporal presence, as only observations that can provide visual identification of the killer whales were included. This ensured that other whales were not mistaken for killer whales. Ten observations had to be disregarded due to lack of visual confirmation in 2022, which make up 24 % of the detections. Thus, 76 % of the observations were supported by photographic evidence, indicating that the citizens have good detection - and photo identification rates when killer whales occur in the fjord. The fjord is narrow and the citizens inhabiting the surrounding areas have gained an increased awareness of and enthusiasm for the killer whales in recent years. Moreover, killer whales are easy to spot with their characteristic features. As a result, there is a strong indication that whenever the whales enter the fjord, they almost certainly get spotted (leading to high detection rates), and their presence is documented. Despite this, an underestimation of their temporal presence can occur if the killer whales enter the fjord during the night and leave again before daylight.

The proportion of records provided by citizen science initiatives, mainly consisting of social media posts, increased remarkably from 2017 to 2021 (Fig. 6). It was hypothesized that killer whale occurrence in Hardangerfjord was a relatively new phenomenon. The scarcity of records on killer whales in Hardangerfjord before 2017 could reflect a true lack of presence or lower observational efforts. Thus, it remains unknown whether this is a new phenomenon or whether it has simply not been discovered due to low observer effort. However, the awareness of the killer whale's occurrence in the fjord is sound, exemplified by the high participation and activity rates on multiple social media platforms. To exemplify, the Facebook group "Spekkhoggara i Hardangerfjord" had 6 447 members at the time of writing and was the biggest platform for killer whale photo identification in this region. This has resulted in a solid citizen-science-based initiative in the Hardangerfjord region when it comes to reporting killer whale observations, which cannot be found at other locations along the Norwegian coast. This study validates previous findings in that the "citizen-science-based" initiative is a useful method in research (Andrachuk et al., 2019, Garcia-Soto et al., 2021). Its usefulness is highly related to the increased availability of good quality footage taken with either digital cameras, smartphones, or drones.

#### Acoustic monitoring

As porpoises and killer whales are the two cetacean species known to frequently occur in Hardangerfjord, it was believed that the acoustic behavior of killer whales would be captured on the CPODs to quantify their presence. More specifically, it was believed that the acoustic

recorders could be used to detect killer whale echolocation clicks and/or whistles, as they hunted for porpoises in the fjord.

The data from the five CPODs contained very few ‘other cetacean’ detections, the category where the potential killer whale echolocation signals would fall within. Only 11 out of the 27 validated ‘other cetacean’ detections occurred in months where the killer whales were visually observed (Fig. 7). The remaining 16 detections occurred at times when the killer whales did not visit the fjord according to the mark-recapture photo identification data (Fig. 7). This may imply the presence of other cetacean species, and pilot whales have been observed inside the fjord occasionally, even though such sightseeing’s are rare (Norwegian Orca Survey, unpublished data). Similarly, the whistle data (< 30 kHz sounds) tended to cluster at random periods in the data (Appendix A, Fig. A9-A13), and did not align with the photo identification data (Fig. 7).

If the killer whales did emit echolocation clicks/whistles in Hardangerfjord, the lack of detections can be because the CPODs simply did not capture them. The killer whales’ acoustics are very directional, and there were only five CPODs placed relatively close to the shore. Alternatively, the CPODs captured the echolocation clicks, but the CPOD.exe program failed to identify them as ‘other cetaceans’, whilst the whistles might not have been extracted correctly from the dataset, causing other sounds to be included. Another explanation is that the killer whales used a predator tactic of silent hunting to avoid detection by prey and optimize predation success, which has been observed in multiple mammal-eating killer whale groups (Barrett-Lennard et al., 1996, Deecke et al., 2005, Filatova et al., 2007, Deecke et al., 2011, Jourdain et al., 2017). Previous studies demonstrate that only sporadic echolocation click trains were emitted by a killer whale group when they were handling seal prey in Norwegian coastal waters (Jourdain et al., 2017), and groups in Shetland only emitted two whistles while traveling (Deecke et al., 2011).

#### Limitations

The primary limitation of using killer whale photo identification data collected by citizen science to estimate killer whales’ temporal presence, is the relatively short data collection period. Yearly re-sightings of the individuals over the past six years indicate some degree of site fidelity in Hardangerfjord, but the short data time series available makes it hard to draw any firm conclusions. This study had only two years (2021-2022) of sufficient observational data available for analysis. This limited time frame may have prevented the complete capture of the long-term trends or fluctuations in this newly discovered phenomenon which is the



temporal presence of killer whales in Hardangerfjord. Therefore, the usefulness of these findings in the predictions of future predator-prey dynamics may be limited.

The primary limitation of this study in using CPODs to estimate killer whales' temporal presence is related to time constraints, which precluded a more extensive analysis of the acoustic data gathered. As this study also focused on establishing an IBM to study the population-level impact of predation on porpoises in Hardangerfjord, the time was not sufficient to further investigate the lacking results in the CPOD data within the scope of this thesis.

## 4.2. THE KILLER WHALE'S PREDATION RATES

### Main findings

The number of porpoises taken annually has been calculated and divided by the porpoise population size estimate to determine the killer whale predation in Hardangerfjord, which has occurred intermittently since 2017. During these estimations, it was assumed that the number of porpoises predated on by killer whales was mainly dependent on the killer whales' temporal presence and bioenergetics. The results indicate that a relatively low number of killer whales (17 individuals) has the potential to consume a large number of porpoises annually, despite their low presence estimates (30 days annually). 399 porpoises were consumed in the worst-case scenario, which composed of 28 % of the porpoise population (Scenario 2 and 7, Table 6).

Multiple scenarios were run to account for the uncertainties in some of the predation rate parameters (Equation 1), this included  $p_{Diet}$  (proportion of diet consisting of porpoise),  $p_{Consumed}$  (proportion of porpoise consumed), and porpoise population size. The estimated, yearly predation rates ranged from 0.12 - 0.28 for the different scenarios investigated (Table 6). This wide range emphasizes the importance of running multiple scenarios when there are uncertainties in the parameters, as small differences in the parameters can have large effects on the result. Due to a lack of information on these values, all of them were investigated when running the predation effect in the IBM.

The evidence presented here supports the prior observations of killer whales predated on harbour porpoises in the Hardangerfjord (Fig. 8). The first scientific record of Norwegian killer whales predated on harbour porpoises occurred in Andfjord waters in 2012 (Cosentino, 2015). Despite this, Norwegian killer whales may have been preying on harbour porpoises for a longer period, but this has gone unnoticed by scientists and the public. There are challenges associated with studying open ocean environments, and the killer whales in Norway have been studied mainly at herring wintering grounds (Similä et al., 1996, Simon et al., 2007a, Jourdain et al.,

2020, Jourdain, 2020, Jourdain et al., 2021, Matika et al., 2022), with limited chance of identifying other prey species. Only recent efforts in other seasons made it possible to investigate the killer whale diet in a larger sense in the Norwegian region (Cosentino, 2015, Jourdain et al., 2017, Jourdain et al., 2020).

The dietary habits of the two killer whale groups remain unknown, as this has never been properly studied in Hardangerfjord. Drawing from the introductory background information, isotopic mixing models suggested that some Norwegian killer whales are cluster 1 individuals with 46-68 % of their diet consisting of marine mammals, specifically seals (Jourdain et al., 2020). Only predation on harbour porpoises has been observed when the killer whales are in Hardangerfjord (Fig. 8), which might indicate that they are cluster 1 individuals. However, it remains unknown whether they also predate on other prey types like seals and a selection of fish species while present in the fjord. The predation of fish often occurs under the surface and can be hard to quantify visually without underwater footage. Moreover, the whereabouts and diet of the killer whales outside of Hardangerfjord remain unknown. The three scenarios run for the  $pDiet$  value (0.50, 0.75, and 1.00) were chosen to cover the most likely scenarios based on current evidence on prey specialization in Norwegian killer whales.

The proportion of the harbour porpoise that is consumed by killer whales during one predation event remains largely unknown. Killer whales predated on large whales have been observed to consume only certain parts of their prey (e.g., their tongue) (Jefferson et al., 1991, Alava et al., 2013). Moreover, they can consume prey partly when the prey is abundant, like killer whales consuming only the skin of harbour seals or fluke of harbour porpoises in Alaska (Heise et al., 2003). On the contrary, studies on smaller-sized marine mammal prey like bowhead whale calves (Willoughby et al., 2020), sea otters, and sea lion pups (Estes et al., 1998) have documented that the entire prey is consumed. Thus, two scenarios with  $pConsumed$  values of 0.75 and 1.00 were investigated in this thesis to cover the most realistic representations of the predation pattern in Hardangerfjord, as harbour porpoise can be classified as a smaller-sized cetacean prey for killer whales.

The calculated predation rates may be underestimated if the population size estimate of harbour porpoises is too high. However, the effect of population size has been thoroughly investigated by using the lower (Scenario 7), mid-range (Scenario 4), and upper (Scenario 8) population estimates when calculating predation rate (Table 6). The predation rates differed extensively when investigating the different porpoise population sizes (Table 6). These results were not

remarkable, considering the wide porpoise population estimate given by IMR (1339, 95 % CI: 992-1808).

It can be argued that the integration of the killer whales' bioenergetics and presence estimates is a sufficient method when estimating the killer whale's predation rates. This is a novel approach that has not been previously applied to Norwegian killer whale populations. If the predation rates are quantified accurately, the method can provide valuable insight into the ecological impact killer whale predation can have on a prey species. Similar methods have been employed in various studies in other regions, where they argue for their usefulness in assessing top-down control by predators (Kitchell et al., 1977, Schindler et al., 2002, Williams et al., 2004, Bolt et al., 2009, Noren, 2011). Accurate estimations of predation rates in a system can advise on decision-making processes and develop management strategies for maintaining biodiversity in Hardangerfjord.

#### The driving force behind

The driving force behind the newly discovered predation phenomenon in Hardangerfjord is not yet fully understood. Studies have shown that there is a direct link between prey availability and movement patterns among killer whales (Similä et al., 1996, Krahn et al., 2002, Forney et al., 2006, Noren and Hauser, 2016). There are high inter-individual and inter-annual variations within the Norwegian killer whales' diet, and they have been observed switching between specialized feeding behaviours seasonally and feeding opportunistically when other prey is available (Jourdain et al., 2020, Jourdain, 2020). This is because marine ecosystems are dynamic, and prey fluctuates over time.

In the case of the killer whale's recent occurrence and predation on harbour porpoise in Hardangerfjord, this could be a new pattern caused by a prey switch or an altered range pattern caused by prey fluctuations. Prior investigations on killer whales have indicated that they can conduct dietary shifts when preferred prey is limited (Springer et al., 2003, Williams et al., 2004, Estes et al., 2009, Testa et al., 2012, Vongraven and Bisther, 2014). The near total collapse of NSS herring in 1970 due to overfishing may have forced killer whale populations that depended on herring to switch to marine mammal prey types (Vongraven and Bisther, 2014). Theoretically, adaptations to new hunting techniques following a prey switch can have been facilitated by phenotypic plasticity and the whale' capability of learning (Riesch et al., 2012, Samarra and Miller, 2015). However, the findings presented in this thesis cannot verify either theory.

## Limitations

Additional underestimation of the number of porpoises killed annually can occur if the porpoise energy content estimate is too high, the estimated days present is too low ( $> 30$ ), or surplus killing. These uncertainties have not been investigated by running multiple scenarios in this thesis, as the availability of observational data bearing on these potential issues does not exist for the porpoises and killer whales in Hardangerfjord. Moreover, there is a limit to how many scenarios which was plausible to run considering given time constraints.

The energy estimates derived from other species closely resembling harbour porpoises were used to solve the problem of incomplete data on the harbour porpoise's energy content. Even though closely related species can have an equivalent amount of muscle, intestine, and fat, the estimate is inevitably subject to some errors. This is because environmental factors, and individual - and dietary differences, can influence the composition of these tissues, leading to discrepancies in the estimates.

Moreover, there are additional uncertainties due to limited knowledge of the killer whales' DPER (daily prey energy requirement). The yearly DPER estimates in this study were based on the body mass of resident killer whales in the eastern Pacific Ocean (Noren, 2011), as estimates for Norwegian killer whales only existed for adult males (Matika et al., 2022). Because the current study concentrates on Norwegian killer whales, whose body mass may vary from the southern resident ones, an error in these estimates may occur. Additionally, the potential higher DPERs of young, adolescent males and lactating female killer whales were not included due to the lack of consistent evidence and high interindividual variation between killer whale populations.

## 4.3. THE POPULATION-LEVEL IMPACT OF KILLER WHALE PREDATION ON THE PORPOISE POPULATION IN HARDANGERFJORD

### Main findings

The individual-based model presented here makes it possible to assess the population dynamics of Hardangerfjord porpoises over time, when subjected to different predation rates by killer whales. Such a model is valuable for effective porpoise management, as it models a system on individual level and gives a thorough understanding of the predators' role in the ecosystem (Beauchamp et al., 2007). The results show that if the predation pattern observed in 2021-2022 continues over a 20-year period, the harbour porpoise population in the highest predation scenario ( $p = 0.28$ ) will be reduced to 10 % of its initial size. In contrast, the population

experienced a small reduction to 95 % of the initial population size before stabilizing, in the scenario with the lowest predation rate ( $p = 0.12$ ). Based on energetic arguments, this study demonstrates that predation by killer whales could exert a negative impact on the porpoise population, potentially threatening them with the risk of extinction. However, the magnitude of this negative effect is highly dependent on the different values used for the parameters in the predation rate estimate (Table 6).

In the lower predation rate scenarios (Scenario 5, 6, and 8), the population experienced a slight reduction before stabilizing at an equilibrium population size of respectively 95, 92, and 89 % of initial numbers. As this model is based on energetic principles, the population carrying capacity is dictated by food availability in the reference scenario without predation. This aligns with previous literature stating that the equilibrium population size for mammals would likely be dictated by food availability in the absence of anthropogenic factors (which were not investigated in this model) (Sinclair, 1989). Once predation was added to the model in lower levels, it contributed to controlling the population carrying capacity, which has been observed in particular species before (Sinclair, 1989). In these scenarios, the harbour porpoise population size is slightly lowered, but it stabilizes at viable levels and the population is not at risk of going extinct.

These results are greatly contradicted by the higher predation rate scenarios, as the majority of the scenarios (scenarios 1-4 and 7) had continuously declining trends in the population size. IUCN considers marine mammals to be more vulnerable to extinction if the population is small or declining (IUCN, 2022). If any of these scenarios realistically represents the predation-prey dynamics between killer whales and harbour porpoises in the fjord, the porpoise would be classified as ‘threatened’ according to the IUCN red list after 20 years. More specifically, in predation scenarios 2 and 7, the population size continuously decreased over time and was reduced by 70 % after 10 years of predation occurring. This would classify the population as ‘endangered’ already after 10 years, as it meets the criterium of a population decrease of at least 50 % during the past 10 years or three generations (IUCN, 2022).

Similarly, when running scenario 4 ( $p = 0.21$ ) with a dynamic effect (Scenario 9-10), the emerging population size differed. It took respectively six and 12 years for the population to be reduced to approximately 75 and 50 % of the initial size, and the populations stabilized at these levels for the remaining simulation time (Fig. 13). Hence, when predation only occurred at times when the current population size was above 75 or 50 % of initial size, the population size was noticeably less reduced compared to the non-dynamic predation scenario (Fig. 13). This

was particularly applicable to the 75 % scenario. When the killer whales only occasionally return to the study area, the porpoise population experiences a slight reduction in size before it stabilizes at a lower, but viable level over time. However, it's important to note that this pattern was run to test for the effect of a simple, dynamic pattern and may not truly represent reality. Regardless, they can provide useful insight. With a dynamic site fidelity in the fjord, the killer whales can cover their energetic needs, whilst still maintaining a stable level of harbour porpoise.

This study did not have a sufficiently reliable data to conclude which scenario that most likely represented the reality. Regardless, these findings provide evidence of top-down control in marine systems and are the first step towards comprehending how killer whales have the potential to control marine mammal prey populations in Norwegian waters. The literature on killer whales reducing prey populations substantially provides contradictory findings, and it remains controversial whether predation alone contributed to the observed declines (Mizroch and Rice, 2006, DeMaster et al., 2006, Trites et al., 2007, Kuker and Barrett-Lennard, 2010). Moreover, there is often a lack of evidence on the top-down control mechanism in marine systems (Williams et al., 2004, Baum and Worm, 2009). The harbour porpoises are vulnerable to high bycatch levels in gillnet fisheries in Norwegian waters (Bjørge et al., 2013, Moan et al., 2020), and they are present in particularly high densities in Hardangerfjord. Thus, it is important to understand the effect predation can have, to successfully manage and preserve biodiversity in the fjord. Generally, the presence of marine mammals in aquatic ecosystems can be crucial to the health and functioning of such systems, which is why they are frequently regarded as keystone species and markers of a system's ecological health (Nelms et al., 2021).

#### Suitability of method

As highlighted in the introduction, IBMs allow scientists to model systems with higher flexibility and realism (Goss-Custard and Sutherland, 1997, Grimm et al., 2005, Grimm and Railsback, 2012). They are particularly suitable for studying population dynamics, as they allow one to explicitly study the relationship between an individual's adaptive behaviour and the emergent patterns within a set system (Grimm and Railsback, 2013). Since the IBM presented here is grounded in theoretical ecological principles, like foraging and fitness optimization, it is more reliable in forecasting future outcomes than models heavily dependent on historical data, especially in the face of environmental changes (Goss-Custard and Sutherland, 1997, Stillman and Goss-Custard, 2010, Nabe-Nielsen, 2014).

The porpoise's behavior and interaction with the environment gave rise to emergent patterns in the population that realistically reflected field observations. This included recreating realistic age distributions (Appendix A, Fig. A) (Lockyer and Kinze, 2003), a stable population size without predation (Fig. 9), and a realistic distribution and movement in the fjord. The age structure (Appendix A, Fig. A14) remained stable during the full extent of the simulation time, arguably as the added predation process did not discriminate on age. Additionally, the porpoise's energy level varied in line with the seasonal food levels (Fig. 10), in a similar pattern like the one observed when running the original model. Thus, it is reasonable to propose that the original porpoise IBM developed by Nabe-Nielsen et al. (2014) was transferable to the study area of Hardangerfjord once the parameters had been recalibrated and adjustments to the model had been made.

The predation rate was added as an additional mortality component in this IBM. Consequently, the porpoises could not respond with evasive behaviour in response to the presence of a killer whale predator. However, the predation rates were implemented in the IBM in a monthly pattern, since the killer whales occurred in Hardangerfjord to a different extent every month (Fig. 7). Moreover, the seasonal variation in porpoise energy level created a temporal variation in the emerging porpoise population size over time (Fig. 10). Thus, the model captured the temporal variation in both the predation effect and the residing harbour porpoise population size. These two temporal components interact in the model and can affect the emerging population size over time as predation occurs. This justifies the use of an IBM in this thesis.

#### Causes of death

Multiple factors need to be accounted for when discussing the porpoise mortality component in the model. Firstly, fewer individuals died of low energy once predation was initiated. In the reference scenario (without predation), all individuals died either of low energy, reaching maximum age or being abandoned by their mother (Appendix A, Fig. A15). However, very few died from low energy once predation was initiated and this pattern was more apparent in the higher predation rate scenarios (Appendix A, Fig. A16-A17). 76 and 61 % of the mortality were caused by killer whale predation in the highest and lowest predation scenarios, respectively. The population decreased as individuals were consumed by killer whales, but this also caused food to become more available in the system. Accordingly, the energy level of the remaining porpoises was higher, and fewer risked dying of low energy. This fits the model assumptions that the population size is density-dependent (Nabe-Nielsen et al., 2014). Existing literature

presents similar findings in that mammal populations are mainly under density dependent regulations (Sinclair, 1989, Sibly and Hone, 2002, Begon and Townsend, 2021).

In the model, all porpoise age classes had the same probability of being eaten by killer whales, which might not be realistic for the two killer whale groups in question. Drawing from the background information, the young, sick, or old individuals in a population can be more vulnerable to predation (Errington, 1946, Jefferson et al., 1991, Curio, 2012), and predators are expected to take advantage of this. Prior investigations report evidence of killer whales targeting pinniped pups almost exclusively (Scammon, 1874, Reisinger et al., 2011, Pistorius et al., 2012), and mainly the calves in cetacean populations (Visser et al., 2010, Pitman et al., 2015, Pitman et al., 2017, Capella et al., 2018, Frediani et al., 2020). However, results vary between different regions and populations, and many have been observed preying on adult individuals as well (Jefferson et al., 1991, Ford et al., 2005, Ford and Reeves, 2008, Cure et al., 2013, Ashe et al., 2021). The harbour porpoise is a mammal with ‘fast’ life history strategies, considering their early maturity and short gestation periods (Read and Hohn, 1995, Murphy et al., 2020). Heppell et al. (2000) illustrated how populations of fast-living mammals are particularly vulnerable to offspring survival. Thus, if predation does occur to a higher degree on porpoise calves, the negative, perturbing effects on the population can be underestimated here.

#### Limitations

Hardangerfjord was simulated as a closed system with no migration. This was done for practical reasons, as no data existed on the fjord populations’ genetics nor their degree of exchange with the porpoises along the outer, Western coast. Evidence of higher porpoises acoustic activity during winter season indicate that some migration may occur (Neemela, 2022). Nevertheless, based on current data available, it can be argued that the porpoises within the fjord represent an ecological population with a low exchange rate with outer, coastal areas. Consequently, the porpoises in the model constituted an ecologically distinct population and were thus more vulnerable to going extinct when facing disturbances. A non-zero migration rate would enable additional individuals to enter the population over time and increase the likelihood that some porpoises migrate out of the fjord to escape the killer whales during their stay. Thus, the population decrease might be overestimated in this model if some migration does occur.

The creation of a simulation model where population dynamics are tightly linked to food availability is particularly challenging due to lack of information on food distribution in the fjord. The original model by Nabe-Nielsen et al. (2014) also lacked food distribution data, but



solved this by using satellite-telemetry observations of porpoises in the study area. They assumed that the food level was directly connected to porpoise presence, and thus modeled the food level accordingly. There are significant variations in the seasonal movement patterns for harbour porpoises between geographical locations. The porpoise population in inner Danish was observed to migrate southwards from spring to winter, whilst the ones in Skagerrak migrated westwards into the North Sea during the same time (Sveegaard et al., 2011). No satellite or seasonal migration data existed for the porpoise population in Hardangerfjord, so it was decided on using the same food variability pattern as Nabe-Nielsen et al. (2014) by resampling their maxent estimates with replacement. Even though this resampling approach preserves the variability of the maxent data overall, it does not maintain the spatial correlations of the data. In consequence, the food in the Hardangerfjord landscape appears more random to a porpoise and the memory of past foraging success is less useful to them than in the original model.

Another limitation is the lack of historical data on the porpoise population size before and after 2020. IMR surveyed the porpoise abundance in the summer of 2020, whilst the data series on killer whale presence and predation observations were initiated in 2017 (Norwegian Orca Survey, unpublished data). Accordingly, there is a risk that the population size already experienced a decline prior to 2020. Without any prior - or post-population estimates, any potential porpoise population decrease cannot be accounted for. Such information would have provided field-based evidence of whether the killer whale predation had initiated a negative effect on the porpoises' dynamics after the first seven years. Regardless, with the current wide, porpoise abundance estimate, a reduction would be hard to quantify even with prior data available.

Furthermore, the total DPER of a killer whale group can change over time as the individuals grow, die, or when new calves enter or adults enter/leave the group. Nevertheless, this value was kept constant during the 20-year simulations in the IBM, due to the lack of knowledge on the two killer whale group's genetics, longevity and how their group structure may change over time. Other regions show evidence of the killer whales reaching maximum ages of 50-90 years (Olesiuk et al., 1990). Thus, the energy requirement of the adult, females ( $> 12$ ) in the two groups will remain relatively stable over the 20-year simulation time, but the energy requirement of the total group can change as new individuals are born and grow to adults, or mature males leave.

#### 4.4. FUTURE IMPROVEMENTS AND APPLICATIONS

With evidence of killer whale predation potentially lowering porpoise populations to an extent where they are at risk of going extinct, there are future improvements that can be made to the model to further understand this predator-prey dynamic. The future improvements and applications regarding the killer whale's presence will be described in the following subsection, followed by an elaboration on the predation rates and the IBM.

##### The killer whales' temporal presence

The mark-recapture and photo identification data from 2021-2022 used to estimate the killer whale's presence has a limited data collection period that should be extended in future research. This will give a better image of the killer whale's dynamics, and whether they will continue to enter the fjord in the same temporal pattern observed in 2021-2022 or not. Observational evidence from 2023 (Norwegian Orca Survey, unpublished data), during which time this discussion was written, indicate that killer whales enter the fjord much less frequently compared to 2021 and 2022. They have been observed in other locations along the Western coast of Norway to a higher extent, like in Sognefjord, off Bergen and Stavanger. This supports the theory of an interannual occurrence pattern in Hardangerfjord, indicating a probable variation in their migration behaviour. Such a pattern would result in an interannual pattern in the predation rates over time as well. Alternatively, the killer whale's occurrence may subside over a longer period or for good. The paucity of data available on Norwegian killer whales' migration patterns can be greatly improved by the continued use of citizen science in the future, specifically in Hardangerfjord where land-based detections are high.

The optimal, methodological approach for the acoustic data would be the inclusion of conventional sound recordings of the specific killer whales alongside the CPOD data. This is needed to determine whether they are acoustically active at all, and potentially their characterization. For now, no acoustic data exist for these two killer whale groups. The findings in the CPOD data could be compared to other killer whale groups, but since acoustic activity and dialects can change sufficiently between different killer whale groups, recordings of these two groups specifically would be useful. The sound recordings could be used to validate potential echolocation clicks in the CPOD data that failed to be classified as 'other cetaceans'. Moreover, it would be very interesting to investigate the CPOD data more thoroughly for killer whale whistles, given that they are extracted in a way that aligns with the characteristics in the recordings. However, given the complex nature of killer whale vocalizations and the fact that

CPODs have never been used to investigate killer whales' acoustics before, further investigation is warranted in future studies with more ample time resources.

#### The killer whales' predation rates

The predation rate estimates would be strengthened by improving the region-specific understanding of the harbour porpoises and killer whales in the fjord overall. This would narrow down the wide range of possible predation rates and give a more accurate rate to implement into the IBM. Specifically, additional studies are needed to examine the killer whale's diet as they reside in the fjord (*DPER*, *pDiet*, *pConsumed*, and porpoise energy content). This can be done by sampling dead harbour porpoises and estimating their energy content, analyzing killer whales stomach contents and fecal samples, or use noninvasive methods like stable isotopic analysis. Citizen science and aerial-, boat- or land-based surveys can be used in the Hardangerfjord to obtain valuable information about the killer whales' hunting strategies, prey selection, and energy expenditure. In light of new data on the porpoise's energy content and the killer whales' diet and energy requirements, the rate of predation should be revised accordingly in future applications of this model.

#### The individual-based harbour porpoise model

Now that an energy-dependent IBM for the porpoise population in Hardangerfjord has been established, the model can be easily extended by adding a variety of disturbances and potentially implementing killer whales as independent agents. As individual agents, the killer whales would be their own individuals in the model, with specific movements, age structure, and fertility parameters. However, more knowledge on the two killer whale groups' behaviour and movement is needed to progress with this. This extension would make it possible for the porpoises to alter their behaviour in response to killer whale presence, and the killer whales would have a given predation success rate. It would also enable the killer whale's predation rate to change over time according to the group's change in energy demand as individuals get older, leave, or die.

There are several additional threats against the harbour porpoise population that has not been considered in this thesis, and which should be covered in the model in future studies. Other, probable threats the porpoise populations face globally include ship traffic, substance- and noise pollution, fisheries bycatch, climate change, and maritime development (Davidson et al., 2012, Nelms et al., 2021). Even though bottom-set gillnet fisheries remain sparse in Hardangerfjord (Bjørge, pers. comm), the population in Hardangerfjord can be at risk of predation and other

threats. Diseases and parasite loads can generate stochastic mortality fluctuations in the porpoise population. None of these factors were included in the model and could've potentially affected the porpoise population dynamics and increased the likelihood of the population going extinct. Nabe-Nielsen et al. (2014) found evidence of multiple disturbances having an additive effect on the relative population size, and hence it would be anticipated that adding other forms of disturbance to the model will further lower the population size.

It would be of particularly high interest to model the effect of ship traffic with its accompanied noise on the porpoise's population dynamics. Hardangerfjord has a remarkable geographical formation with its narrow and deep structure, making it particularly vulnerable as noise may transmit more intensely back and forth between underwater cliff faces. Such intense noise disturbance can negatively affect the porpoise's foraging abilities and migration patterns, as they rely on echolocation for these activities (Manzetti and Stenersen, 2010, Institute of Marine Research, 2010). There is daily ship traffic from ferry routes, ships related to the aquaculture industry, large cruise ships, and an unknown amount of private boats (Manzetti and Stenersen, 2010). Studies have shown that the low-level noises from boats can reach porpoises up to 1000 m away and cause behavioural responses (Dyndo et al., 2015). However, Nabe-Nielsen et al. (2014) found that ships did not impact the long-term population size of porpoise in Inner Danish waters. Thus, information on the fjords ship traffic should be added to the current IBM in the future to investigate whether the same conclusions can be drawn here.

Moreover, it would be of most importance to further investigate the abundance of the porpoises' prey species, and how it varies seasonally. With empirical evidence of its distribution, a maxent model fit for Hardangerfjord could be used to predict a realistic food distribution. This would make the model more suitable for Hardangerfjord and give a realistic image of the mechanisms that govern porpoise population dynamics in the fjord. The prey abundance estimates could be investigated with trawl surveys. The porpoise abundance should also be further investigated. This can be done by putting satellite trackers on porpoise individuals or by conducting abundance surveys over a longer period, and preferably four times annually to account for seasonal variations. This could provide further insight into the possibilities of porpoises conducting seasonal migrations in and out of the fjord. The satellite tracking could also provide information on whether the porpoise movement used in the model aligns with the porpoise's movement in Hardangerfjord. Overall, porpoise abundance estimates would allow for investigations into how the porpoise population is affected as predation occurs over time and can give a more realistic predation rate estimate that can be implemented in the model.

## 5 CONCLUSIONS

This study aimed to quantify the presence of killer whales in Hardangerfjord and investigate the population-level impact of their predation on the harbour porpoise population. The use of citizen science was a successful method to quantify the killer whale's presence in the fjord, but the same cannot be said for the acoustic data. The citizen science approach indicates that the killer whales have been present in the fjord in an intermittent pattern since 2017. Data from 2021 and 2022 gave an estimated presence value of 30 days annually. However, more research is needed to determine whether their occurrence is a new phenomenon. Evidence put forward confirms that the killer whales do predate on harbour porpoises, and it can be argued that prey availability is a main driver for their movement. The combined use of bioenergetics and predator presence estimates was a sufficient method for estimating the killer whales' predation rate. Ten predation rate scenarios were investigated in the IBM, where the parameters  $pDiet$ ,  $pConsumed$ , and porpoise population size varied.

The use of an IBM made it possible to explore the harbour porpoise population trajectories under a number of scenarios, such as different killer whale predation rates. Nevertheless, the results presented here are first and foremost simulation-based and theoretical, and only realistic insofar as the underlying assumptions are reasonable. The results from the IBM indicate that killer whale predation has the potential, based on energetic arguments, to negatively affect the porpoise population size to an extent where they are at risk of going extinct. The different scenarios investigated had big implications for the population size after predation occurred over 20 years, where the population decreased by 5 % compared to 90 % in the lowest and highest predation scenario, respectively. Overall, the IBM succeeded at recreating natural porpoise movements within the fjord, a density-dependent regulation of the population, and in connecting mortality to energy level.

However, it is important to note that this is a pilot study, and there are multiple uncertainties related to the parameters used in the methods. The approach is sufficient to address the various hypotheses, but the conclusions derived from these results are weakened by uncertainties in the predation rate – and IBM parameters. To better understand the implication of these results, extensive knowledge is needed on the predator-prey dynamics, and particularly the predators' and prey's population size and diets. Thus, further research is needed to determine whether there is a prominent risk of the porpoise population going extinct.

To conclude, this study has presented evidence of the potential top-down effect killer whales can have on marine mammal prey like harbour porpoises with a dense population in a small area. The Hardangerfjord represent a unique study area where large, migratory animals like the killer whales and their predation impact on the porpoise prey population can be studied thoroughly. Dependent on the predation scenarios investigated, the killer whales execute top-down control on the porpoise population size by lowering the carrying capacity or bringing them close to extinction. Overall, this thesis illustrates how the use of predictive, spatially explicit models like IBMs, can be beneficial in enhancing population management in marine ecosystems in the future.

## REFERENCES

Using Endnote, Harvard Style.

- AEBISCHER, N. J., COULSON, J. & COLEBROOK, J. 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature*, 347, 753-755.
- ALAVA, J. J., SMITH, K. J., O'HERN, J., ALARCÓN, D., MERLEN, G. & DENKINGER, J. 2013. Observations of killer whale (*Orcinus orca*) attacks on Bryde's whales (*Balaenoptera edeni*) in the Galapagos Islands. *Aquatic Mammals*, 39, 196.
- ANDRACHUK, M., MARSCHKE, M., HINGS, C. & ARMITAGE, D. 2019. Smartphone technologies supporting community-based environmental monitoring and implementation: a systematic scoping review. *Biological Conservation*, 237, 430-442.
- ASHE, E., WILLIAMS, R., MORTON, A. & HAMMOND, P. S. 2021. Disentangling Natural and Anthropogenic Forms of Mortality and Serious Injury in a Poorly Studied Pelagic Dolphin. *Frontiers in Marine Science*, 8.
- AU, W. W. 1993. *The sonar of dolphins*, New York, Springer-Verlag New York.
- AU, W. W., FORD, J. K. B., HORNE, J. K. & NEWMAN ALLMAN, K. A. 2004. Echolocation signals of free-ranging killer whales (*Orcinus orca*) and modeling of foraging for chinook salmon (*Oncorhynchus tshawytscha*). *The Journal of the Acoustical Society of America*, 115, 901-909.
- BAIRD, R. W., ABRAMS, P. A. & DILL, L. M. 1992. Possible indirect interactions between transient and resident killer whales: implications for the evolution of foraging specializations in the genus *Orcinus*. *Oecologia*, 89, 125-132.
- BAIRD, R. W. & DILL, L. M. 1996. Ecological and social determinants of group size in transient killer whales. *Behavioral Ecology*, 7, 408-416.
- BARRETT-LENNARD, L. G., FORD, J. K. & HEISE, K. A. 1996. The mixed blessing of echolocation: differences in sonar use by fish-eating and mammal-eating killer whales. *Animal behaviour*, 51, 553-565.
- BAUM, J. K. & WORM, B. 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, 78, 699-714.
- BEAUCHAMP, D. A., WAHL, D. & JOHNSON, B. M. 2007. Predator-prey interactions. In: GUY, C. S. & BROWN, M. L. (eds.) *Analysis and interpretation of freshwater fisheries data*. Bethesda, Maryland: American Fisheries Society.
- BEGON, M. & TOWNSEND, C. R. 2021. *Ecology: from individuals to ecosystems*, John Wiley & Sons.
- BIGG, M. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Report of the International Whaling Commission*, 32, 655-666.
- BJØRGE, A. 2003. The Harbour Porpoise (*Phocoena phocoena*) in the North Atlantic: Variability in habitat use, trophic ecology and contaminant exposure. *NAMMCO Scientific Publications*, 5, 223-228.

- BJØRGE, A., SKERN-MAURITZEN, M. & ROSSMAN, M. C. 2013. Estimated bycatch of harbour porpoise (*Phocoena phocoena*) in two coastal gillnet fisheries in Norway, 2006–2008. Mitigation and implications for conservation. *Biological Conservation*, 161, 164-173.
- BJØRGE, A. & TOLLEY, K. A. 2009. Harbor Porpoise: *Phocoena phocoena*. In: PERRIN, W. F., WÜRSIG, B. & THEWISSEN, J. G. M. (eds.) *Encyclopedia of Marine Mammals (Second Edition)*. London: Academic Press.
- BJØRGE, A., ØIEN, N. & KÖNINGSON, S. 2019. Do the harbour porpoises have permanent residency in Norwegian fjords? Project proposal. *Institute of Marine Research*.
- BJØRGE, A., AAREFJORD, H., KAARSTAD, S., KLEIVANE, L. & ØIEN, N. Harbor porpoise (*Phocoena phocoena*) in Norwegian waters. 1991. International Council for the Exploration of the Sea.
- BOLT, H. E., HARVEY, P. V., MANDLEBERG, L. & FOOTE, A. D. 2009. Occurrence of killer whales in Scottish inshore waters: temporal and spatial patterns relative to the distribution of declining harbour seal populations. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 19, 671-675.
- BOYLES, J. G. & BRACK, V., JR. 2009. Modeling Survival Rates of Hibernating Mammals with Individual-Based Models of Energy Expenditure. *Journal of Mammalogy*, 90, 9-16.
- BRAULT, S. & CASWELL, H. 1993. Pod-Specific Demography of Killer Whales (*Orcinus Orca*). *Ecology*, 74, 1444-1454.
- BROOKS, J. L. & DODSON, S. I. 1965. Predation, Body Size, and Composition of Plankton: The effect of a marine planktivore on lake plankton illustrates theory of size, competition, and predation. *Science*, 150, 28-35.
- CAPELLA, J. J., FELIX, F., FLOREZ-GONZALEZ, L., GIBBONS, J., HAASE, B. & GUZMAN, H. M. 2018. Geographic and temporal patterns of non-lethal attacks on humpback whales by killer whales in the eastern South Pacific and the Antarctic Peninsula. *Endangered Species Research*, 37, 207-218.
- CARPENTER, S. R., KITCHELL, J. F. & HODGSON, J. R. 1985. Cascading trophic interactions and lake productivity. *BioScience*, 35, 634-639.
- CARWARDINE, M. 2019. *Handbook of whales, dolphins and porpoises*, London, Bloomsbury Publishing.
- CASEY, J. M., BAIRD, A. H., BRANDL, S. J., HOOGENBOOM, M. O., RIZZARI, J. R., FRISCH, A. J., MIRBACH, C. E. & CONNOLLY, S. R. 2017. A test of trophic cascade theory: fish and benthic assemblages across a predator density gradient on coral reefs. *Oecologia*, 183, 161-175.
- CHLEONIA LIMITED. 2016. *Chleonia Limited - Wildlife Acoustic Monitoring* [Online]. Available: [www.chelonia.co.uk](http://www.chelonia.co.uk) [Accessed 17.04.2023].
- COSENTINO, A. M. 2015. First record of Norwegian killer whales attacking and feeding on a harbour porpoise. *Marine Biodiversity Records*, 8.
- COSENTINO, M., GUARATO, F., TOUGAARD, J., NAIRN, D., JACKSON, J. C. & WINDMILL, J. F. C. 2019. Porpoise click classifier (PorCC): A high-accuracy classifier to study harbour porpoises



- (*Phocoena phocoena*) in the wild. *The Journal of the Acoustical Society of America*, 145, 3427-3434.
- CURE, C., ANTUNES, R., ALVES, A. C., VISSER, F., KVADSHEIM, P. H. & MILLER, P. J. O. 2013. Responses of male sperm whales (*Physeter macrocephalus*) to killer whale sounds: implications for anti-predator strategies. *Scientific Reports*, 3, 1579.
- CURIO, E. 2012. *The ethology of predation*, Springer Science & Business Media.
- CUSHING, D. H. 1975. *Marine ecology and fisheries*, Oxford, Cambridge University Press.
- DAHLHEIM, M. E. & MATKIN, C. O. 1994. Assessment of injuries to Prince William Sound killer whales. *Marine mammals and the Exxon Valdez*, 163-171.
- DALHEIM, M., SCHULMAN-JANIGER, A., BLACK, N., TERNULLO, R., ELLIFRIT, D. & BALCOMB III, K. 2008. Eastern temperate North Pacific offshore killer whales (*Orcinus orca*): occurrence, movements, and insights into feeding ecology. *Marine mammal science* 24(3): 719–729 24, 719-729.
- DARWIN, C. 2004. *On the origin of species, 1859*, London, John Murray.
- DAVIDSON, A. D., BOYER, A. G., KIM, H., POMPA-MANSILLA, S., HAMILTON, M. J., COSTA, D. P., CEBALLOS, G. & BROWN, J. H. 2012. Drivers and hotspots of extinction risk in marine mammals. *Proceedings of the National Academy of Sciences*, 109, 3395-3400.
- DAVIS, R., FUJIMAN, L., WILLIAMS, T., COLLIER, S., HAGEY, W., KANATOUS, S., KOHIN, S. & HORNING, M. 1999. Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science*, 283, 993-996.
- DAWKINS, R. & KREBS, J. R. 1979. Arms races between and within species. *Proceedings of the Royal Society B, Biological Sciences*, 205, 489-511.
- DE BRUYN, P. N., TOSH, C. A. & TERAUDS, A. 2013. Killer whale ecotypes: is there a global model? *Biological Reviews*, 88, 62-80.
- DEECKE, V. B., FORD, J. K. & SLATER, P. J. 2005. The vocal behaviour of mammal-eating killer whales: communicating with costly calls. *Animal Behaviour*, 69, 395-405.
- DEECKE, V. B., NYKÄNEN, M., FOOTE, A. D. & JANIK, V. M. 2011. Vocal behaviour and feeding ecology of killer whales *Orcinus orca* around Shetland, UK. *Aquatic Biology*, 13, 79-88.
- DEECKE, V. B., SLATER, P. J. & FORD, J. K. 2002. Selective habituation shapes acoustic predator recognition in harbour seals. *Nature*, 420, 171-173.
- DEMASTER, D. P., TRITES, A. W., CLAPHAM, P., MIZROCH, S., WADE, P., SMALL, R. J. & VERHOEF, J. 2006. The sequential megafaunal collapse hypothesis: testing with existing data. *Progress in Oceanography*, 68, 329-342.
- DENNY, M. 2008. *How the Ocean Works: An Introduction to Oceanography*, Princeton University Press.
- DYNDO, M., WIŚNIEWSKA, D. M., ROJANO-DOÑATE, L. & MADSEN, P. T. 2015. Harbour porpoises react to low levels of high frequency vessel noise. *Scientific reports*, 5.

- EDRÉN, S. M. C., WISZ, M. S., TEILMANN, J., DIETZ, R. & SÖDERKVIST, J. 2010. Modelling spatial patterns in harbour porpoise satellite telemetry data using maximum entropy. *Ecography*, 33, 698-708.
- EMODNET. 2020. *EMODnet High Resolution Seabed Mapping project II* [Online]. [Accessed 28.04.2023].
- ERRINGTON, P. L. 1946. Predation and Vertebrate Populations. *The Quarterly Review of Biology*, 21, 144-177.
- ESTES, J., DOAK, D., SPRINGER, A. & WILLIAMS, T. 2009. Causes and consequences of marine mammal population declines in southwest Alaska: a food-web perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1647-1658.
- ESTES, J. A. & DUGGINS, D. O. 1995. Sea Otters and Kelp Forests in Alaska: Generality and Variation in a Community Ecological Paradigm. *Ecological Monographs*, 65, 75-100.
- ESTES, J. A., TINKER, M. T., WILLIAMS, T. M. & DOAK, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science*, 282, 473-476.
- FERGUSON, S. H., HIGDON, J. W. & WESTDAL, K. H. 2012. Prey items and predation behavior of killer whales (*Orcinus orca*) in Nunavut, Canada based on Inuit hunter interviews. *Aquatic Biosystems*, 8, 1-16.
- FILATOVA, O. A., FEDUTIN, I. D., BURDIN, A. M. & HOYT, E. 2007. The structure of the discrete call repertoire of killer whales *Orcinus orca* from Southeast Kamchatka *Bioacoustics*, 16, 261-280.
- FONTAINE, M. C., BAIRD, S. J., PIRY, S., RAY, N., TOLLEY, K. A., DUKE, S., BIRKUN, A., FERREIRA, M., JAUNIAUX, T. & LLAVONA, A. 2007. Rise of oceanographic barriers in continuous populations of a cetacean: the genetic structure of harbour porpoises in Old World waters. *BMC biology*, 5, 1-16.
- FOOTE, A. D., NEWTON, J., PIERTNEY, S. B., WILLERSLEV, E. & GILBERT, M. T. P. 2009. Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. *Molecular Ecology*, 18, 5207-5217.
- FORD, J. K. 1989. Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *Canadian Journal of Zoology*, 67, 727-745.
- FORD, J. K. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Canadian journal of zoology*, 69, 1454-1483.
- FORD, J. K. 2009. Killer whale: *Orcinus orca*. *Encyclopedia of marine mammals*. Elsevier.
- FORD, J. K., ELLIS, G. M., BARRETT-LENNARD, L. G., MORTON, A. B., PALM, R. S. & BALCOMB III, K. C. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology*, 76, 1456-1471.
- FORD, J. K. B., ELLIS, G. A., MATKIN, D. R., BALCOMB, K. C., BRIGGS, D. & MORTON, A. B. 2005. Killer whale attacks on minke whales: Prey capture and antipredator tactics. *Marine Mammal Science*, 21, 603-618.

- FORD, J. K. B. & REEVES, R. R. 2008. Fight or flight: antipredator strategies of baleen whales. *Mammal Review*, 38, 50-86.
- FORNEY, K. A., WADE, P. R. & ESTES, J. 2006. Worldwide distribution and abundance of killer whales. *Whales, whaling and ocean ecosystems*. Berkeley, CA: University of California Press.
- FREDIANI, J. G., BLACK, N. A. & SHARPE, F. 2020. Postmortem Attractions: Humpback Whales Investigate the Carcass of a Killer Whale-Depredated Gray Whale Calf. *Aquatic Mammals*, 46, 402-410.
- GARCIA-SOTO, C., SEYS, J. J., ZIELINSKI, O., BUSCH, J. A., LUNA, S., BAEZ, J. C., DOMEGAN, C., DUBSKY, K., KOTYNSKA-ZIELINSKA, I. & LOUBAT, P. 2021. Marine citizen science: Current state in Europe and new technological developments. *Frontiers in Marine Science*, 241.
- GENOVART, M., NEGRE, N., TAVECCHIA, G., BISTUER, A., PARPAL, L. & ORO, D. 2010. The young, the weak and the sick: evidence of natural selection by predation. *PLoS One*, 5, e9774.
- GOETZ, S., READ, F. L., FERREIRA, M., PORTELA, J. M., SANTOS, M. B., VINGADA, J., SIEBERT, U., MARÇALO, A., SANTOS, J. & ARAÚJO, H. 2015. Cetacean occurrence, habitat preferences and potential for cetacean–fishery interactions in Iberian Atlantic waters: results from cooperative research involving local stakeholders. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 25, 138-154.
- GOSS-CUSTARD, J. D. & SUTHERLAND, W. J. 1997. Individual behaviour, populations and conservation. *Behavioural ecology: an evolutionary approach*, 4, 373-395.
- GRIMM, V., BERGER, U., DEANGELIS, D. L., POLHILL, J. G., GISKE, J. & RAILSBACK, S. F. 2010. The ODD protocol: a review and first update. *Ecological modelling*, 221, 2760-2768.
- GRIMM, V. & RAILSBACK, S. F. 2012. Pattern-oriented modelling: a ‘multi-scope’ for predictive systems ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 298-310.
- GRIMM, V. & RAILSBACK, S. F. 2013. Individual-based modeling and ecology. *Individual-Based Modeling and Ecology*. Princeton university press.
- GRIMM, V., REVILLA, E., BERGER, U., JELTSCH, F., MOOIJ, W. M., RAILSBACK, S. F., THULKE, H.-H., WEINER, J., WIEGAND, T. & DEANGELIS, D. L. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science*, 310, 987-991.
- HALL, A. J., MCCONNELL, B. J., ROWLES, T. K., AGUILAR, A., BORRELL, A., SCHWACKE, L., REIJNDERS, P. J. H. & WELLS, R. S. 2006. Individual-based model framework to assess population consequences of polychlorinated biphenyl exposure in bottlenose dolphins. *Environmental health perspectives*, 114 Suppl 1, 60-64.
- HAMMOND, P. S., BERGGREN, P., BENKE, H., BORCHERS, D. L., COLLET, A., HEIDE-JØRGENSEN, M. P., HEIMLICH, S., HIBY, A. R., LEOPOLD, M. F. & ØIEN, N. 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *Journal of Applied Ecology*, 39, 361-376.
- HEISE, K., BARRETT-LENNARD, L. G., SAULITIS, E., MATKIN, C. & BAIN, D. 2003. Examining the evidence for killer whale predation on Steller sea lions in British Columbia and Alaska. *Aquatic Mammals*, 29, 325-334.

- HEPPELL, S. S., CASWELL, H. & CROWDER, L. B. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data *Ecology*, 81, 654-665.
- HERMAN, D., BURROWS, D., WADE, P., DURBAN, J., MATKIN, C., LEDUC, R., BARRETT-LENNARD, L. & KRAHN, M. M. 2005. Feeding ecology of eastern North Pacific killer whales *Orcinus orca* from fatty acid, stable isotope, and organochlorine analyses of blubber biopsies. *Marine Ecology Progress Series*, 302, 275-291.
- HIJMANS, R. J. 2021. *Raster: Geographic Data Analysis and Modeling, R package version* [Online]. Available: <https://cran.r-project.org/web/packages/raster/index.html> [Accessed 20.04.23].
- IAMMWG, C. C. & SIEMENSMA, M. 2015. A Conservation Literature Review for the Harbour Porpoise (*Phocoena phocoena*). *JNCC Report*.
- IMR & NAMMCO 2019. Report of the joint IMR/NAMMCO international workshop on the status of harbour porpoises in the North Atlantic. *Tromsø, Norway*, 236.
- INNES, S., LAVIGNE, D., EARLE, W. & KOVACS, K. 1987. Feeding rates of seals and whales. *The Journal of Animal Ecology*, 115-130.
- INSTITUTE OF MARINE RESEARCH. 2010. *Havforskningsrapporten 2010* [Online]. hi.no: Havforskningsinstituttet. Available: <https://www.hi.no/resources/Arsrapport-2010.pdf> [Accessed 18.03.2023].
- IUCN 2022. Red List Criteria Summary Sheet. Version 2022-2.
- JEFFERSON, T. A., STACEY, P. J. & BAIRD, R. W. 1991. A review of killer whale interactions with other marine mammals: predation to co-existence. *Mammal review*, 21, 151-180.
- JENNINGS, S. & KAISER, M. J. 1998. The effects of fishing on marine ecosystems. *Advances in marine biology*. Elsevier.
- JOURDAIN, E. 2020. *Dietary variations and specializations of killer whales (Orcinus orca) in Norway*. University of Oslo.
- JOURDAIN, E., ANDVIK, C., KAROLIUSSEN, R., RUUS, A., VONGRAVEN, D. & BORGÅ, K. 2020. Isotopic niche differs between seal and fish-eating killer whales (*Orcinus orca*) in northern Norway. *Ecology and Evolution*, 10, 4115-4127.
- JOURDAIN, E., GOH, T., KUNINGAS, S., SIMILÄ, T., VONGRAVEN, D., KAROLIUSSEN, R., BISTHER, A. & HAMMOND, P. S. 2021. Killer whale (*Orcinus orca*) population dynamics in response to a period of rapid ecosystem change in the eastern North Atlantic. *Ecology and Evolution*, 11, 17289-17306.
- JOURDAIN, E. & KAROLIUSSEN, R. 2021. Photo-Identification Catalogue of Norwegian killer whales 2007-2021. Figshare.
- JOURDAIN, E., VONGRAVEN, D., BISTHER, A. & KAROLIUSSEN, R. 2017. First longitudinal study of seal-feeding killer whales (*Orcinus orca*) in Norwegian coastal waters. *PLoS One*, 12, e0180099.
- JOURDAIN, E., AASEN, V. B., ERDAL, O. V. & JOHNSEN, S. 2022. Identification Catalogue of the Killer whales that frequent inner Vestlandet. Figshare.

- JULIANO, S. A. 2007. Population dynamics. *Journal of the American Mosquito Control Association*, 23, 265.
- JØRGENSEN, S. E. & FATH, B. D. 2011. 9 - Individual-Based Models. In: JØRGENSEN, S. E. & FATH, B. D. (eds.) *Developments in Environmental Modelling*. Elsevier.
- KANWISHER, J. 1965. Physiology of a small cetacean. *Hvalradets Skrifter*, 48, 45.
- KITCHELL, J. F., STEWART, D. J. & WEININGER, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Board of Canada*, 34, 1922-1935.
- KLEIBER, M. 1975. *The fire of life: An introduction to animal energetics*. Robert E, New York: London, John Wiley & Sons, Inc.
- KOONS, D. N., ILES, D. T., SCHAUB, M. & CASWELL, H. 2016. A life-history perspective on the demographic drivers of structured population dynamics in changing environments. *Ecology letters*, 19, 1023-1031.
- KRAHN, M. M., WADE, P. R., KALINOWSKI, S. T., DAHLHEIM, M. E., TAYLOR, B. L., HANSON, M. B., YLITALO, G. M., ANGLISS, R. P., STEIN, J. E. & WAPLES, R. S. 2002. Status review of southern resident killer whales (*Orcinus orca*) under the Endangered Species Act.
- KRIETE, B. 1994. *Bioenergetics in the killer whale, Orcinus orca*. PhD, University of British Columbia.
- KUKER, K. & BARRETT-LENNARD, L. 2010. A re-evaluation of the role of killer whales *Orcinus orca* in a population decline of sea otters *Enhydra lutris* in the Aleutian Islands and a review of alternative hypotheses. *Mammal Review*, 40, 103-124.
- LEARMONTH, J. A., MURPHY, S., LUQUE, P. L., REID, R. J., PATTERSON, I. A. P., BROWNLOW, A., ROSS, H. M., BARLEY, J. P., BEGONA SANTOS, M. & PIERCE, G. J. 2014. Life history of harbor porpoises (*Phocoena phocoena*) in Scottish (UK) waters. *Marine Mammal Science*, 30, 1427-1455.
- LEFORT, K. J., GARROWAY, C. J. & FERGUSON, S. H. 2020. Killer whale abundance and predicted narwhal consumption in the Canadian Arctic. *Global Change Biology*, 26, 4276-4283.
- LEONARD, D. M. & ØIEN, N. I. 2020. Estimated abundances of cetacean species in the Northeast Atlantic from two multiyear surveys conducted by Norwegian vessels between 2002-2013. *NAMMCO Scientific Publications*, 11.
- LETNIC, M., RITCHIE, E. G. & DICKMAN, C. R. 2012. Top predators as biodiversity regulators: the dingo *Canis lupus dingo* as a case study. *Biological Reviews*, 87, 390-413.
- LINK, J. 2002. Does food web theory work for marine ecosystems? *Marine ecology progress series*, 230, 1-9.
- LOCKYER, C. 1996. Investigation of aspects of the life history of the harbour porpoise, *Phocoena phocoena*, in British waters. *Oceanographic Literature Review*, 10, 1041.
- LOCKYER, C. 2003. Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: Biological parameters. *NAMMCO Scientific Publications*, 5, 71-89.

- LOCKYER, C. & KINZE, C. 2003. Status, ecology and life history of harbour porpoise (*Phocoena phocoena*), in Danish waters. *NAMMCO Scientific Publications*, 5, 143-175.
- MANZETTI, S. & STENERSEN, J. H. V. 2010. A critical view of the environmental condition of the Sognefjord. *Marine pollution bulletin*, 60, 2167-2174.
- MATIKA, A. F., JOURDAIN, E., CADE, D. E., KAROLIUSSEN, R. & HAMMOND, P. S. 2022. Feeding characteristics and prey profitability in five herring-feeding killer whales (*Orcinus orca*) in northern Norway. *Marine Mammal Science*, 38, 1409-1424.
- MILLER, L. & WAHLBERG, M. 2013. Echolocation by the harbour porpoise: life in coastal waters. *Frontiers in Physiology*, 4, 1-6.
- MIZROCH, S. A. & RICE, D. W. 2006. Have North Pacific killer whales switched prey species in response to depletion of the great whale populations? *Marine Ecology Progress Series*, 310, 235-246.
- MOAN, A., SKERN-MAURITZEN, M., VØLSTAD, J. H. & BJØRGE, A. 2020. Assessing the impact of fisheries-related mortality of harbour porpoise (*Phocoena phocoena*) caused by incidental bycatch in the dynamic Norwegian gillnet fisheries. *ICES Journal of Marine Science*, 77, 3039-3049.
- MURPHY, S., PETITGUYOT, M. A. C., JEPSON, P. D., DEAVILLE, R., LOCKYER, C., BARNETT, J., PERKINS, M., PENROSE, R., DAVISON, N. J. & MINTO, C. 2020. Spatio-Temporal Variability of Harbor Porpoise Life History Parameters in the North-East Atlantic. *Frontiers in Marine Science*, 7.
- MØHL, B. & ANDERSEN, S. 1973. Echolocation: high-frequency component in the click of the Harbour Porpoise (*Phocoena phocoena*). *The Journal of the Acoustical Society of America*, 54, 1368-1372.
- NABE-NIELSEN, J., SIBLY, R. M., TOUGAARD, J., TEILMANN, J. & SVEEGAARD, S. 2014. Effects of noise and by-catch on a Danish harbour porpoise population. *Ecological Modelling*, 272, 242-251.
- NABE-NIELSEN, J., TOUGAARD, J., TEILMANN, J., LUCKE, K. & FORCHHAMMER, M. C. 2013. How a simple adaptive foraging strategy can lead to emergent home ranges and increased food intake. *Oikos*, 122, 1307-1316.
- NABE-NIELSEN, J., VAN BEEST, F. M., GRIMM, V., SIBLY, R. M., TEILMANN, J. & THOMPSON, P. M. 2018. Predicting the impacts of anthropogenic disturbances on marine populations. *Conservation Letters*, 11, e12563.
- NABE-NIELSEN, J. S., R M. TOUGAARD, J. TEILMANN, J. SVEEGAARD, S. 2014. Effects of noise and by-catch on a Danish harbour porpoise population – Appendix A.
- NATHAN, R., GETZ, W. M., REVILLA, E., HOLYOAK, M., KADMON, R., SALTZ, D. & SMOUSE, P. E. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, 105, 19052-19059.
- NEEMELA, M. 2022. *Seasonal and diel patterns of harbour porpoise (Phocoena phocoena) activity in Hardangerfjord, Norway* Master thesis, University of Tartu.

- NELMS, S. E., ALFARO-SHIGUETO, J., ARNOULD, J. P., AVILA, I. C., NASH, S. B., CAMPBELL, E., CARTER, M. I., COLLINS, T., CURREY, R. J. & DOMIT, C. 2021. Marine mammal conservation: over the horizon. *Endangered Species Research*, 44, 291-325.
- NICHOL, L. M. & SHACKLETON, D. M. 1996. Seasonal movements and foraging behaviour of northern resident killer whales (*Orcinus orca*) in relation to the inshore distribution of salmon (*Oncorhynchus* spp.) in British Columbia. *Canadian Journal of Zoology*, 74, 983-991.
- NOREN, D. P. 2011. Estimated field metabolic rates and prey requirements of resident killer whales. *Marine Mammal Science*, 27, 60-77.
- NOREN, D. P. & HAUSER, D. D. 2016. Surface-based observations can be used to assess behavior and fine-scale habitat use by an endangered killer whale (*Orcinus orca*) population. *Aquatic Mammals*, 42, 168-183.
- NOREN, S. R. & EDWARDS, E. F. 2007. Physiological and behavioral development in delphinid calves: Implications for calf separation and mortality due to tuna purse-seine sets. *Marine Mammal Science*, 23, 15-29.
- NORWEGIAN ORCA SURVEY. 2021. *Norwegian Orca ID* [Online]. Norwegianorca-id.no. Available: <https://www.norwegianorca-id.no/> [Accessed 11.12.2022].
- NØTTESTAD, L., SIVLE, L. D., KRAFFT, B. A., LANGÅRD, L., ANTHONYPILLAI, V., BERNASCONI, M., LANGØY, H. & FERNÖ, A. 2014. Prey selection of offshore killer whales *Orcinus orca* in the Northeast Atlantic in late summer: spatial associations with mackerel. *Marine Ecology Progress Series*, 499, 275-283.
- OLESIUK, P. F., BIGG, M. A. & ELLIS, G. M. 1990. Life history and population dynamics of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission, Special*, 12, 209-243.
- PEBESMA E 2018 Simple Features for R: Standardized Support for Spatial Vector Data *The R Journal*, 10(1), 439–446.
- PEREZ, M. A., MCALISTER, W. B. & MOONEY, E. E. 1990. Estimated feeding rate relationship for marine mammals based on captive animal data. *NOAA technical memorandum NMFS F/NWC ; 184* 30.
- PISTORIUS, P. A., MEYER, M. A., REISINGER, R. R. & KIRKMAN, S. P. 2012. Killer whale predation on subantarctic fur seals at Prince Edward Island, Southern Indian Ocean. *Polar Biology*, 35, 1767-1772.
- PITMAN, R. L., DEECKE, V. B., GABRIELE, C. M., SRINIVASAN, M., BLACK, N., DENKINGER, J., DURBAN, J. W., MATHEWS, E. A., MATKIN, D. R., NEILSON, J. L., SCHULMAN-JANIGER, A., SHEARWATER, D., STAP, P. & TERNULLO, R. 2017. Humpback whales interfering when mammal-eating killer whales attack other species: Mobbing behavior and interspecific altruism? *Marine Mammal Science*, 33, 7-58.
- PITMAN, R. L., TOTTERDELL, J. A., FEARNBACH, H., BALLANCE, L. T., DURBAN, J. W. & KEMPS, H. 2015. Whale killers: Prevalence and ecological implications of killer whale predation on humpback whale calves off Western Australia. *Marine Mammal Science*, 31, 629-657.

- POWER, M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology*, 73, 733-746.
- QUINTELA, M., BESNIER, F., SELIUSSEN, B., GLOVER, K. A. & LINDSTRØM, U. 2020. Population structure of bycaught harbour porpoise (*Phocoena phocoena*) in Norway. *Marine Biology Research*, 16, 141-147.
- READ, A. J. 1990. Age at sexual maturity and pregnancy rates of harbour porpoises *Phocoena phocoena* from the Bay of Fundy *Canadian Journal of Fisheries and Aquatic Sciences*, 47, 561-565.
- READ, A. J., DRINKER, P. & NORTHRIDGE, S. 2006. Bycatch of marine mammals in US and global fisheries. *Conservation biology*, 20, 163-169.
- READ, A. J. & HOHN, A. A. 1995. Life in the fast lane: the life history of harbor porpoises from the Gulf of Maine. *Marine Mammal Science*, 11, 423-440.
- REISINGER, R. R., DE BRUYN, P., TOSH, C. A., OOSTHUIZEN, W. C., MUFANADZO, N. T. & BESTER, M. N. 2011. Prey and seasonal abundance of killer whales at sub-Antarctic Marion Island. *African Journal of Marine Science*, 33, 99-105.
- RIESCH, R., BARETT-LENNARD, L. G., ELLIS, G. M., FORD, J. K. B. & DEECKE, V. B. 2012. Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? *Biological Journal of the Linnean Society*, 106, 1-17.
- RIESCH, R., FORD, J. K. & THOMSEN, F. 2006. Stability and group specificity of stereotyped whistles in resident killer whales, *Orcinus orca*, off British Columbia. *Animal Behaviour*, 71, 79-91.
- RIPPLE, W. J. & BESCHTA, R. L. 2012. Trophic cascades in Yellowstone: The first 15 years after wolf reintroduction. *Biological Conservation*, 145, 205-213.
- ROCHE, C., GUINET, C., GASCO, N. & DUHAMEL, G. 2007. Marine mammals and demersal longline fishery interactions in Crozet and Kerguelen Exclusive Economic Zones: an assessment of depredation levels. *CCAMLR Science*, 14, 67-82.
- SAMARRA, F. I. P. & MILLER, P. J. O. 2015. Prey-induced behavioural plasticity of herring-eating killer whales. *Marine Biology*, 162, 809-821.
- SANTOS, M. & PIERCE, G. J. 2003. The diet of harbour porpoise (*Phocoena phocoena*) in the northeast Atlantic: A review. *Oceanography and Marine Biology, An Annual Review, Volume 41*, 363-369.
- SCAMMON, C. M. 1874. *The Marine Mammals of the North Western Coast of North America, described and illustrated together with an Account of the American Whale-Fishery*, J. H. Carmany and Co, San Francisco G. P. Putnam's Son, New York
- SCHINDLER, D. E., ESSINGTON, T. E., KITCHELL, J. F., BOGGS, C. & HILBORN, R. 2002. Sharks and tunas: fisheries impacts on predators with contrasting life histories. *Ecological Applications*, 12, 735-748.
- SCHMITT, W., AUTERI, D., BASTIANSEN, F., EBELING, M., LIU, C., LUTTIK, R., MASTITSKY, S., NACCI, D., TOPPING, C. & WANG, M. 2016. An example of population-level risk assessments for small



- mammals using individual-based population models. *Integrated Environmental Assessment and Management*, 12, 46-57.
- SCHMITZ, O. J. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. *Ecology Letters*, 6, 156-163.
- SIBLY, R. M. & HONE, J. 2002. Population growth rate and its determinants: an overview. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 357, 1153-1170.
- SIMILÄ, T., HOLST, J. C. & CHRISTENSEN 1996. Occurrence and diet of killer whales in northern Norway: seasonal patterns relative to the distribution and abundance of Norwegian spring-spawning herring. *Canadian Journal of Fisheries and Aquatic Sciences*, 53, 769-779.
- SIMON, M., MCGREGOR, P. K. & UGARTE, F. 2007a. The relationship between the acoustic behaviour and surface activity of killer whales (*Orcinus orca*) that feed on herring (*Clupea harengus*). *Acta ethologica*, 10, 47-53.
- SIMON, M., WAHLBERG, M. & MILLER, L. A. 2007b. Echolocation clicks from killer whales (*Orcinus orca*) feeding on herring (*Clupea harengus*). *The Journal of the Acoustical Society of America*, 121, 749-752.
- SINCLAIR, A. 1989. Population regulation of animals. *Ecological concepts*, 197-241.
- SPRINGER, A. M., ESTES, J. A., VAN VLIET, G. B., WILLIAMS, T. M., DOAK, D. F., DANNER, E. M., FORNEY, K. A. & PFISTER, B. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences*, 100, 12223-12228.
- SRINIVASAN, M., SWANNACK, T. M., GRANT, W. E., RAJAN, J. & WÜRSIG, B. 2018. To feed or not to feed? Bioenergetic impacts of fear-driven behaviors in lactating dolphins. *Ecology and Evolution*, 8, 1384-1398.
- STEELE, J. H. 1998. From carbon flux to regime shift. *Fisheries Oceanography*, 7, 176-181.
- STEVENS, A. N. 2012. Predation, herbivory, and parasitism. *Nature Education Knowledge*, 3, 36.
- STILLMAN, R. A. & GOSS-CUSTARD, J. D. 2010. Individual-based ecology of coastal birds. *Biological Reviews*, 85, 413-434.
- SVEEGAARD, S., TEILMANN, J., TOUGAARD, J., DIETZ, R., MOURITSEN, K. N., DESPORTES, G. & SIEBERT, U. 2011. High-density areas for harbor porpoises (*Phocoena phocoena*) identified by satellite tracking. *Marine Mammal Science*, 27, 230-246.
- TESTA, J. W., MOCK, K. J., TAYLOR, C., KOYUK, H., COYLE, J. R. & WAGGONER, R. 2012. Agent-based modeling of the dynamics of mammal-eating killer whales and their prey. *Marine Ecology Progress Series*, 466, 275-291.
- THOMSEN, F., FRANCK, D. & FORD, J. 2001. Characteristics of whistles from the acoustic repertoire of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. *The Journal of the Acoustical Society of America*, 109, 1240-1246.

- THOMSEN, F., FRANCK, D. & FORD, J. K. 2002. On the communicative significance of whistles in wild killer whales (*Orcinus orca*). *Naturwissenschaften*, 89, 404-407.
- THORSNÆS, G. 2021. *Hardangerfjorden* [Online]. snl.no: Store norske leksikon. [Accessed 02.03.2022].
- TREGENZA, N. 2013. *Validating cetacean detections* [Online]. chleonia.co.uk. Available: <https://www.chelonia.co.uk/> [Accessed 10.05 2022].
- TRITES, A. W., DEECKE, V. B., GREGR, E. J., FORD, J. K. & OLESIUK, P. F. 2007. Killer whales, whaling, and sequential megafaunal collapse in the North Pacific: a comparative analysis of the dynamics of marine mammals in Alaska and British Columbia following commercial whaling. *Marine mammal science*, 23, 751-765.
- VERFUß, U. K., MILLER, L. A., PILZ, P. K. D. & SCHNITZLER, H.-U. 2009. Echolocation by two foraging harbour porpoises (*Phocoena phocoena*). *Journal of Experimental Biology*, 212, 823-834.
- VERITY, P. G. & SMETACEK, V. 1996. Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Marine Ecology Progress Series*, 130, 277-293.
- VESTER, H. & HAMMERSCHMIDT, K. 2013. First record of killer whales (*Orcinus orca*) feeding on Atlantic salmon (*Salmo salar*) in northern Norway suggest a multi-prey feeding type. *Marine Biodiversity Records*, 6, 1-5.
- VISSER, I. N., ZAESCHMAR, J., HALLIDAY, J., ABRAHAM, A., BALL, P., BRADLEY, R., DALY, S., HATWELL, T., JOHNSON, T., JOHNSON, W., KAY, L., MAESSEN, T., MCKAY, V., PETERS, T., TURNER, N., UMUROA, B. & PACE, D. S. 2010. First Record of Predation on False Killer Whales (*Pseudorca crassidens*) by Killer Whales (*Orcinus orca*). *Aquatic Mammals*, 36, 195-204.
- VONGRAVEN, D. & BISTHER, A. 2014. Prey switching by killer whales in the north-east Atlantic: observational evidence and experimental insights. *Journal of the Marine Biological Association of the United Kingdom*, 94, 1357-1365.
- WEISE, M. J., HARVEY, J. T. & COSTA, D. P. 2010. The role of body size in individual-based foraging strategies of a top marine predator. *Ecology*, 91, 1004-1015.
- WELLARD, R., ERBE, C., FOUUDA, L. & BLEWITT, M. 2015. Vocalisations of killer whales (*Orcinus orca*) in the Bremer Canyon, Western Australia. *PLOS ONE*, 10, e0136535.
- WILLIAMS, T. M., ESTES, J. A., DOAK, D. F. & SPRINGER, A. M. 2004. Killer appetites: assessing the role of predators in ecological communities. *Ecology*, 85, 3373-3384.
- WILLIAMS, T. M., RUTISHAUSER, M., LONG, B., FINK, T., GAFNEY, J., MOSTMAN-LIWANAG, H. & CASPER, D. 2007. Seasonal Variability in Otariid Energetics: Implications for the Effects of Predators on Localized Prey Resources. *Physiological and Biochemical Zoology*, 80, 433-443.
- WILLOUGHBY, A. L., FERGUSON, M. C., STIMMELMAYR, R., CLARKE, J. T. & BROWER, A. A. 2020. Bowhead whale (*Balaena mysticetus*) and killer whale (*Orcinus orca*) co-occurrence in the US Pacific Arctic, 2009–2018: evidence from bowhead whale carcasses. *Polar Biology*, 43, 1669-1679.
- YOUNG, N. M. & LUDICELLO, S. 2007. Worldwide bycatch of cetaceans: an evaluation of the most significant threats to cetaceans, the affected species and the geographic areas of high risk

and the recommended actions from various independent institutions. *NOAA technical memorandum NMFS-OPR 36*.

AAREFJORD, H., BJORGE, A., KINZE, C. & LINDSTEDT, I. 1996. Diet of the harbour porpoise (*Phocoena phocoena*) in Scandinavian waters. *Oceanographic Literature Review*, 10, 1041.

## APPENDIX

### DESIGN CONCEPTS

#### Sub-models corresponding to processes presented in the ‘Process overview and scheduling’

The sub-models presented are almost identical to the ones presented in Nabe Nielsen et al’s (2014) Appendix A: “Effects of noise and by-catch on a Danish harbour porpoise population”. However, some parameters have been altered and sub-models related to the predation by killer whales have been added. The original sub-models related to the ships and wind turbine processes in the landscape have been removed. The addition to the original model is highlighted in green, whilst the removed components are highlighted in red. The details of the simulation processes are presented in order of execution, and when necessary, the formulas involved in the calculations and the reference parameter values are presented. The literature used to support the choice of parameter values is provided in the main text and Table A2.

#### Process overview

**Table A1:** An overview of the processes repeated every half hour steps in the individual-based harbour porpoise model. The model follows the same processes as described by the original model (Nabe Nielsen et al 2014), but the processes that has been removed from, or added/altered to this model has been highlighted in red and green, respectively.

<i>Processes repeated each half hour step</i>	
<i>Update landscape</i>	<i>For food patches:</i> Load the food level in every food patch (Eqn. A1)
	<b><i>For ships and wind turbines: Ask any nearby porpoises to get frighten and take a step away from them directly. The amount of noise they are subjected to determines how long the step will be. The duration of the step is reduced by half at the completion of the prior step, and it is reset to zero after a set number of steps (<math>t_{deter}</math>).</i></b>
<i>Porpoise move</i>	<i>Spatial memory behaviour:</i> Porpoises get ready to take a step towards the patches where they have previously obtained food. The distance to the patches, how much food the animals previously found there, and to what extent their memory of them has faded all affect how long the step is (Nabe-Nielsen et al., 2013).
	<i>Correlated random walk (CRW) behaviour:</i> After a CRW, the porpoises prepare to take a step. The amount of food the animals just discovered determines the length of the step (which serves as a proxy for how much they should anticipate finding if performing an undirected CRW step)
	<i>Calculate the steps combined:</i> Turn in the given direction indicate by the combined effects of their spatial memory, CRW, and deterrent behaviors (Eqn. A2).

	<p><i>Given that the upcoming water depth &lt; minimum water depth (<math>w_{min}</math>): To face the direction of deepest water, take a turn of 40° (or 70°, 120°, or 180° if needed).</i></p>
	<p><i>Move ahead: The step's length is dictated by the CWR step length.</i></p>
<b>Change dispersal/back-track status:</b>	<p><i>IF the energy decreases for three consecutive days and no current dispersing/back tracking is occurring:</i></p> <ol style="list-style-type: none"> <li>1) Begin dispersing.</li> <li>2) Turn in the direction of the 20 x 20 km block with the highest average maximum food level among the q blocks (see Table A2).</li> </ol>
	<p><i>IF the energy level was greater 6–9 days ago than it has been over the past three days AND not dispersing //</i></p> <p style="text-align: center;"><i>OR dispersing AND closing in on target block //</i></p> <p style="text-align: center;"><i>OR dispersing AND being unable to access deep water (<math>&gt;w_{disp}</math>):</i></p> <ol style="list-style-type: none"> <li>1) Begin back-tracking.</li> <li>2) Turn around 180° from where you were specifically one day ago.</li> </ol>
	<p><i>IF dispersing/back-tracking AND the energy levels are at their highest point in the past week //</i></p> <p style="text-align: center;"><i>OR stuck in low-water areas:</i></p> <ol style="list-style-type: none"> <li>1) Stop dispersing / backtracking</li> </ol>
<b>Disperse/back-track:</b>	<p style="text-align: center;"><i>IF dispersing:</i></p> <ol style="list-style-type: none"> <li>1) Make a 20° turn in the direction of the deepest water.</li> <li>2) IF water depth &lt; minimum dispersal depth OR if the coastal distance is &lt; <b>50 m</b>: turn <math>\leq 30^\circ</math> to maximize the possible distance from land.</li> </ol>
	<p style="text-align: center;"><i>IF back-tracking:</i></p> <ol style="list-style-type: none"> <li>1) IF 1-4 km from land, turn up to 80° to maintain distance.</li> <li>2) ELSE turn up to 80° in the directional area that is 1-4 km away from shore.</li> </ol>
	<p style="text-align: center;"><i>IF dispersing OR back-tracking: Move <math>d_{disp}</math> steps forward.</i></p>
<b>Update energy level and survival probability:</b>	<p><i>Consume food:</i> Porpoises acquire more energy as they travel through food patches, but they consume less of the food as their energy levels rise (Eqn. A3). They always leave at least 0.01 food units in a patch and never consume more than 99%.</p>
	<p style="text-align: center;"><i>Reduce food levels in visited patches to match porpoise consumption.</i></p>
	<p><i>Spend energy:</i> Every step, lower the energy levels by a specific amount:</p> <ul style="list-style-type: none"> <li>◦ Spend <math>E_{use}</math> per step, if month is May–September.</li> <li>◦ ELSE spend 1.15 <math>E_{use}</math> if month is April or October.</li> <li>◦ ELSE spend 1.30 <math>E_{use}</math> if month is November–March.</li> <li>◦ IF lactating individual, spend 1.50 <math>E_{use}</math> per step.</li> <li>◦ <b>IF age &lt; 3.44, multiply energy use by 1.5.</b></li> </ul>
	<p style="text-align: center;"><i>IF random-float 1 &gt; survival probability (Eqn. A4):</i></p> <ol style="list-style-type: none"> <li>1) IF with lactating calf: let calf die.</li> <li>2) ELSE die</li> </ol>
<b>Processes repeated every simulation day</b>	

<b>Update porpoise age</b>	<i>IF age &gt; 24: die</i>
<b>Killer whale predation</b>	<b>If the year &gt; 6: Add a yearly predation rate, spread out on the 12 months based on the killer whales' presence estimates.</b>
<b>Update pregnancy status</b>	<i>IF not pregnant AND the day of year is the mating date: the individual has a probability h of getting status as 'pregnant'.</i>
	<i>IF pregnant AND it is <math>t_{gest}</math> days since pregnancy started: Give birth to porpoise calf and begin lactating, update pregnancy status to 'not pregnant'.</i>
	<i>IF having lactating calf AND it is <math>t_{nurs}</math> days since giving birth: A new individual enters the population with a probability of 0.5 (given an equal sex ratio and that only females are included in the model).</i>
<b>Update landscape</b>	<i>IF the day is 60, 150, 210 or 300: Read the seasonal Maxent data. Between 300 and 60 (winter): Rescale values to 0–1. Other seasons: rescale values to ensure that the total of all patches' maximum food amounts remains constant in the landscape.</i>  <i>IF it is day 1 of the year: calculate new porpoise mating dates.</i>

## Equations used in sub-models

The same equations as presented in Nabe Nielsen et al (2014) has been used here but has been rewritten. The equations for calculating the effect of ships and noise have been removed in this individual based harbour porpoise model:

*Update food levels in patches:* When  $M_k[t]$  is the Maxent level at the  $k$  position of a patch at time  $t$  and  $r_U$  is the food replenishment rate, the food level in a patch is calculated as

$$E_k[t + 1] = E_k[t] + r_U \times E_k[t] \left( 1 - \frac{E_k[t]}{M_k[t]} \right) \quad \text{Eqn. A1}$$

*Calculate combined step:* The vector describing the next step (without considering land and dispersal),  $\mathbf{V}^*$ , is determined by the spatial memory contribution,  $\mathbf{V}_R$ , the CRW contribution,  $\mathbf{V}_S$ , and the deterrence behaviour contribution,  $\mathbf{V}_D$ . The length of the step is determined by the length of the CRW contribution,  $\|\mathbf{V}_S\|$ .

$$\mathbf{V}^* = \frac{\mathbf{V}_R + \mathbf{V}_S + \mathbf{V}_D}{\|\mathbf{V}_R + \mathbf{V}_S + \mathbf{V}_D\|} \times \|\mathbf{V}_S\| \quad \text{Eqn. A2}$$

*Consume food:* The range for a porpoise's energy level at time  $t$ ,  $E_p[t]$ , is 0 to 20. Time is measured in steps of half an hour. If a patch's food level is  $E_k$ , the energy level after eating but before using energy,  $E_p^*[t+1]$ , drops linearly with the patch's energy level given that it is greater than 10.

$$E_p^*[t + 1] = \begin{cases} E_p[t] + E_k[t] \frac{20 - E_p[t]}{10} & \text{if } E_p[t] \geq 10; \\ E_p[t] + E_k[t] & \text{if } E_p[t] < 10. \end{cases} \quad \text{Eqn. A3}$$

*Survival probability:* The survival probability,  $s$ , is based on a constant called the survival probability constant,  $\beta$ . This constant shows how the porpoise's energy level affects how likely it is that it will live one time step:

$$s_p = 1 - e^{-\beta E_p} \quad \text{Eqn. A4}$$

## Flow diagram for the porpoise population

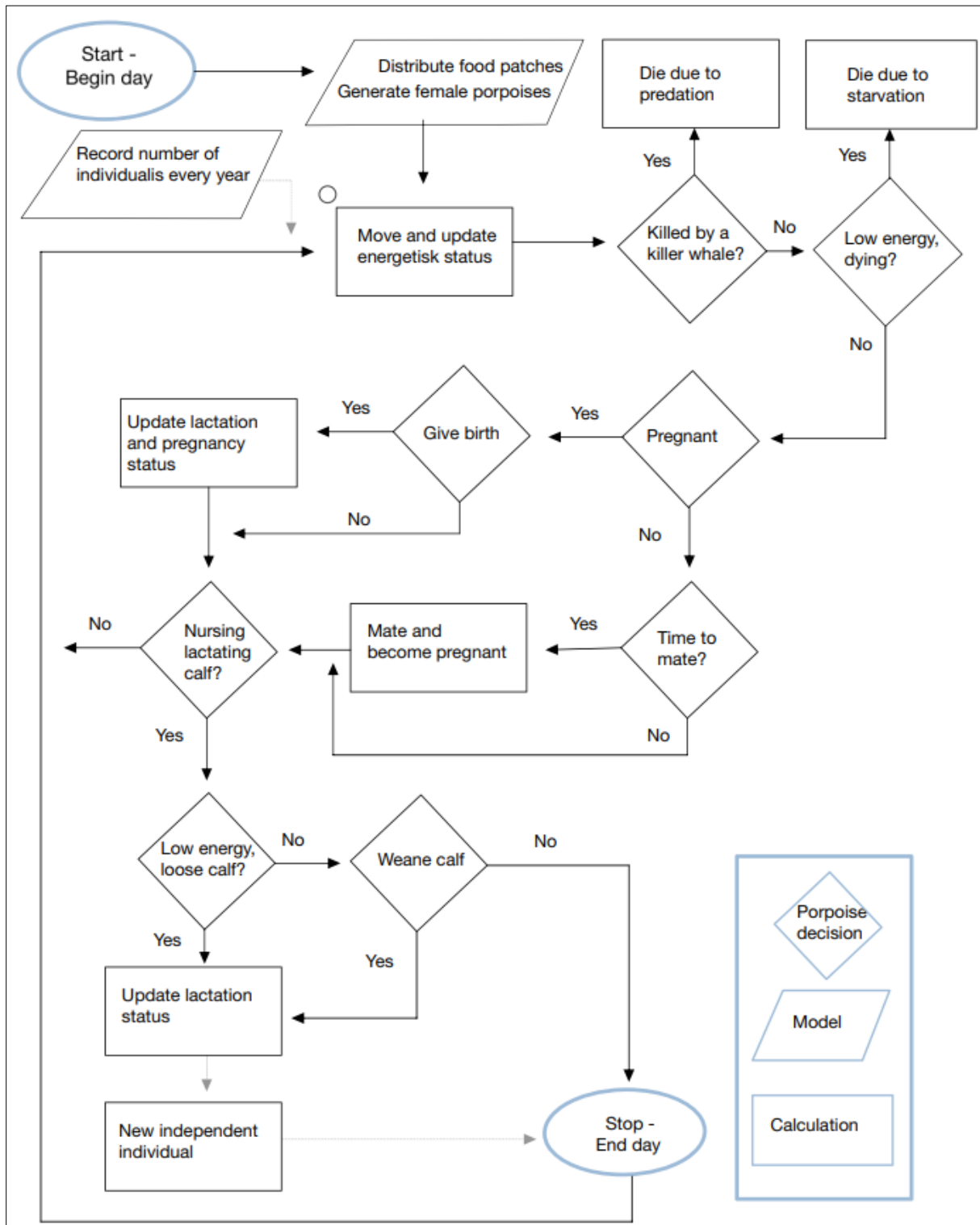


Figure A1: Flow chart showing how the population part of the model works. Only female porpoises are included.



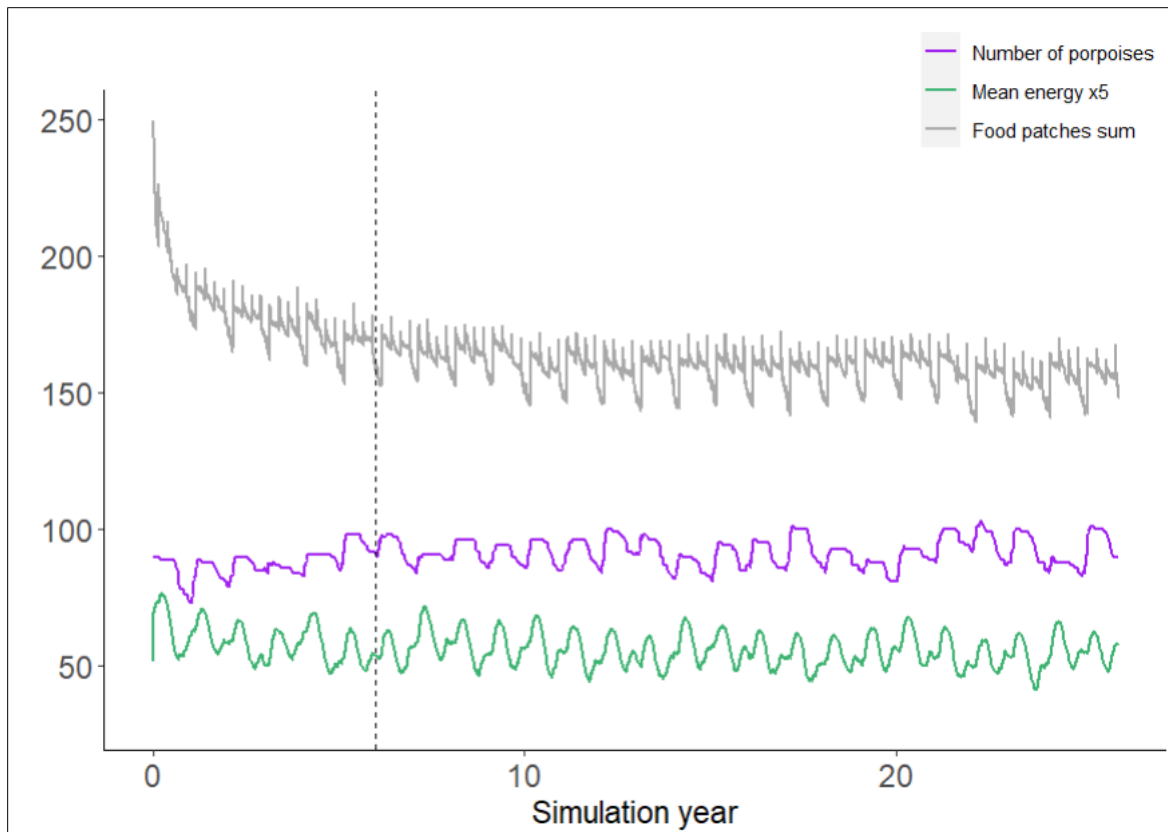
## Parameters

**Table A2:** An overview of the parameters used in the individual based harbour porpoise model. The table is taken from the original model by Nabe-Nielsen et al (2014), and the values that are written in green, bold font are the ones that was re-calibrated from the original model to fit the specific area of Hardangerfjord.

Parameter	Standard value	Description and units
$c$	8	Deterrence coefficient [unitless] (calibrated).
$d_{deter}$	300	Standard deterrence distance [m] (calibrated).
$d_{disp}$	1.6	Dispersal distance per time step [km] (J. Teilmann, unpublished satellite data).
$E_{use}$	<b>5.0</b>	<b>Energy use per half-hour step in May–September (calibrated).</b>
$h$	0.68	Probability of becoming pregnant (Read and Hohn, 1995).
$q$	<b>5</b>	<b>Number of potential dispersal targets = 40×40 km blocks (calibrated visually).</b>
$r_U$	<b>0.11</b>	<b>Food replenishment rate [unitless] (Nabe-Nielsen et al., 2013)</b>
$t_{deter}$	5	Deterrence time; number of time steps the deterrence effect lasts [time steps] (arbitrary).
$t_{gest}$	300	Gestation time [days] (Lockyer et al., 2003).
$t_{nurs}$	240	Nursing time [days] (Lockyer et al., 2003, Lockyer and Kinze, 2003a).
$U_{max}$	1	Maximum energy content in a food patch.
$w_{disp}$	4	Minimum water depth when dispersing [m] (visual calibration).
$w_{min}$	1	Minimum water depth [m] required by porpoises (J. Tougaard, pers. comm).
$\beta$	0.4	Survival probability constant (calibrated).

### Determining simulation time

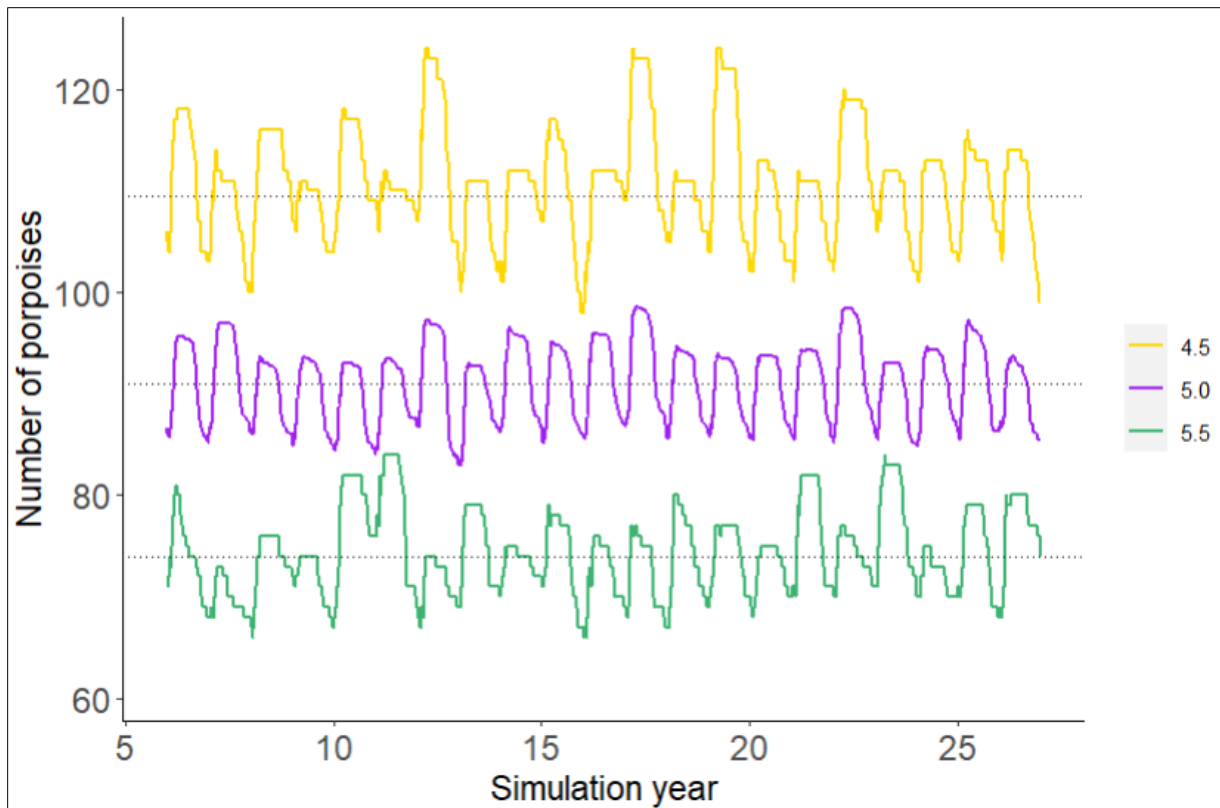
The model was run with the re-calibrated parameters (Table A1) and a predation probability of 0.05 to determine the time it took for the population to stabilize. The food level and population size stabilized before year 6 (Fig x).



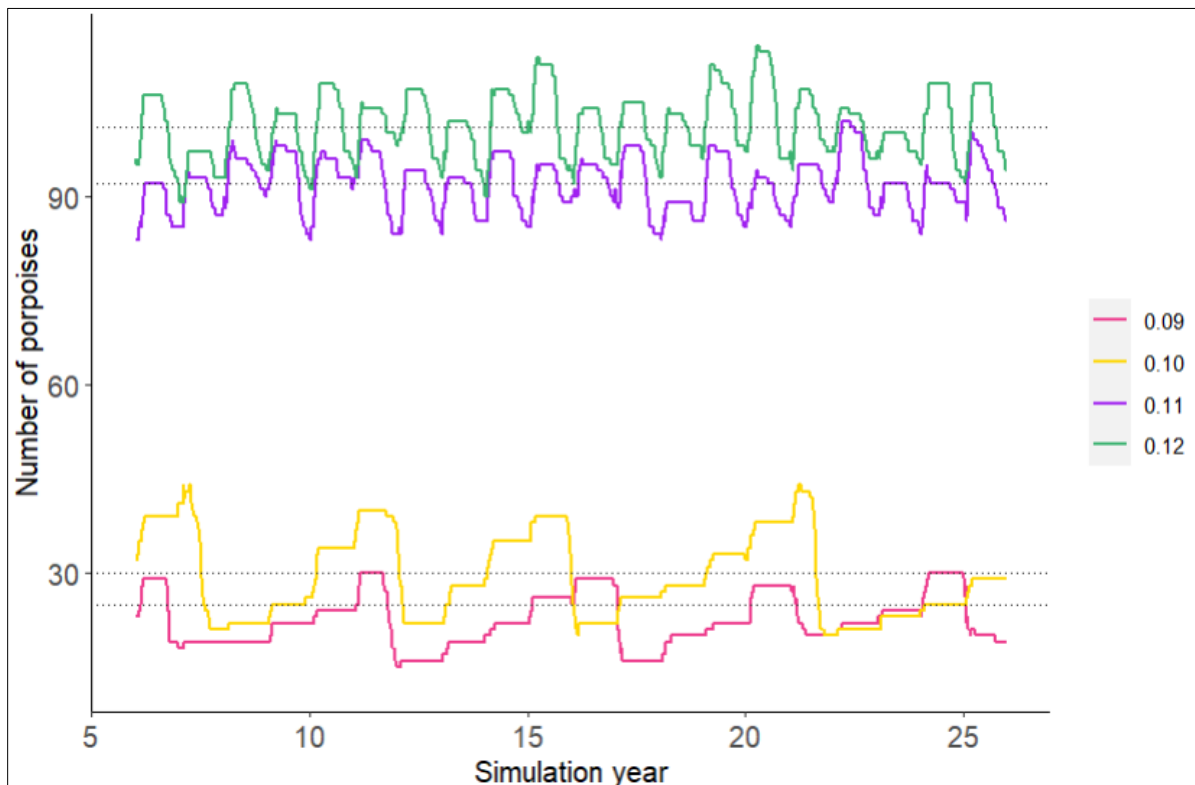
**Figure A2:** Simulated population dynamics based on the reference scenario ( $E_{Use} = 5.0$ ,  $r_U = 0.11$ ,  $B = 0.4$ ) in a landscape without predation. The green line shows the mean energy level  $\times 5$  of the porpoises, the purple line shows the porpoise population size, and the grey line shows the summarized amount of food in the landscape. This is plotted against simulated time, from year 0 to 26. The vertical, dashed line represents year 6, when the model has stabilized. Each individual is a super individual and only female porpoises are represented.

### Sensitivity analysis

Sensitivity analysis was done to test for how sensitive the model was to variations in  $E_{Use}$  (Fig A3) and  $r_U$  (Fig A4), parameters that had to be changed to fit the porpoise population in the Hardangerfjord.



**Figure A3:** Calibration of energy use per half-hour step ( $E_{0.5}$ ) when the  $rU$  (0.11) and  $B$  (0.4) is kept constant. Simulations were run in a landscape without predation. The population size is given in number of porpoise super-individuals, each representing several adult female porpoises.

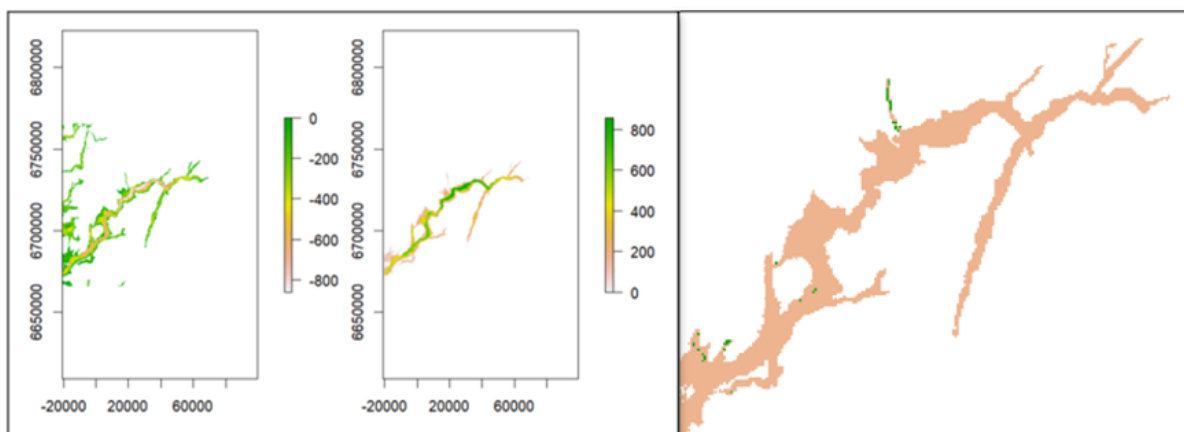


**Figure A4:** Calibration of food replenishment rate per half-hour step ( $r_U$ ) when the  $E_{0.5}$  (0.5) and  $B$  (0.4) is kept constant. The population size is given in number of porpoise super-individuals, each representing several adult female porpoises.

## Generating spatial data

Raster files were generated in R to make the spatial data that was to be implemented in the Individual based model. A raster file consists of a matrix of cells structured into rows and columns to represent a spatially explicit area. Firstly, the extent of the simulation universe was established and included unprojected coordinates of the lower left corner of the map, its cell sizes and how many rows and columns. The bathymetry data were projected from the European Marine Observation and Data network (EMODnet) onto the study area; the Hardangerfjord and surrounding coastal land. EMODnet contains a variation of marine data, among them bathymetric data (Martín Míguez et al., 2019).

This gave an explicit map over the Hardangerfjord (Fig A5). However, the map had to be slightly altered and masked to include only the desired area, which included removing coastal areas outside of the fjord and preventing porpoises to leave the fjord by adding a strip of land by the fjords mouth opening (Fig A5). Moreover, the map had to be slightly altered as some of the fjord arms had cells that were too shallow to be recognized as water, thus these had to be changed from land cells to water cells to represent the fjord more accurately (Fig A5). Additionally, the bathymetric file was used when another raster file (disttocoast.asc) was generated to add the distance to nearest point on the coastline for each cell in water. This was important for the porpoises dispersal movement as they will move away from or along the coast during dispersal (Nabe-Nielsen et al., 2014).



**Figure A5:** The original bathymetry map projected from EMODnet. The altered bathymetry map where coastal areas were removed, a strip of land was added at the fjords mouth and some water cells were added (left). The pink map includes an illustration of the Hardangerfjord where the green patches are the newly added water cells (right).

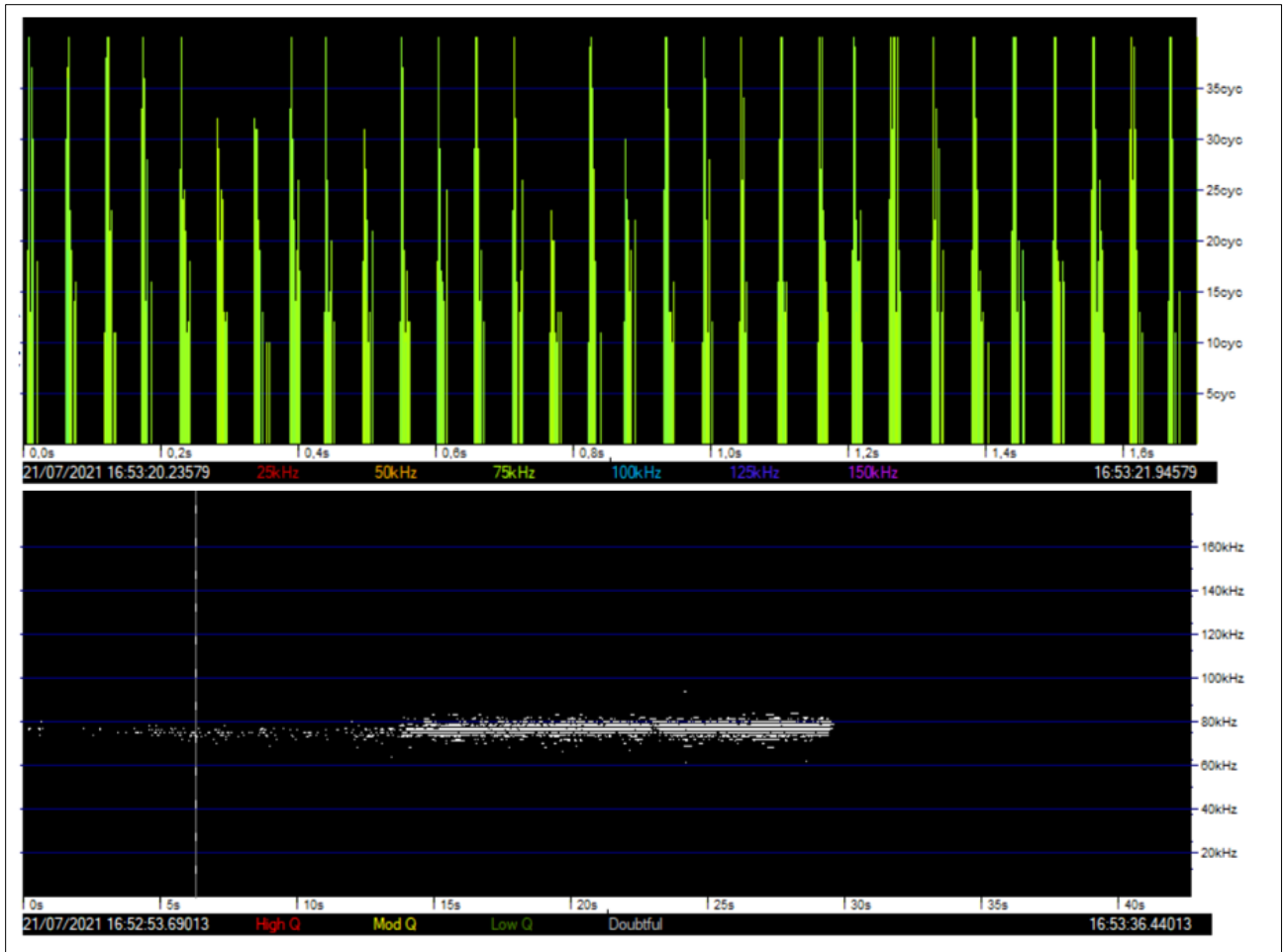
A new raster file (blocks.asc) had to be made to further divide the Hardangerfjord area into distinct blocks with each block covering the water of the fjord. The blocks are important for the porpoise's dispersal activity, as it is modeled that they will move randomly towards one of the

five blocks with highest food quality when their energy is low over a set time. Each block consists of a 20 x 20 km (50 x 50 cells) area, and 11 blocks were calibrated visually to give a realistic representation of the fjord. The food quality in each block was determined by creating a third raster file (patches.asc), that randomly placed food patches (1 x 1 cell) and their maximum energy content (1.0) in the 11 blocks (1.35). These food parameters were calibrated so that the population size remained at a stable size over time. Additionally, the maximum food level in the model depends on time of year to include a seasonal variation in the food availability. However, the season-specific availability of prey remains unknown in the Hardangerfjord. As an approximation, it was assumed that the season-specific pattern is comparable with the data in Nabe-Nielsen et al (2014). Thus, a fourth raster file was made (quartes.asc) to make sure that the randomly distributed food patches are replaced quarterly by resampling with replacement the quarterly maximum levels in the data from Nabe-Nielsen 2014. These season-specific maximum food levels were estimated from areas with high porpoise density recorded by satellite tags in Danish waters.

## **RESULTS**

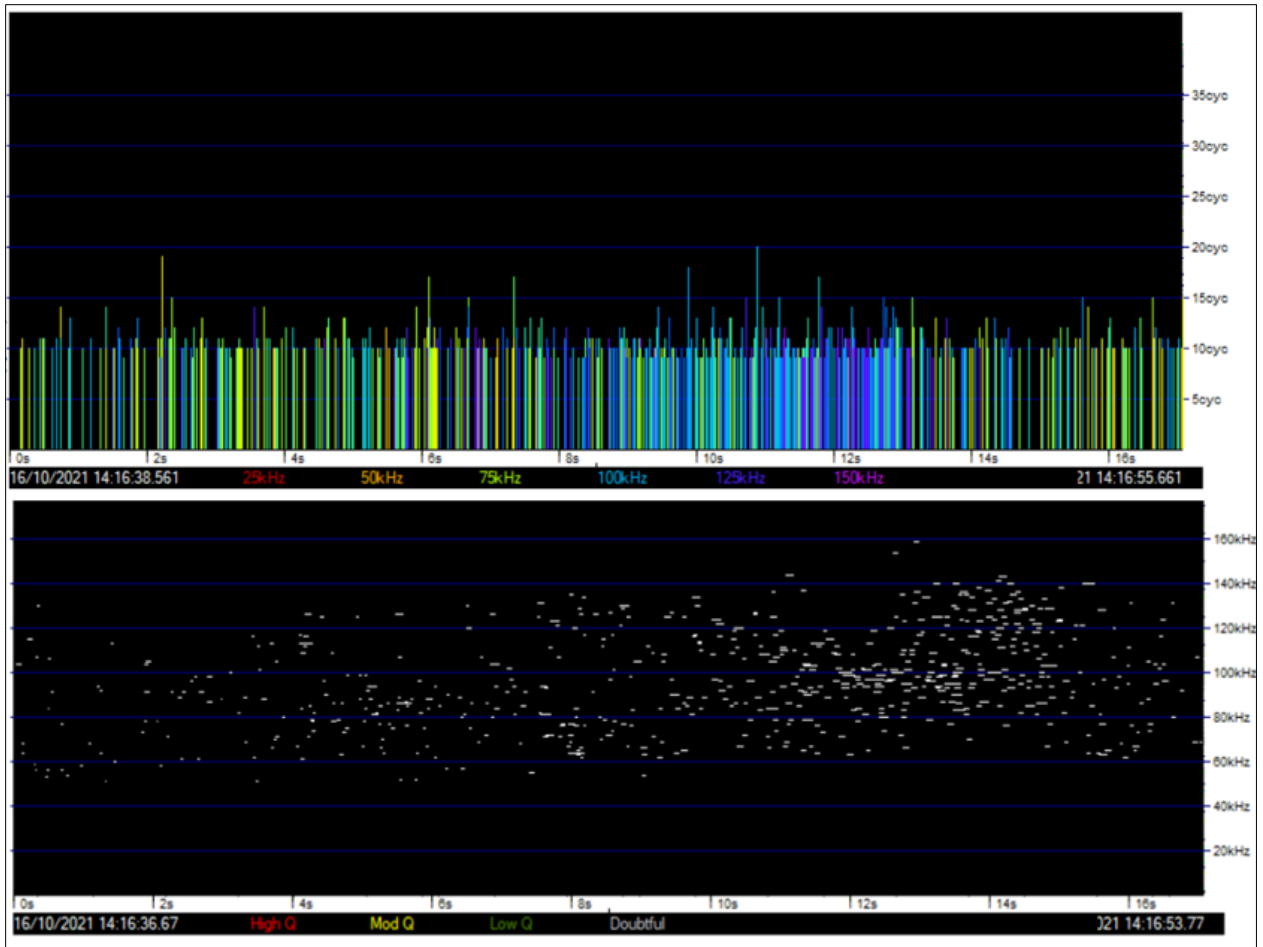
### **The acoustic monitoring**

A true ‘other cetacean’ click train should have a low duration (< 15 cycles), continuously changing click rates and a large range of frequencies (Tregenza, 2013). The Torsnes station had one ‘other cetacean’ detection during the study period, which occurred on 21.07.2021. This detection does not resemble an ‘other cetacean’ species with it has high duration clicks (20-35 cycles) occurring in very consistent intervals, and a narrow frequency band of 72-80 kHz (Fig. A6).

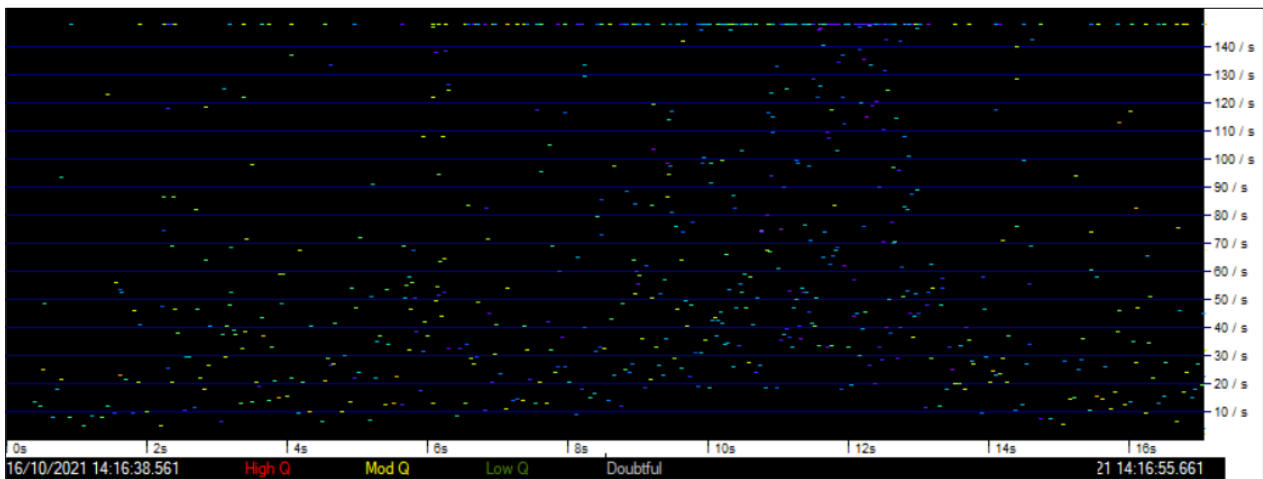


**Figure A6:** The duration of clicks (upper figure) and the frequency (lower figure) of the ‘other cetacean’ detection on 21/07/2021 in the Torsnes CPOD.

The Årsnes and Bagnstrond stations both had ‘other cetacean’ detections that fit the characteristics of a broad band species. Only the detection from Årsnes station on 16.10.2021 is shown here to illustrate the characteristics of a positive ‘other cetacean’ detection in the dataset (Fig. A7-A8). In general, the frequency range was broad (40-140 kHz) and the click rates were continuously changing.

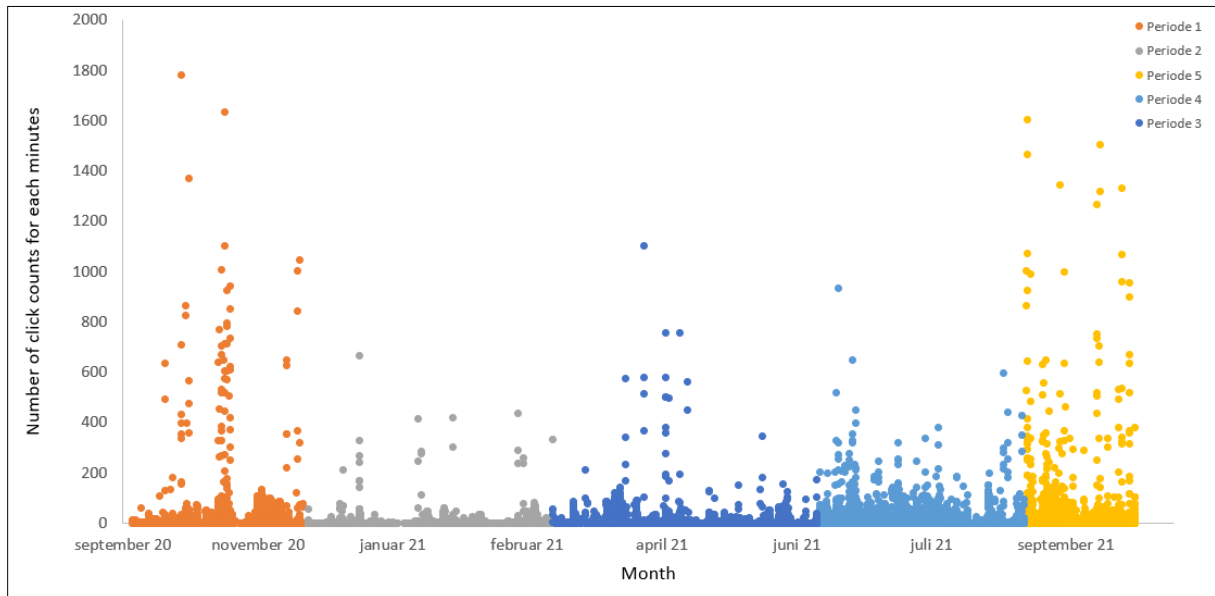


**Figure A7:** The number of cycles (upper figure) and the frequency (lower figure) of the ‘other cetacean’ detection on 16/10/2021 in the Årsnes CPOD.

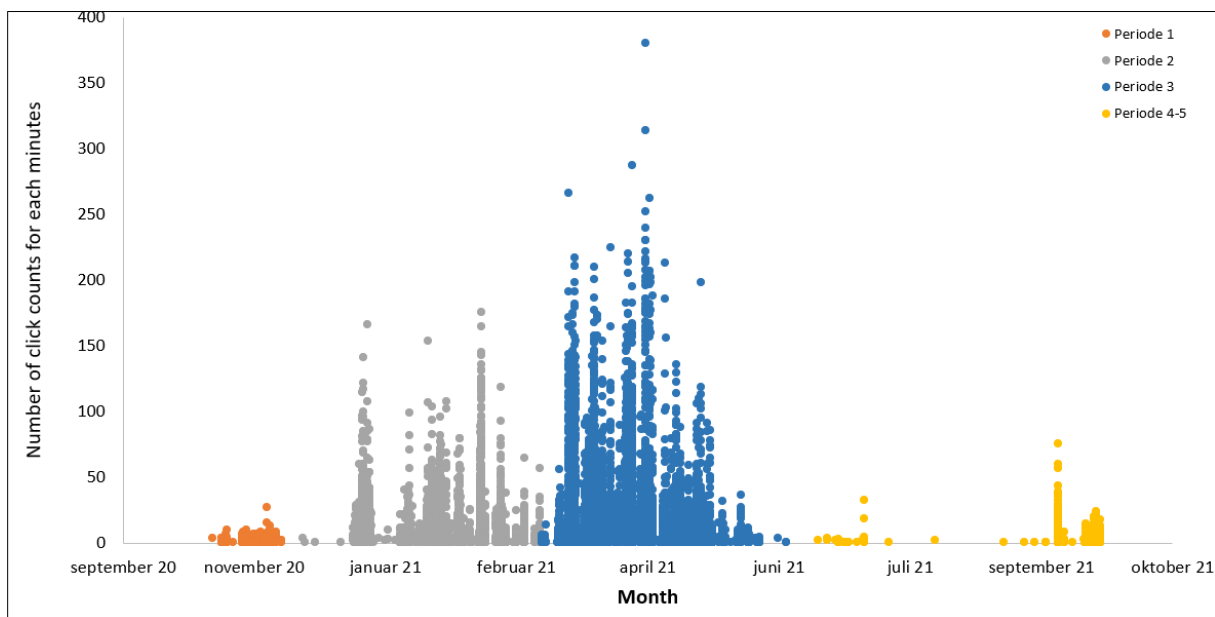


**Figure A8:** The click rates of the ‘other cetacean’ detection on 16/10/2021 in the Årsnes CPOD.

The sound detections with frequency below 30 kHz were exported from the CPOD data and plotted against time for all the five CPOD stations (Fig. A9-A13).

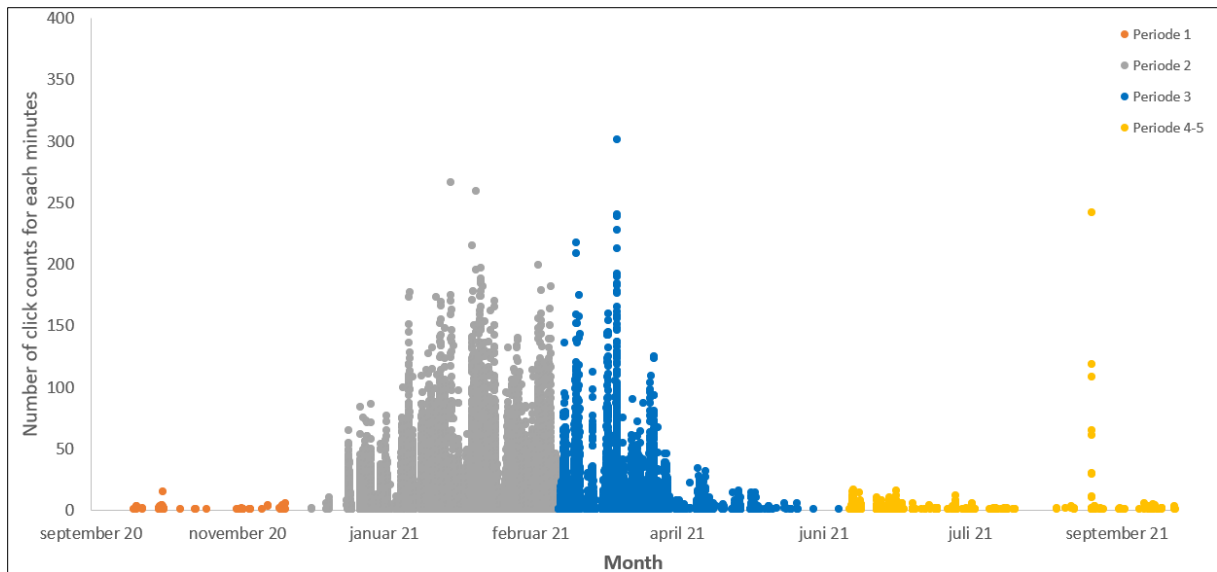


**Figure A9:** Number of click counted for each minute with a kHz < 30 for the CPODs placed at Bagnstrond for the period 27.09.2020 - 28.10.2021.

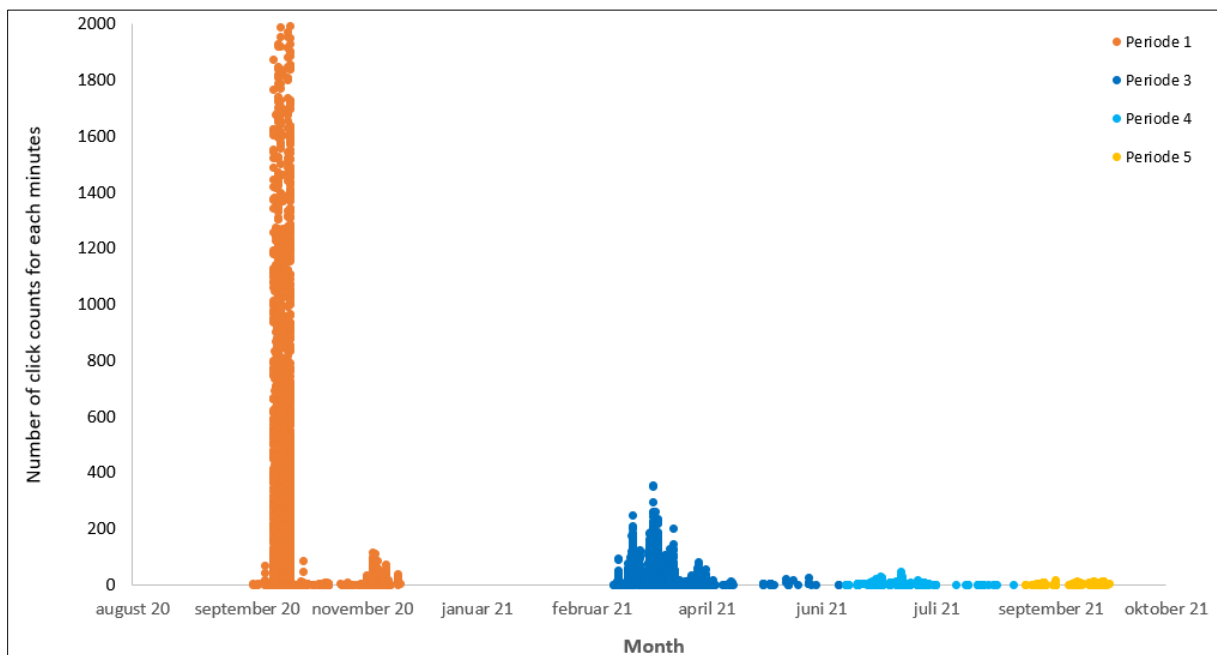


**Figure A10:** Number of click counted for each minute with a kHz < 30 for the CPODs placed at Ystanes for the period 27.09.2020 - 28.10.2021.

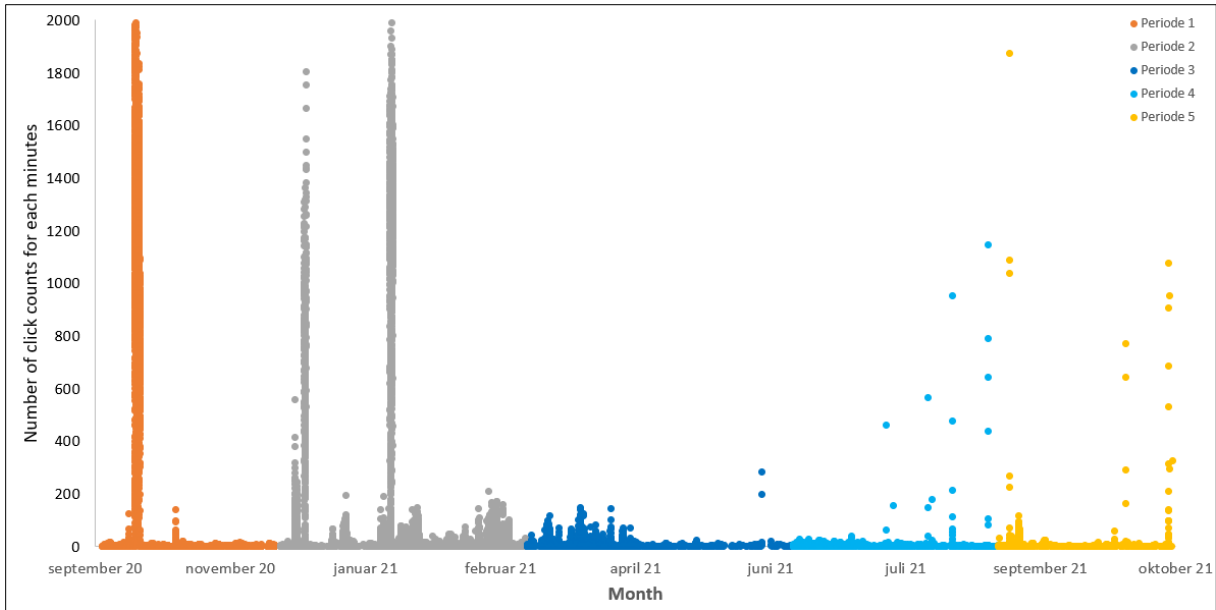




**Figure A11:** Number of click counted for each minute with a kHz < 30 for the CPODs placed at Smedvik for the period 27.09.2020 - 28.10.2021.



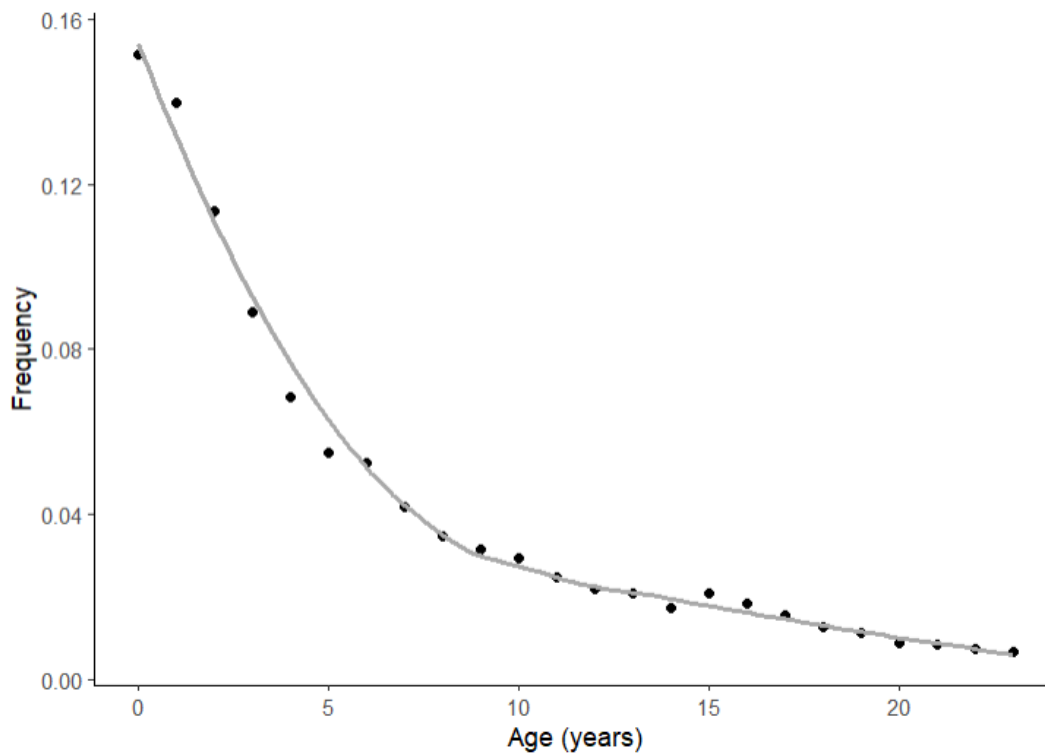
**Figure A12:** Number of click counted for each minute with a kHz < 30 for the CPODs placed at Torsnes for the period 27.09.2020 - 28.10.2021.



**Figure A13:** Number of click counted for each minute with a kHz < 30 for the CPODs placed at Årsnes for the period 27.09.2020 - 28.10.2021.

### Dynamics of the porpoise population

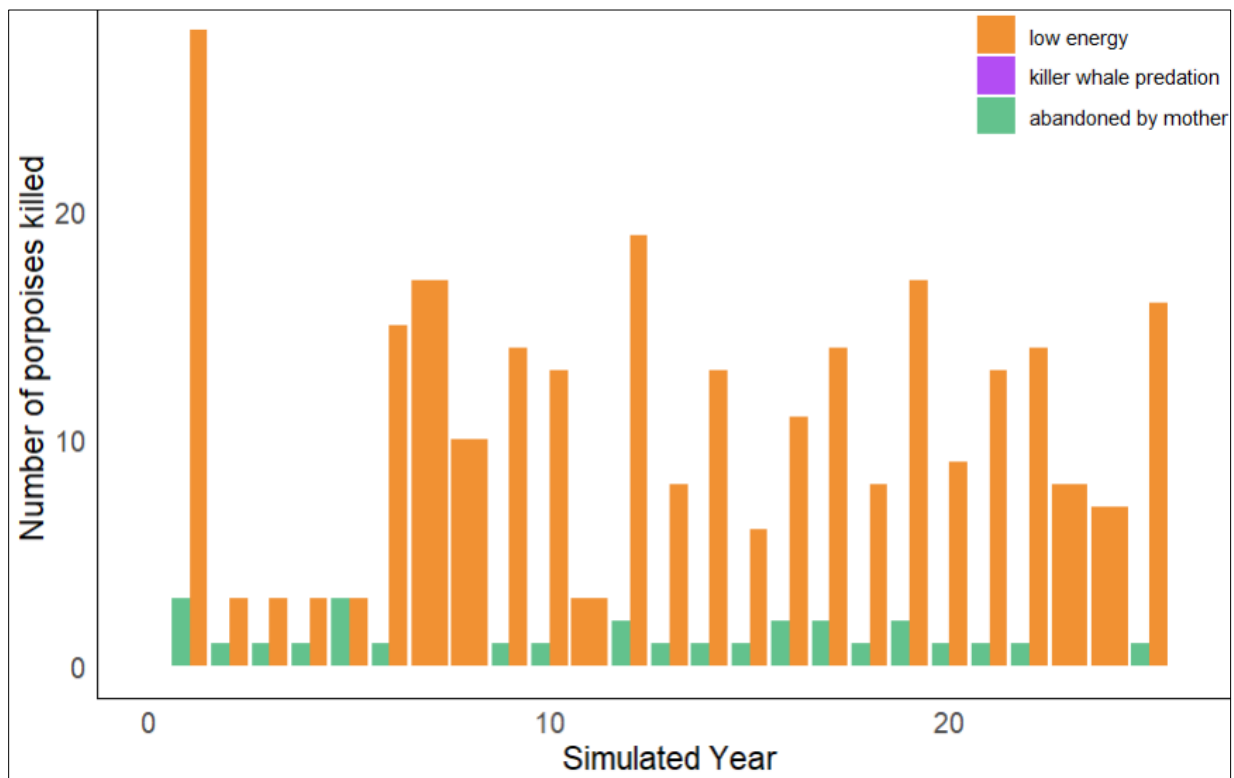
The age class distribution of the individuals that died in model was very similar to the ones presented in other studies on harbour porpoise (Nabe-Nielsen et al., 2014, Lockyer and Kinze, 2003b). The age distribution looked the same when the predation scenarios was simulated.



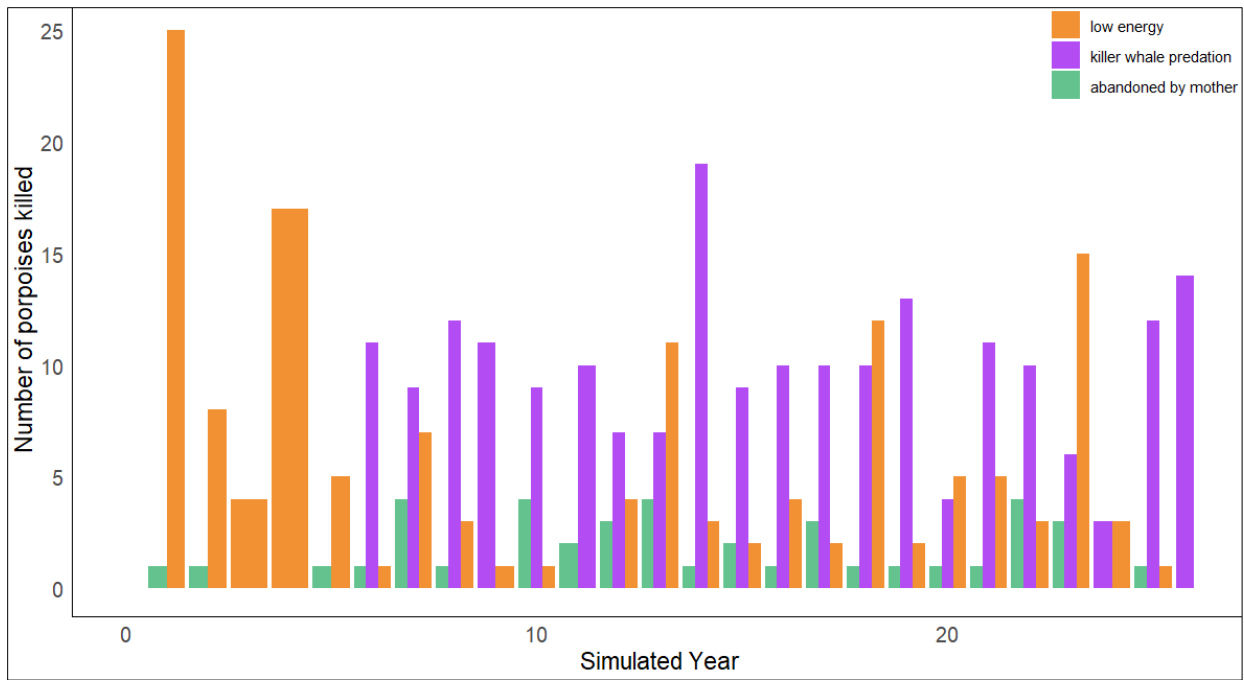
**Figure A14:** The age distribution of dead individuals in simulations for the reference scenario ( $rU = 0.11$ ,  $Euse = 5.0$ ,  $B = 0.4$ ).

### Cause of death

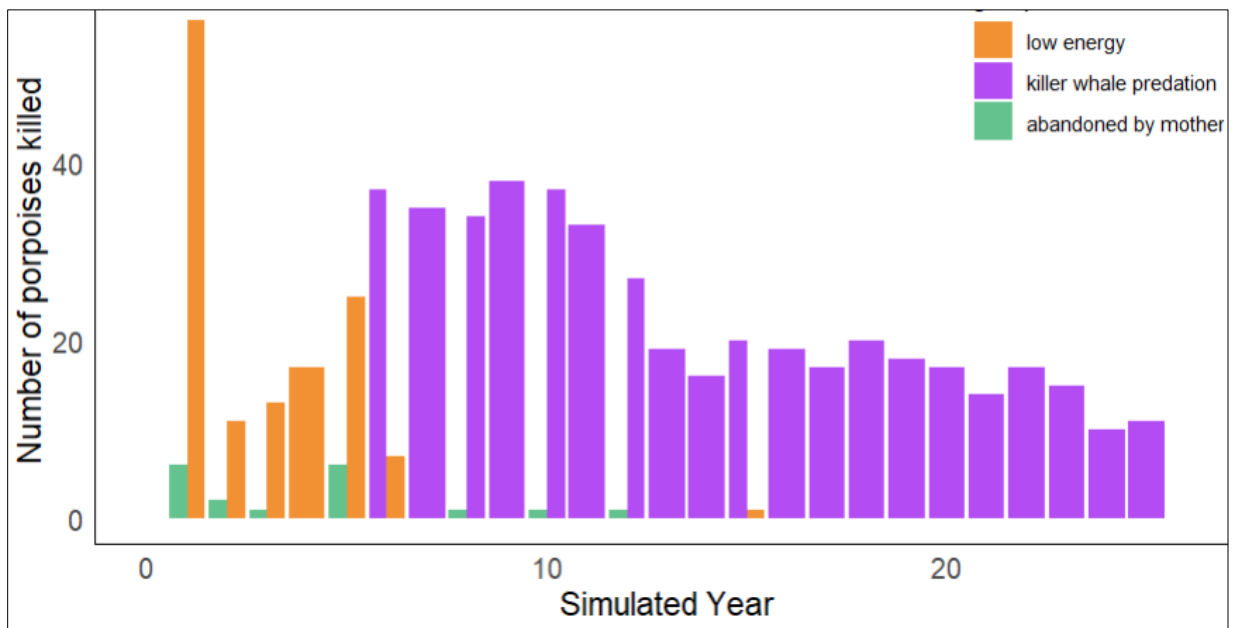
There were changes in cause of death when the model was run without predation (Fig A15), compared to when it was run with the lowest ( $p = 0.12$ ) (Fig A16) and highest ( $p = 0.28$ ) (Fig A17) predation rate scenario. The individuals dying from reaching maximum age was not included in the graphic illustrations as few died from this.



**Figure A15:** The causes of death for the porpoises dying in specific year in the reference scenario where no predation is happening. Most of the mortalities are caused by porpoises dying of low energy, and the ones being abandoned by their mother are calves that have been left and died if their mother had low energy.



**Figure A16** The causes of death for the porpoises dying in specific years in the scenario with lowest predation rate ( $p = 0.12$ ) where predation occur in year 6-26. Most of the mortalities after year 6, when predation was initiated, were caused by porpoises being killed by killer whales. But some still died of low energy or being abandoned by their mother as calves.



**Figure A17:** The causes of death for the porpoises dying in specific years in the scenario with the highest predation rate ( $p = 0.28$ ) where predation occur in year 6-26. Most of the mortalities after year 6, when predation was initiated, were caused by porpoises being killed by killer whales. Few died of low energy or being abandoned by their mother as calves.

## Appendix literature

- LOCKYER, C., DESPORTES, G., HANSEN, K., LABBERTÉ, S. & SIEBERT, U. 2003. Monitoring growth and energy utilization of the harbour porpoise (*Phocoena phocoena*) in human care. *Harbour porpoises in the North Atlantic*, 5, 143-175.
- LOCKYER, C. & KINZE, C. 2003a. Status, ecology and life history of harbour porpoise (*Phocoena phocoena*), in Danish waters. In: HAUG, T., DESPORTES, G., VÍKINGSSON, G. A. & WITTING, L. (eds.) *Harbour porpoises in the North Atlantic*. Tromsø: The North Atlantic Marine Mammal Commission.
- LOCKYER, C. & KINZE, C. 2003b. Status, ecology and life history of harbour porpoise (*Phocoena phocoena*), in Danish waters. *NAMMCO Scientific Publications*, 5, 143-175.
- MARTÍN MÍGUEZ, B., NOVELLINO, A., VINCI, M., CLAUS, S., CALEWAERT, J.-B., VALLIUS, H., SCHMITT, T., PITITTO, A., GIORGETTI, A. & ASKEW, N. 2019. The European Marine Observation and Data Network (EMODnet): visions and roles of the gateway to marine data in Europe. *Frontiers in Marine Science*, 6, 313.
- NABE-NIELSEN, J., SIBLY, R. M., TOUGAARD, J., TEILMANN, J. & SVEEGAARD, S. 2014. Effects of noise and by-catch on a Danish harbour porpoise population. *Ecological Modelling*, 272, 242-251.
- NABE-NIELSEN, J., TOUGAARD, J., TEILMANN, J., LUCKE, K. & FORCHHAMMER, M. C. 2013. How a simple adaptive foraging strategy can lead to emergent home ranges and increased food intake. *Oikos*, 122, 1307-1316.
- READ, A. J. & HOHN, A. A. 1995. Life in the fast lane: The life history of harbor porpoises from the Gulf of Maine. *Marine Mammal Science*, 11, 423-440.
- TREGENZA, N. 2013. *Validating cetacean detections* [Online]. chleonia.co.uk. Available: <https://www.chelonia.co.uk/> [Accessed 10.05 2022].