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Haulout Behavior of Harbor Seals (*Phoca vitulina*) along the Norwegian Coast

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Abstract

Harbor seals (*Phoca vitulina*) are a natural part of temperate and arctic coastal ecosystems and are dependent on regularly coming to shore and haul out. Colonies are distributed along most of the Norwegian coastline, often in close proximity to humans. It is thus important to increase knowledge about the seals' behavior, to facilitate sound management and conservation. Spatial and temporal variation in haul-out patterns have previously been documented, as has effects of environmental conditions. In this study I had access to data records from 31 harbor seals equipped with GPS phone tags in three distinct geographical regions along the Norwegian coastline from 2007 to 2020. Environmental conditions, seasonal and circadian patterns, sex and lunar cycle were tested in a GLMM framework with individuals as random effects and the response variable being the beta distributed proportion of time spent hauled out in 2 h summary periods. I discovered a lower probability of hauling out in northern Norway than in Skagerrak. Seasonal variation in haul-outs were also found between the two areas. A higher probability of nightly haul-outs was found in both areas, with a more pronounced nocturnal pattern in Skagerrak. Windspeed was found to have a negative effect in both areas. Water level had a negative effect and air temperature had a positive effect on haul-out behavior in northern Norway. I also discovered a significantly lower probability of hauling out during full moon in the north, compared with the last quarter half-moon. These findings strengthen pre-existing knowledge about geographical differences and variable responses to environmental and temporal factors associated with haul-out behavior and is to my knowledge the first study to identify behavioral differences in response to external factors between harbor seal colonies in Skagerrak and northern Norway.

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Acknowledgements

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Lastly, to my curiously inquiring and wonderful son, Bjørn: I love you.

— Nina Hille Bringsdal

November 19th, 2021 Mandal

1 Introduction

As semi-aquatic marine mammals, all pinniped species are dependent on regularly coming to shore and haul out (Cronin and McConnell 2008). One of the most widely distributed pinnipeds in the world is that of the mid-sized harbor seal (*Phoca vitulina*, Linnaeus 1758), and hauling out of the water onto skerries, sandbanks, ice floes and rock faces in the inter-tidal zone is an important part of harbor seals' life histories (Pauli and Terhune 1987; Patterson and Acevedo-Gutiérrez 2008; Burns 2009; Bjørge et al. 2010; Cordes et al. 2011; Boehme et al. 2016; Rosing-Asvid et al. 2020). A common site is seen in Figure 1, which shows vigilant harbor seals hauled out on a part of a rock that is clearly under water at high tide, and thus makes for a fast flush if needed. Harbor seals are adapted to a life along the coastline. Coastal systems have a naturally high variability, with changing weather conditions and wave- and current patterns through the seasons, and human activities are adding to this variability by heavy utilization of this productive and sensitive area (Field, Hempe, and Summerhayes 2002). In Norway, harbor seals can be found along most of the open, rocky coastline, but also in estuaries, fjords, and even up rivers (Bjørge 1991; Nilssen et al. 2010) Harbor seals are dependent on optimal haul-out sites for rest between foraging bouts, for thermoregulation (e.g., Watts 1996; Paterson et al. 2012), to undergo an annual molting cycle (shedding of pelt coat), for giving birth and nursing pups (e.g., Thompson et al. 1991; Bjørge et al. 2010), to interact with conspecifics and get relief from interspecific competition (killer whales, *Orcinus orca*, see e.g., London et al. (2012), sharks, see Lucas and Stobo (2000), and several other sea- and shore based predators, see NAMMCO), where the sites serve as safe zones. As central place foragers, harbor seals are known to perform foraging bouts from centrally located, near-shore haul-out sites with access to productive feeding grounds (which can vary), and they show relatively high site fidelity (Orians and Pearson 1979; Yochem et al. 1987; Thompson and Miller 1990; Simpkins et al. 2003; Boveng et al. 2003; Cunningham et al. 2009; Bjørge et al. 2010; Cordes et al. 2011; Grigg et al. 2012; London et al. 2012; Ramasco 2015). Long distance travel far away from their natal place may also occur (Peterson et al. 2012).

1.1 Haul-out behavior of harbor seals

Harbor seal haul-out behavior has been thoroughly studied on different scales, from fine scaled and individual, seasonal, and even decennial, all over the Northern Hemisphere (Brown and Mate 1983; Härkönen, Harding, and Lunneryd 1999; Ramasco 2008; Cordes et al. 2011; London et al. 2012; Rosing-Asvid et al. 2020).

Haul-out behavior of pinnipeds varies considerably, both spatially (e.g., regional differences) and temporally (e.g., seasonal, or annual variation), as well as with individual physical condition, and by the age- and sex composition of a colony (Thompson et al. 1991; Härkönen, Harding, and Lunneryd 1999; Simpkins et al. 2003; Small, Pendleton, and Pitcher 2003; Härkönen and Harding 2001; Ramasco 2015; Boehme et al. 2016). Where prey is less abundant, or in areas with more human disturbance, harbor seals have been found to haul out less (Pauli and Terhune 1987; Huber et al. 2001; Hoover-Miller et al. 2013; Blundell and Pendleton 2015). It is therefore of vital importance to conduct studies in local areas of the population range and be wary of extrapolating findings on studies of seal colonies and generalize the findings on the whole harbor seal population all along the (100915 km long) Norwegian coastline (islands included, Regjeringen). Both environmental conditions and population structure as well as timing of life history events such as molting, have relative effects on haul-out behavior (Härkönen, Harding, and Lunneryd 1999; Cunningham et al. 2009; Daniel et al. 2003; Mogren et al. 2010; Cordes et al. 2011; NAMMCO). Both environmental factors and individual traits act together on how haul-out behavior is being expressed, and it has been documented that the probability of harbor seals hauling out varies between regions, between seasons, and between the sexes (Thompson et al. 1998; Cunningham et al. 2009).

Environmental conditions are external factors that are highly influential on harbor seal haul-out behavior, and several studies have been performed to explore the possible effects of e.g., tides, windspeeds, air pressure, wave intensity, cloud cover, precipitation, air temperature, time-of-day, solar radiation, and lunar phases Granquist and Hauksson (2016). Tidal state is commonly found to have a negative effect on the proportion of time spent hauled out (e.g., Frost, Lowry, and Ver Hoef 1999; Simpkins et al. 2003; London et al. 2012; Hamilton et al. 2014). It is common to explain this effect by haul-out sites becoming less available (Granquist and Hauksson 2016). Windspeeds usually have a detrimental effect on haul-outs (e.g. Granquist and Hauksson 2016), and harbor seals tend to prefer to haul out more under fair and warm weather conditions (e.g., Simpkins et al. 2003). Additional to energy optimization, one reason for the positive effect of temperature is that by increasing the temperature of their skin, the seals increase the molting cycle and maximize regrowth of pelt after molting (Boily 1995; Paterson et al. 2012). Cronin et al. (2009) found that harbor seals left their haul-out sites more often right after a full moon, indicating a lunar influence on haul-out behavior, and moon light intensity changes with cloud cover (Hamilton et al. 2014). Environmental factors also vary both in space and time (Small, Pendleton, and Pitcher 2003). Some follow a relatively cyclic pattern whilst other factors can be more complex to predict. For example, tidal amplitudes are easy to predict, but can vary to a greater or lesser extent in different geographical regions (Thompson et al. 1991; London et al. 2012; Hamilton et al. 2014). Wave action (both in-shore and off-shore), precipitation, windpseed, and wind-direction related to local topography, affect haul-out behavior to varying degrees (Pauli and Terhune 1987; Granquist and Hauksson 2016). Harbor seals need to deal with the effects accorded to spatially and temporally varying environmental factors, and it is generally agreed upon that haul-out behavior is influenced by tidal fluctuations, seasonal variation, time-of-day as well as a preference of hauling out with higher air temperatures, less precipitation and lower windspeeds (Yochem et al. 1987; Thompson 1989; Roen and Bjørge 1995; Boveng et al. 2003; Simpkins et al. 2003; Cronin

Figure 1. Harbor seals hauled out at low tide at Hvaler in outer Oslofjord, Norway. (Photo by Carla Freitas).

et al. 2009; Granquist and Hauksson 2016). Fine scale studies of colonies are thus important to be able to distinguish the relative importance of area specific variation of environmental conditions.

The proportion of seals hauling out at the same time is largest during the pupping and molting seasons, with the highest peaks in July and August (Granquist and Hauksson 2016). In Norway, the pupping and breeding period finds place between June and July, and the molting period from late July to the middle of August (Institute of Marine Research; Granquist and Hauksson 2016). They spend more time at sea during the winter months (e.g., Watts 1996; Patterson and Acevedo-Gutiérrez 2008), but with less winter haul-outs in northern Norwegian harbor seal populations, as on Svalbard, compared to southern populations (Hamilton et al. 2014; Rosing-Asvid et al. 2020). And since harbor seal haul-out behavior varies by age and sex, it is reasonable to believe that the composition of a colony is an important factor when investigating haul-out behavior (Härkönen, Harding, and Lunneryd 1999).

Population estimates of harbor seals are usually based on surveys that are performed by counting individuals at haul-out sites at times when it is thought that the largest proportion of the population is simultaneously out of the water, i.e., during the molting period (from August 10 to early September in Norway), at low tide (± 2 hours), during noon or afternoon (Heide-Jørgensen and Härkönen 1988; Watts 1996; Härkönen, Harding, and Lunneryd 1999; Patterson and Acevedo-Gutiérrez 2008; Mogren et al. 2010; Marine Research 2020; North Atlantic Marine Mammal Commission 2021). This fraction is then used as a minimum population estimate (Pauli and Terhune 1987; Cordes et al. 2011). The study of haul-out behavior can improve survey designs by implementation of correction factors, and thus increase the probability of obtaining the actual population estimate, instead of a minimum (Yochem et al. 1987; Simpkins et al. 2003; Cordes et al. 2011).

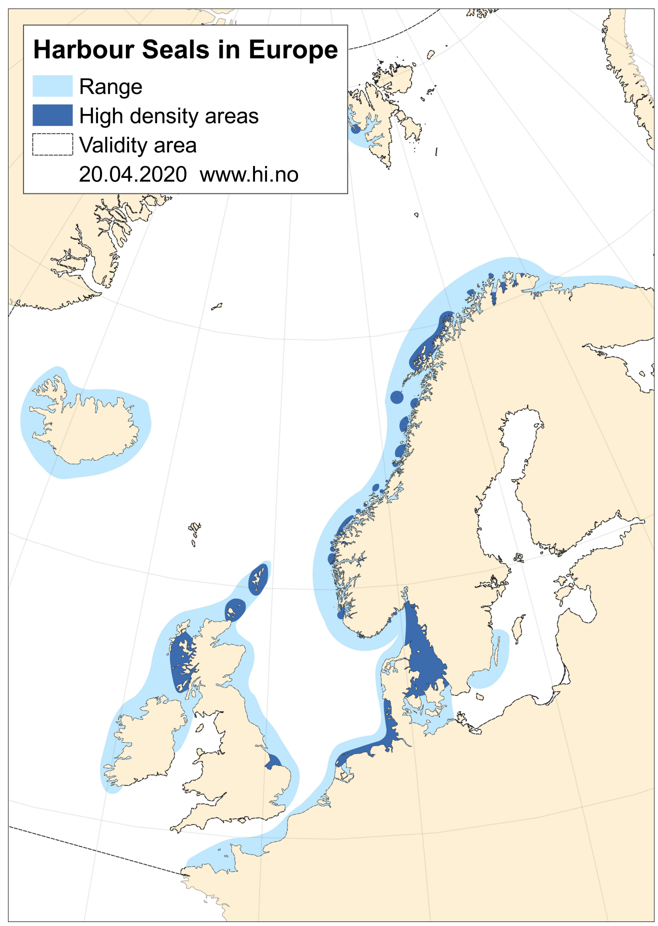

Figure 2. Distribution of harbor seal colonies in Europe (A. Bjørge and Nilssen, 2020).

1.2 Conflicts and Management

The Northern Atlantic harbor seals are

distributed on eastern and western coasts of the North Atlantic Ocean (eastern and western sub-species *P. v. vitulina* and *P. v. concolor* (DeKay 1842), respectively) (Bjørge et al. 2010). A map of harbor seal distribution in Europe is depicted in Figure 2. L. W. Andersen and Olsen (2010) have identified at least 12 genetically distinct populations here (see Figure 32 in Appendix). Northern Atlantic harbor seals have been subject to population fluctuations all through their range (L. W. Andersen and Olsen 2010). The animals are vulnerable to viral epidemics, and grim examples are the Phocine Distemper Virus (PVD) epizootics in 1988 and 2002, which took out about 50% of the harbor seal population in northwestern Europe, including Skagerrak-Kattegat (Dietz, Heide-Jørgensen, and Härkönen 1989; Härkönen et al. 2006; Bjørge et al. 2010; Duignan et al. 2014).

As coastal piscivores and curious pinnipeds, harbor seals interact with nearshore fisheries and fish farms, and this puts them at risk of becoming entangled in e.g., bottom-set gill nets (with death by drowning being the ultimate consequence) and lethal removal by fish farm operations (Bjørge et al. 2002).[1]

Further, harbor seals are potential carriers of parasitic nematodes (*Pseudoterranova decipiens* species complex) that can be transferred to commercially important fish species (mainly Atlantic cod, *Gadus morhua* and monkfish, *Lophius piscatorus*, (Linnaeus 1758)), which can have economic consequences for businesses involved (Bjørge et al. 2010; Desportes and McClelland 2014).

Since harbor seals show relatively high site fidelity and are vitally dependent on them (Yochem et al. 1987; Simpkins et al. 2003; Cunningham et al. 2009; Bjørge et al. 2010; Cordes et al. 2011), they are vulnerable to human coastal disturbances, especially during the breeding and nursing season (Bjørge 2014). High levels of disturbance can increase mortality in pups and alter previously observed haul-out behavior in some areas (London et al. 2012; Bjørge 2014; Granquist and Sigurjónsdóttir 2014). Harbor seals are also able to adjust and habituate to humans, as mentioned by Bjørge (2014), and clearly shown by Konrad and Levine (2021).

Conflicts with stakeholders and fisheries (e.g., Bjørge et al. 2002; Sørlie et al. 2020), human disturbance and pollution (e.g., London et al. 2012; Granquist and Hauksson 2016; ICES 2020), viral epidemics and climate change (Bjørge et al. 2010; Small, Pendleton, and Pitcher 2003) are essential reasons for sound management and conservation of Phocids (Small, Pendleton, and Pitcher 2003). The scientific studies of harbor seal behavior, the animals' ecological role, and consequently the procurement of tools to perform more refined monitoring are thus both necessary and critically important as means to greater understanding of marine ecosystem dynamics, trophic relationships, and to provide management agencies with constantly better ways to perform population estimates through surveys on both regional- and national scales (Small, Pendleton, and Pitcher 2003; Ramasco 2008; Cunningham et al. 2009; Mogren et al. 2010; Cordes et al. 2011; Boehme et al. 2016; Granquist and Hauksson 2016).

The Institute of Marine Research advice that the Norwegian harbor seal population must be regulated on both ecological and social considerations. Even though not a member of the EU, and thus not directly subjected to

[1]Following executive order FOR-2019-28-1593, lethal removal at fish farms was made illegal in Norway in 2019 (NAMMCO).

legal responsibilities under the Habitats Directive (Council Directive 92/43/EEC), Norway is a signatory to the Bern Convention (Convention on the Conservation of European Wildlife and Natural Habitats, Council Decision 82/72/EEC). Further, Norway as a coastal nation is instructed by the UN's Convention on the Law of the Sea (UNCLOS) to cooperate with other coastal nations in the conservation and management of marine mammals, including the harbor seal (Institute of Marine Research 2010). This means in short that the nation is legally bounded to work towards achieving international cooperation for conservation of ecosystems and wildlife – whether endangered or not (Epstein 2013). With white paper nr. 20 (2019-2020), the Norwegian Government submitted goals to keep working on and consolidating an integrated, ecosystem-based ocean management plan system, with e.g., Ministry of Trade, Industry and Fisheries as a steering committee and the Institute of Marine Research (IMR) as an advisory group on management, assisted by the Marine Mammal Advisory Board (Institute of Marine Research 2010). Within this system lies the management of harbor seals. "The Government's goal is to maintain the distribution of the harbor seals and ensure viable populations within their natural range. To achieve this goal, the Government will limit the decline in the stock and stabilize it at the 2006 level" (white paper nr. 46 (2009-2009) on Norwegian sea mammal policy), see also Fiskeri- og kystdepartementet 2010). In effect meaning protection of the species as well as taking coastal fisheries- and aquaculture interests into account. The population is assumed as stable when around 7000 individuals are counted during the molting period, which is done annually in sub-areas, resulting in a national population estimate of harbor seals every 5 years. The last completed national survey (2011 - 2015) resulted in 7,552 counts, which is slightly above the management plan's objective. The recent national survey is going to be finalized in the second half of 2021 but results from the sub-areas covered (all except Finnmark in the north) during 2016 - 2020 show a decrease in many areas, and an increase in Skagerrak (NAMMCO; Institute of Marine Research; North Atlantic Marine Mammal Commission 2021).

Haul-out behavior of harbor seals on a regional scale, as a function of biological and environmental covariates are thus an essential framework to draw inference from, concerning both management and conservation purposes.

1.3 Biotelemetry

Biotelemetry is the tracking of wild animals, and satellite transmitters with Platform Transmitter Terminals (PTTs) have been used to track and monitor movements of individual animals since the 1980s (Robinson et al. 2006; Meynecke and Liebsch 2021). Location tracking of marine mammals that spend a lesser or greater time below the surface (e.g., pinnipeds) have been greatly improved in accuracy by the innovation of GPS Fastloc-systems (Dujon, Lindstrom, and Hays 2014). Combining this technology with the Global Systems for Mobile Communication (GSM) network, it also greatly reduces costs of data transmissions SMRU.

1.4 Aims of this study

My main goal is to investigate haul-out behavior of harbor seals, based on data from tagged seals recorded over several time periods, in three zoogeographically distinct regions (L. W. Andersen and Olsen 2010; Bjørge, Øien, and Fagerheim 2007), along the Norwegian coastline. This can potentially lead to a better understanding of harbor seal biology and produce correction factors to aid in the precision of existing national population surveys.

The main research questions I want to try to answer are:

- How do selected environmental factors affect haul-out behavior of harbor seals in Skagerrak and in northern Norway?
- Does the probability of haul-outs differ between the geographical areas? Expressed in another way: are there differences in the probability of haul-outs on a spatial scale in the data?
  - If so, can differences in haul-out probabilities between Norwegian Skagerrak and northern Norway be explained by selected environmental factors, biological traits, time-of-year, and/or time-of-day?

Environmental and temporal factors, such as windspeed, air temperature, water level, precipitation, solar elevation, time of day, time of year, and lunar effects will be tested as explanatory variables (covariates) in a generalized linear mixed model (GLMM) framework, where the response variable is the beta distributed proportion of harbor seals hauled out during a specific time period calculated in hours (i.e., haul-out behavior).

I believe that the analysis of haul-out behavior of harbor seals in two distinct geographical areas along the Norwegian coastline could be a potentially good framework to draw inference from. Hopefully this can contribute to creating more fine-scaled precision tools for both national and local conservation and management, and thus consequently aid in the precision of existing national population surveys.

2 Methods

2.1 Study Areas

This study included telemetry data from a total of 31 harbor seals deployed with GPS phone tags along the Norwegian coast between 2007 and 2019, from the southwestern waters in Skagerrak, to the northeastern coast above the Arctic circle in Vesterålen, and all the way up to the fjord of Porsanger, an inlet of the Arctic Ocean and the Barents Sea (Table 1 and Figure 3).

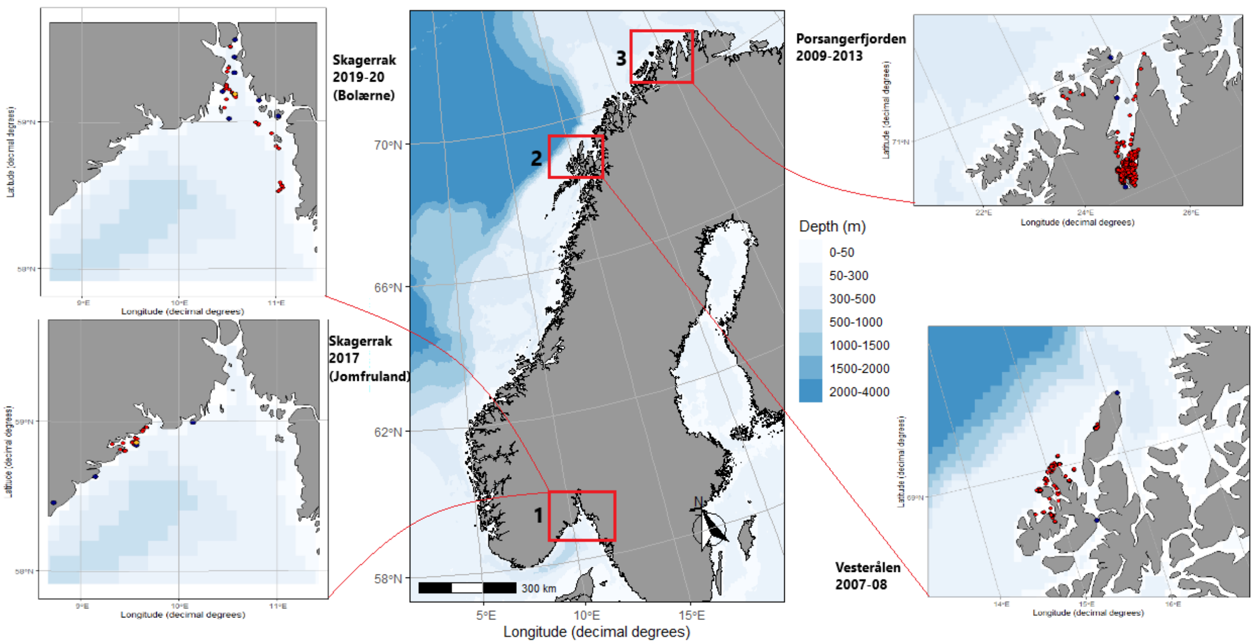

Figure 3. Map of Norway. Map of Norway showing the three areas where harbor seals were tagged with GPS phone transmitters: 1) Norwegian Skagerrak (Jomfruland, Kragerø 2017, Bolærne, Ytre Hvaler 2019-20), 2) Porsangerfjorden (2009-13), and 3) Vesterålen (2007-08). Red points are coordinates of haul-outs, blue points are coordinates for the weather stations where weather- and water level data were retrieved, and yellow points in the two Skagerrak close-ups represent exact location where animals were tagged. The graphed GPS-positions of haul-outs were retrieved from tag data (SMRU). Weather station coordinates were retrieved from Google Maps and Norgeskart.no. The maps were made in R with the ggOceanMap-package, Vihtakari 2021.

2.1.1 Skagerrak

The strait of Skagerrak runs between the southeast coast of Norway and the west coast of Sweden, and the reference tide level (Chart Datum) at Helgeroa in Larvik (58°59′42 North and 9°51′22 East) is 56 cm (Normal zero 2000, see Sjødivisjonen 2020). The area connects the North Sea via the Kattegat area with brackish water from the Baltic Sea, and the nutrient rich Norwegian Coastal Current (NCC) originates here (Kunnskapsutvikling Skagerrak-Kattegat-Oslofjorden 2019; Albretsen et al. 2011). The Norwegian Trench, with depths down to 700 m, runs through Skagerrak, and the shallower coastline is speckled with numerous islands and protected, semi-protected and exposed skerries (harbor seals' preferred haul-out spots). Norwegian

Skagerrak is the area from Lindesnes (Agder county) in the south, up to the Oslo fjord and Ytre Hvaler National Park (between 58°40′5 to 59°32′45 North, and 9°40′31 to 10°34′49 East). The annual mean temperature in the Norwegian Skagerrak is currently approximately 8.5 - 10 $°C$, and the annual amount of precipitation at the weather station situated on Torungen (58°23′931 North, 8°47′25 East), based on averaged data from 2017, 2019 and 2020, was annually averaged to 1016 mm (NCCS).

2.1.2 Vesterålen

Vesterålen is an exposed archipelago in Nordland and Troms County above the Arctic circle, northeast of Lofoten (69°01′14 North, 15°05′58 East), and the area is speckled with numerous skerries and islands. The reference tide level at the secondary port of Andenes (69°19′ North, 16°19.09′ East), belonging to the standard port of Tromsø, is 145 cm (Normal zero 2000, see Sjødivisjonen 2020). The island district faces the deep bathyal zone of the Norwegian Sea due west, at the end of the continental shelf (approximately 20 - 30 km out, Ramasco 2008), and with much shallower waters along the continental shelf itself (<200 m). Annual average precipitation and mean temperature in the area lie approximately between 1352 mm and 2.1 $°C$ (Sortland), and 1260 mm and 4.0 $°C$ (Nyksund) (Climate-Data.org).

2.1.3 Porsangerfjorden

The fjord of Porsanger is the fourth largest fjord in Norway (approximately 130 km long) and is located well above the Arctic circle at 70°31′14.4 North and 25°27′49.3 East. The fjord is an inlet of the Barents Sea in the Arctic Ocean. Both larger and smaller islands and skerries are found here, and due to its extent inland it serves as a more sheltered location than e.g., the archipelago of Vesterålen. The reference tide level at the standard port of Honningsvåg (70°59′ North, 25°59′ East) at the outlet of the fjord, is 186 cm (Normal zero 2000, see Sjødivisjonen 2020). Annual average precipitation and mean temperature in the area lies approximately between 686 mm and -0.2 $°C$ (Lakselv), and 871 mm and 2.1 $°C$ (Honningsvåg) (Climate-Data.org), reflecting a wetter and more temperate climate where the fjord reaches the sea compared to the innermost part of the fjord.

2.2 Study Animals and Transmitter Technology

2.2.1 Locations of deployments

The 11 harbor seals from Skagerrak included in this study were captured and tagged in two areas at three locations of the Norwegian Skagerrak in 2017 and 2019 (Table 2). Five individuals were tagged at Flatskjær, Bolærne in November of 2019 (59°11′20.0 North and 10°34′01.1 East). Four individuals were tagged in Ødegårdskilen, Jomfruland in August of 2017 (58°51′18.1 North and 9°33′36.1 East). Two individuals were tagged on Gjesskjæra, Jomfruland in August, 2017 (58°51′50.1 North and 9°34′18.3 East).

20 harbor seals were captured and tagged in two areas of Northern Norway between 2007 and 2012 (Table 3). 15 of these were captured and tagged by Børselv in Porsangerfjorden between September 2009 and September of 2012 (70°31′14.4 North and 25°27′49.3 East), and the remaining five seals in this study were tagged at Stø in Vesterålen in August of 2007 (69°01′14.4 North and 15°05′57.9 East).

Table 1. Central coordinates of deployments, names of locations on map, and year.

Locations	Coordinates	Name on map	Year of deployment
Skagerrak (Jomfruland)	58°51’18.1 N, 9°33’36.1 E	Ødegårdskilen	2017
Skagerrak (Jomfruland)	58°51’50.1 N, 9°34’18.3 E	Gjesskjæra	2017
Skagerrak (Bolærne)	59°11’20.8 N, 10°34’01.1 E	Flatskjær, Bolærne	2019
Porsangerfjorden	70°31’14.4 N, 25°27’49.3 E	Børselv	2009, -10, -11, -12
Vesterålen (Øksnes)	69°01’14.4 N, 15°05’57.9 E	Stø	2007

Table 2. Table of individual IDs of 11 harbor seals captured and deployed with GPS phone tags in Skagerrak from 2017 to 2019. Included are also biological data of each individual, the start- and end date of data transmission, the duration of active tags in days, number of observations, and tagging location.

ID Skagerrak 2017-19	Sex	Weight (kg)	Length (cm)	Start date	End date	Days	Observations	Location
pv68-F53-Iris-14	F	53	120	14-Nov-19	28-Mar-20	135	1600	Flatskjær, Bolærne
pv68-F56-Karin-14	F	56	125	14-Nov-19	21-Mar-20	128	1516	Flatskjær, Bolærne
pv68-M40-Pedro-14	M	40	113	14-Nov-19	12-Mar-20	119	1408	Flatskjær, Bolærne
pv68-M42-Einar-14	M	42	116	14-Nov-19	27-Feb-20	105	1256	Flatskjær, Bolærne
pv68-M47-Vemund-14	M	47	122	14-Nov-19	25-Dec-19	41	492	Flatskjær, Bolærne
pv35b-04-11	M	85	162	25-Aug-17	27-Aug-17	2	27	Gjesskæra (north side)
pv35b-05-11	F	62	137	25-Aug-17	31-Dec-17	128	1539	Gjesskæra (north side)
pv35b-06-11	M	75	149	25-Aug-17	16-Sep-17	22	270	Ødegårdskilen, Jomfruland
pv35b-08-11	M	75	149	29-Aug-17	04-Sep-17	6	45	Ødegårdskilen, Jomfruland
pv35b-09-11	M	90	150	25-Aug-17	26-Aug-17	1	18	Ødegårdskilen, Jomfruland
pv35b-10-11	F	34	115	28-Aug-17	20-Sep-17	23	54	Ødegårdskilen, Jomfruland

2.2.2 Tag functionality and technology

The telemetry tags used in this study were SMRU GPS phone tags with a GPS Fastloc 3 system, quad-band modem (GSM engine) and external antennas.

With a weight range of around 330 - 370g g the tags were approximately weightless in sea water. The battery life time was limited to 7 - 11 months (L. W. Andersen and Olsen 2010; Ramasco, Biuw, and Nilssen 2014; SMRU). The general longevity of batteries was conditional on configurations of desired connection attempts, but tags were ultimately lost the next molting period after tagging between August and September (Mogren et al. 2010).

Table 3. Table of individual IDs of all harbor seals captured and deployed with GPS phone tags in northern Norway from 2007 to 2013 (Porsangerfjord and Vesterålen, respectively). Included are also biological data of each individual, the start- and end date of data transmission, the duration of active tags in days, number of observations, and tagging location.

ID northern Norway 2007-13	Sex	Weight (kg)	Length (cm)	Start date	End date	Days	Observations	Location
pv35-01-11	M	34	115	01-Sep-12	29-Dec-13	484	5814	Børselv
pv35-02-11	M	24	85	03-Sep-12	22-Oct-12	49	594	Børselv
pv35-03-11	M	22	96	01-Sep-11	22-Oct-11	51	666	Børselv
pv30-01-09	M	21	87	01-Sep-09	09-Jul-10	311	3564	Børselv
pv30-02-09	M	24	94	20-Sep-10	10-Jan-11	112	1224	Børselv
pv30-03-09	M	41	108	31-Aug-10	30-Jan-11	152	1836	Børselv
pv30-05-09	M	30	105	04-Sep-09	30-Mar-10	207	2484	Børselv
pv30-06-09	F	31	104	01-Sep-09	27-May-10	268	3192	Børselv
pv30-07-09	M	29	96	21-Oct-09	28-Jan-10	99	1184	Børselv
pv30-08-09	M	25	101	05-Sep-10	19-Jun-11	287	3444	Børselv
pv30-09-09	F	29	90	03-Sep-10	11-Jul-11	311	3552	Børselv
pv30-10-09	M	28	100	21-Sep-10	13-Oct-10	22	264	Børselv
pv30-11-09	F	22	93	06-Sep-09	07-Jun-10	274	3288	Børselv
pv30-12-09	M	24	100	08-Sep-09	19-Dec-09	102	1224	Børselv
pv30-13-09	F	28	101	22-Sep-10	03-Jun-11	254	2928	Børselv
gp10-641-07	F	23	86	30-Aug-07	01-Apr-07	215	2064	Stø (Øksnes)
gp10-655-07	F	22	92	30-Aug-07	03-Dec-07	95	876	Stø (Øksnes)
gp10-683-07	F	22	90	30-Aug-07	13-Mar-08	196	2352	Stø (Øksnes)
gp10-684-07	F	32	108	30-Aug-07	26-Mar-08	209	2472	Stø (Øksnes)
gp10-685-07	F	20	90	31-Aug-07	17-Feb-08	170	1884	Stø (Øksnes)

Continuous monitoring of interactions with temperature and pressure sensors together with a wet/dry saltwater switch and a real-time clock recorded a three-state model of behavioral categories; if the tag was continuously dry for 10 consecutive minutes, a haul-out started; if the tag was wet for 40 seconds, a surface event was initiated; if the tag was deeper than 1.5 meter for 8 seconds, a dive was initiated (see Figure 4). Summary statistics of surfs, dives and haul-outs were also recorded, and all summary statistics of haul-outs in this study consisted of 2 h consecutive time intervals of the proportion of time spent in behavioral states (e.g., time spent at the surface, in dives, and hauled out). The records of focus in this study were the 2 h summaries of proportion of time hauled out.

2.2.3 Tagging procedures

The capture and tagging procedures varied somewhat due to integration of novel strategies throughout the years from 2007 to 2019, but both the handling and logging protocols were similar in design and execution.

Prior to capture, visual localization of animals was performed, at sites where harbor seals were previously observed to haul out.

In Skagerrak (2017-19), a specially designed pop-up net (100m x 4m) packed inside a modified fire hose was set up around the targeted haul-out site, attached to the seabed with a chain. A rubber air tube packed inside with the net, running the length of the fire hose, was attached to an air tank deployed together with the pop-up net. After the setup, the animals were allowed to adapt and resume normal activity. Capture was attempted at low tide the next day (about 24 h after setup). The site was scanned with binoculars, and the operation continued if animals were observed. With two boats ready (one aluminum and one inflatable) and engines shut off, the pop-up net was activated by a remote control (modified garage door opener technology). If successfully released, the net would immediately pop up from the seabed and encircle the site from seabed to surface. Seals would then escape into the water, and some into the net. An immediate response was initiated by the researchers by driving full speed towards the net. Animals entangled were promptly boarded, disentangled, and secured in specialized bags to restrain movement, and heads were covered with burlap cloths to reduce stressing sensory inputs. All Skagerrak animals in this study were brought ashore prior to the treatment procedure.

When on land, animals were weighed before they were sedated with an intramuscular injection of Zoletil®. During the procedure, a veterinarian monitored heartrates and oxygen uptake. An image of the procedure is presented in Figure 25 in the Appendix A DNA sample was procured from each individual (for population structure analyses). Gender, girth, and length was noted. Before dorsally attaching active transmitters to the neck, the fur needed to be dried and defatted by alcohol/acetone. In Skagerrak, transmitters were glued to the dried, defatted fur right below the skull with the fast-acting superglue Allround Loctite®. The sedation preparate acted as a dissociative, and the animals recovered from the drug within approximately 20 minutes after injection. They were then ready for release and went into the water shortly after.

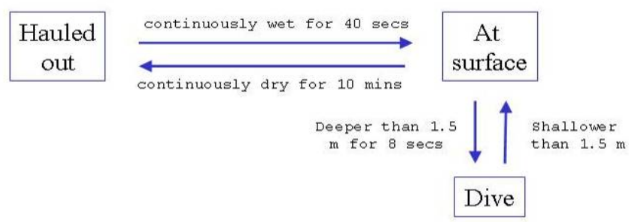

Figure 4. A haul-out starts when the tag has been continuously dry of a period of 10 minutes. A haul-out ends when the tag has been continuously wet for 40 seconds. A dive starts when wet and below 1.5 m for 8 seconds. A dive ends when above 1.5 m for 0 seconds (or dry).

The capture and tagging procedure in Porsangerfjorden and Vesterålen followed the same protocol, with some variation in techniques. I will only mention the differences. Nets (50m x 9m) were used by actively catching seals in the water from a boat. The glue used to attach transmitters to the animals was a two-component epoxy glue, and the heat reaction was closely monitored when applied. Due to heavier sedation, the animals were kept in aluminum boxes in a quiet environment for around 30 minutes to 2 hours before release. For more detailed tagging procedures of the 20 harbor seals from northern Norway, please see Ramasco, Biuw, and Nilssen (2014) (Porsangerfjorden 2009-13) and Ramasco (2008) (Vesterålen 2007-08).

2.3 Data preparation

Predictor variables

Table 4 gives an overview of all variables included in this study. The variables used as predictors were taken and prepared from separate sources. Data exploration was conducted following the protocol by Zuur, Ieno, and Elphick (2010) and Ieno and Zuur (2015).

The **Waterlevel** predictor variable was created from water level data retrieved through the application

Table 4. List of all variables included in the study. Haul-out time represented the proportion of time hauled out during a summary period of 2 h. REF consisted of 31 individual seals (11 from Skagerrak and 20 from northern Norway). Weather statistics were retrieved from NCCS, and water level data from the Norwegian Hydrographic Service. Months were pooled for all years of tracking events in each area. Light was calculated by an algorithm provided by NOAA. Lunar phases were created from an index in R (Girondot 2021). Location was only used in the Northern Norway model. Supporting figure of moon categories can be found in the appendix.

Variable	Description	Type
HAUL.TM	Proportion time hauled out (0, 1) during time inverval (2 h)	Continuous
REF	Individual ID	Categorical
Month	Calendar months from start to end of tracking events	Categorical
Waterlevel	Observed mean water level	Continuous
Air_Temperature	Air temperature, arithm.averaged beetween ports in location	Continuous
Windspeed	Windspeed, arithm. averaged between ports in location	Continuous
Precipitation	Amount of precipitation, arithm. averaged between ports in location	Continuous
Light_cat	Night, Dusk, Day, Dawn calculated by solar elevation	Categorical (4)
Moon_cat	Full Moon, First Quarter, Last Quarter, New Moon, Middling	Categorical (4)
Sex	Gender of individual (Male/Female)	Categorical (2)
Location	Vesterålen (2007-2008) and Porsanger (2009-13)	Categorical (2)

programming interface (API) of the Norwegian Mapping Authority, Hydrographic Service (Norwegian Mapping Authority). The reference level was set at Chart Datum (CD). The water levels for Jomfruland (2017) were measured at the standard port of Helgeroa in Larvik (Vestfold and Telemark county), with nautical chart zero 54.9 cm. The water levels for Bolærne (2019-20) were measured at the port of Viker in Hvaler municipality, a secondary port of Helgeroa, with nautical chart zero 57.0. Water levels for Porsangerfjorden (2009-13) were measured at the standard port of Honningsvåg, with nautical chart zero 167.3 cm. In Vesterålen (2007-08), the measures came from the port of Andenes, a secondary port of Tromsø, with nautical chart zero 133.8 cm.

The weather statistics (**Air Temperature**, **Windspeed** and **Precipitation**) were retrieved from the Norwegian Centre for Climate Services, provided by the Norwegian Meteorological Institute (NCCS). The values of air temperature were measured in ° Celsius and came from hourly values measured 2 m above ground. The values of wind speed were measured at meters per second (m/s) and came from hourly mean of measured mean wind speeds, usually measured 10 m above ground. Values of precipitation in Skagerrak were measured in millimeters (mm) and came from hourly measures. All precipitation statistics from Northern Norway were based on measures per 12 hours. I selected strategically placed weather stations within close proximity to the activity data received from the pooled data from each tracking event (weather stations are represented with black points on the maps in Figure 3). Weather data from Skagerrak 2019 - 2020 were retrieved from six stations around tagging event: Færder Fyr, Gullholmen, Hvaler-Brekke, Nøtterøy - Knarrberg, Strømtangen Fyr and Tofte - Rulleto. In the 2017-event in Skagerrak, weather data was retrieved from four stations: Lyngør Fyr, Jomfruland, Svenner Fyr and Arendal Sentrum. Arendal was selected in this time period, because it was the only station in relatively close proximity to the event that had measurements of precipitation. All weather data from the area of tagging events in the Porsangerfjorden 2009 - 2013 were retrieved from two stations: Honningsvåg Airport (located at the outlet of the fjord) and Banak (in the innermost part of the fjord). Weather data from Vesterålen 2007 - 2008 were retrieved from two stations: Andøya (wind- and temperature data) in the outer skerries of the archipelago, and Sortland (wind-, temperature-, and precipitation data), which were more protected from direct exposure from the Norwegian Sea. Where more than one station gave the same type of weather data in a location, an arithmetic averaging was performed.

All the continuous (i.e., numeric) environmental predictors had significantly different ranges, and were thus pre-processed prior to analysis. I also wanted to create unit-independent features for the models. I centered the data around 0, and scaled with respect to the standard deviation: $x_{standardized} = \frac{x-\mu}{\sigma}$. This did not change the distribution, only the range of the data.

Months were used as categorical variables. All months with observations were pooled together in each of the two locations (i.e, all unique months across years). The reference months of the six data sets were set to be the month of which most tags started to record in the particular data set (i.e., the month of which most seals were tagged). In Skagerrak, November was set as the reference month. September was set as reference month in northern Norway. In Skagerrak, the months with recorded data went from August to March. In northern Norway, months with observations went from September to July.

The five lunar categories in the categorical **Moon Phase** predictor where created in R (Girondot 2021), which generated an index ranging from 1 to 100 that made it possible to derive lunar phases. See Figure 32 in the Appendix for a visual presentation of the lunar phases and how the 'Middling' category relates to the categorical variable.

The categorical **Light** predictor, with four levels referring to night, dawn, day, and dusk, were calculated by algorithms provided by the National Oceanic & Atmospheric Administration (NOAA) (see Bivand and Lewin-Koh 2021 for function details and further references). I first calculated sunrise and sunset in the local areas. Nautical dawn ("morning twilight") and dusk ("evening twilight") was then derived, with 12 degrees for angle of the sun below the horizon. All data from northern Norway was retrieved above the Arctic Circle (i.e., above $66°33'$ North). The polar night in Vesterålen lasts from November 30 to January 12, and the polar night in Porsangerfjorden lasts from November 25 to January 16 ("Time and Date AS 1995 - 2021"). These periods were coded only at night-level. The midnight sun in Vesterålen lasts from approx. May 23 to July 23, and the midnight sun in Porsangerfjorden lasts from approx. May 16 to July 27 ("Time and Date AS 1995 - 2021"). These periods were coded as day-level.

Biological data (i.e., **sex**, weight, and length) on the tagged seals from Bolærne 2019-20 were retrieved from spread sheets procured by Carla Freitas. Michael Poltermann procured me with data from Jomfruland 2017. The biological data on harbor seals in Porsangerfjorden (2009 - 2013) was retrieved from Ramasco, Biuw, and Nilssen (2014), and the data on the Vesterålen-seals (2007 - 2008) were found in Ramasco (2008).

2.4 Statistical Analyses

I wanted to investigate if the selected continuous and categorical environmental and temporal factors affected haul-out behavior of the harbor seals included in this study. Furthermore, I wanted to find out if I could detect interaction effects between selected environmental variables, and if these had significant effects on haul-out behavior. Lastly, I wanted to investigate if there were significant spatial differences in haul-out probability of the populations under the area-specific environmental and temporal conditions. The two distinctly different geographical locations of interest were Skagerrak and northern Norway, respectively.

A large part of the data was non-normally distributed. Furthermore, observations were sampled for each individual ID, which gave multiple observations from each of the harbor seals. This meant that there was dependence between observations and in the error terms. Treating them as independent observations could have led to Type II errors. To be able to deal with the non-normality and nested structure of the data, I used a generalized linear mixed model (GLMM), which is a model framework that takes a link function, and extends the generalized linear model by being able to consider correlations between variables and random effects of nested data structures, i.e., models that include both fixed and random effects (Bolker 2008; Zuur et al. 2009; Ieno and Zuur 2015; Douma and Weedon 2019). The ID (the categorical variable **REF**) was selected *a priori* as random effects, and thus accounted for pseudo-replication in the data. The random effects were assumed to follow a normal distribution.

The response variable in this study (**HAUL.TM**) was given as proportional observations of time spent hauled out during a 2 h time interval, or summary period, and treated as continuous data. The value of the variable was thus proportions between 0 to 1 (i.e., open unit interval (0, 1) = {x | 0 < x < 1}, Smithson and Verkuilen 2006). Initial data exploration revealed it to be right skewed and with high peaked kurtosis. In other words, it had a predominance of values close to zero. A beta distribution was chosen, and the choice was backed up by the decision tree found in Douma and Weedon (2019), and Cullen & Frey graphs (Delignette-Muller and Dutang 2015, see also Figure 31 in the Appendix).

A logit link function was chosen (see Equation 2.1), since the response's mean μ, given the predictors X, was assumed to be linear on the logit scale. Also, a logit link solved the problem of being constrained by $0 < \mu < 1$ and $\phi > 0$:

$$logit(\mu) = log(\frac{\mu}{1-\mu}) = \eta = X\beta \tag{2.1}$$

The logit, or log odds function calculates the expectation of y (the linear predictor), and the inverse (natural logarithm) function transforms back to values between 0 and 1.

The general structure of a model with a beta distributed response is $y \sim Beta(\alpha, \beta)\varepsilon(0, 1)$, where $\alpha, \beta > 0$ are shape parameters. Ferrari and Cribari-Neto (2004) suggest re-parameterization of α and β into μ and ϕ, respectively (Cribari-Neto and Zeileis 2010). The expected value of the mean are thus $E(y) = \mu$, and the variance can be derived from $VAR(y) = \mu(1 - \mu/(1 + \phi))$. The parameter ϕ is the *precision parameter* since, for fixed μ, the larger ϕ the smaller the variance of y. ϕ^-1 is thus a dispersion parameter.

The formula for the maximal model fitted to the two data sets (Skagerrak (N = 8225), and northern Norway (N = 44906)) is shown in the following Equation 2.2 (note that the categorical predictor **Location** was only added to the full model of northern Norway):

$$\begin{aligned}
&HAUL.TM \sim Beta(\mu, \phi) \\
&E(HAUL.TM) = \mu \\
&Var(HAUL.TM) = \mu(1 - \mu/(1 + \phi) \\
&logit(\mu) = log(\frac{\mu}{1 - \mu})
\end{aligned} \tag{2.2}$$

$$\begin{aligned}
logit(\mu) = &\beta_1 + \beta_2 sWindspeed \times \beta_3 sAir_Temperature \times \beta_4 sWaterlevel + \beta_5 sPrecipitation + \\
&\beta_6 Moon_cat + \beta_7 Light_cat + \beta_8 fMonth + \beta_9 Sex(+\beta_{10} Location) + z_i,
\end{aligned}$$

where $z_1 \sim N(0, \sigma^2_{REF})$, i.e., is the normally distributed random intercept.

2.4.1 Model selection

Model fitting was performed using the R package **glmmTMB** (Brooks et al. 2017), which took all arguments needed to fit a beta GLMM with a logit link function and a family function that could specify the beta family as an error distribution. The fitting process used maximum likelihood, and random effects were integrated out by application of the Laplace approximation.

Model selection for the Skagerrak GLMM was performed using the R package **buildmer** (Voeten 2021), with the function `buildglmmTMB`. When the maximal model was purposefully built, the administrative formula processor function was used on it, with backwards and forwards stepwise elimination. Akaike's Information Criterion (AIC) was used as a model selection criterion for estimating the relative quality of the model (e.g., Burnham and Anderson (2004)), and Equation 2.3 shows the general equation.

$$AIC = -2log[L(\hat{\Theta}|data)] + 2K \tag{2.3}$$

The model formulas that were retained (one with backwards, and one with forwards stepwise elimination), were fitted as beta GLMMs. The last step consisted of comparing the two competing best models by the AIC. The formula resulting from the backwards stepwise elimination process had the lowest AIC and was chosen as the best model conditional on the data and the full model formula.

Model selection on the northern Norway GLMM was performed using the R package **MuMIn** and its `dredge` function on the maximal model. The model ran into convergence issues when attempting to apply a stepwise elimination process, and lack of theoretical knowledge on optimization left me with this method. I organized the resulting model selection table by lowest AIC, and the resulting formula was chosen as the best model conditional on the data and the full model formula.

The selected model formulas for Skagerrak and northern Norway, respectively, are found in the sub-chapter "Model formulas and estimates" in the Results-chapter.

2.5 Model Validation

2.5.1 Nakagawa's R-squared

Variance explained and goodness-of-fit was performed by calculating Nakagawa's R^2 (Nakagawa and Schielzeth 2013; Lüdecke, Ben-Shachar, et al. 2021). The following formulas calculated both the marginal R^2 (Equation 2.4), providing the variance explained only by the fixed effects, and the conditional R^2 (Equation 2.5), providing the variance explained by the entire model, i.e., both fixed and random effects.

$$R^2_{GLMM(m)} = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_\gamma^2 + \sigma_\alpha^2 + \sigma_e^2 + \sigma_d^2}, \tag{2.4}$$

$$R^2_{GLMM(c)} = \frac{\sigma_f^2 + \sum_{i=1}^{n} \sigma_l^2}{\sigma_f^2 + \sum_{i=1}^{n} \sigma_l^2 + \sigma_e^2 + \sigma_d^2} \tag{2.5}$$

2.5.2 Residual diagnostics

Residual diagnostics were performed on the generalized linear models using the R package **DHARMa** (Hartig 2021). This package partly aided in overcoming the difficulty of interpreting GLMM residuals. An algorithm standardized the model residuals to values between 0 and 1 and simulated new response data for each observation from the fitted models. This made interpretation more intuitive. A residual was defined as "the value of the empirical density function at the value of the observed data" (Hartig 2021), where a value of 1 would indicate a perfect fit and values of 0 that all simulated values were larger than the observed.

2.5.3 Simulations

Simulations of the models were performed to see if the models performed as expected. The `simulate` function attached to the glmmTMB-package in R was used (Brooks et al. 2017). The simulation process generates computer generated pseudo-random numbers (seed values) from an assumed distribution, and this process re-samples the effects from the estimated distributions (Kumle, Võ, and Draschkow 2021; "Analyst Prep. Simulation and Bootstrapping"). This may thus indicate if the models perform satisfactory or not.

2.6 Interpretatiton of results

Visual representation of fixed effect estimates of the two models were performed with the functions `effect_plot` for single effects, and `plot_model` for interaction effects (Long 2020; Lüdecke 2021). Forest plots were created with the parameters- and see-packages in R (Lüdecke, Pati, et al. 2021; Lüdecke et al. 2020).

The estimated effects of a logistic regression model is on a log odds scale. I converted the output to probabilities by exponentiating them off a logarithmic scale to odds by the formula in Equation 2.6, and converted the odds to probabilities using the formula in Equation 2.7.

$$\frac{exp(ln(odds))}{1 + exp(ln(odds))} \tag{2.6}$$

$$prob = \frac{odds}{1 + odds} \tag{2.7}$$

3 Results

3.1 Descriptive statistics of the response and predictor variables

In the following sub-chapters, descriptive statistics of all the variables included in this study are reported. First, summary tables of central tendencies and percentages of variables are listed. Secondly, tables of proportion of time hauled out during all months represented in the two data sets in contexts of light categories, sex, and moon phase, respectively, are listed. Thirdly, an in-depth description of the properties of the response is reported. Fourth, summaries of individual seals are reported. Lastly, visual representations of the predictor variables are reported, in intuitive time-line and frequency graphs.

3.1.1 Summary statistics of variables

Descriptive statistics of the raw data from Skagerrak and northern Norway are listed in Table 5. Overall N is the total number of haul-out summaries, i.e., observations in the two main data sets. The continuous variables are described by their means, standard deviations (SD), minimum and maximum values. Categorical variables are described by percent share of the total number of summaries/observations. Individual ID represents all harbor seals tracked in Skagerrak between 2017 and 2020, and all seals tracked in northern Norway between 2007 and 2013, respectively.

Table 5. All variables incorporated in the maximal beta GLMMs fitted to the Skagerrak and northern Norway data, respectively. Continuous variables' respective means (with SD) and medians (with maximum and minimum values), as well as the percentage of each level in the categorical variables' overall observational count.

Skagerrak 2017 - 2020				Northern Norway 2007 - 2013			
Variables	Overall N (8225)	Variables	Overall N (8225)	Variables	Overall N (8225)	Variables	Overall N (44.401)
Haul-out time		Light categories		Haul-out time		Sex	
Mean (SD)	0.181 (0.362)	Day	2793 (34.0%)	Mean (SD)	0.141 (0.311)	F	22608 (50.3%)
Median [Min, Max]	0 [0, 1.00]	Dusk	593 (7.2%)	Median [Min, Max]	0 [0, 1.00]	M	22298 (49.7%)
Waterlevel		Night	4234 (51.5%)	Waterlevel		Individual ID (REF)	
Mean (SD)	66.0 (24.9)	Dawn	605 (7.4%)	Mean (SD)	167 (69.1)	gp10-641-07	2044 (4.6%)
Median [Min, Max]	63.8 [-0.900, 170]	Lunar phase		Median [Min, Max]	166 [-16.4, 355]	gp10-655-07	857 (1.9%)
Missing	6 (0.1%)	FM	252 (3.1%)	Missing	38 (0.1%)	gp10-683-07	2333 (5.3%)
Precipitation		FQ	288 (3.5%)	Precipitation		gp10-684-07	2457 (5.5%)
Mean (SD)	0.142 (0.470)	LQ	300 (3.6%)	Mean (SD)	0.156 (1.26)	gp10-685-07	1881 (4.2%)
Median [Min, Max]	0 [0, 7.70]	Middling	7115 (86.5%)	Median [Min, Max]	0 [0, 46.2]	pv30-01-09	3564 (8.0%)
Missing	25 (0.3%)	NM	270 (3.3%)	Air Temperature		pv30-02-09	1224 (2.8%)
Air Temperature		Sex		Mean (SD)	0.922 (6.63)	pv30-03-09	1830 (4.1%)
Mean (SD)	5.19 (4.28)	F	4709 (57.3%)	Median [Min, Max]	1.35 [-19.4, 24.5]	pv30-05-09	2484 (5.6%)
Median [Min, Max]	4.90 [-4.82, 18.2]	M	3516 (42.7%)	Missing	2716 (6.1%)	pv30-06-09	3192 (7.2%)
Missing	1 (0.0%)	Individual ID		Windspeed		pv30-07-09	1184 (2.7%)
Windspeed		pv35b-04-11	27 (0.3%)	Mean (SD)	5.99 (3.24)	pv30-08-09	3444 (7.8%)
Mean (SD)	6.84 (3.77)	pv35b-05-11	1539 (18.7%)	Median [Min, Max]	5.60 [0, 21.3]	pv30-09-09	3552 (8.0%)
Median [Min, Max]	6.13 [0.500, 21.5]	pv35b-06-11	270 (3.3%)	Missing	2833 (6.4%)	pv30-10-09	264 (0.6%)
Missing	470 (5.7%)	pv35b-08-11	45 (0.5%)	Months		pv30-11-09	3288 (7.4%)
Months		pv35b-09-11	18 (0.2%)	Sep	6150 (13.9%)	pv30-12-09	1224 (2.8%)
Nov	1340 (16.3%)	pv35b-10-11	54 (0.7%)	Oct	7020 (15.8%)	pv30-13-09	2928 (6.6%)
Dec	2150 (26.1%)	pv68-F53_Iris-14	1600 (19.5%)	Nov	6216 (14.0%)	pv35-01-11	5442 (12.3%)
Jan	1488 (18.1%)	pv68-F56_Karin-14	1516 (18.4%)	Dec	6060 (13.6%)	pv35-02-11	594 (1.3%)
Feb	1324 (16.1%)	pv68-M40_Pedro-14	1408 (17.1%)	Jan	4953 (11.2%)	pv35-03-11	615 (1.4%)
March	696 (8.5%)	pv68-M42_Einar-14	1256 (15.3%)	Feb	3621 (8.2%)	Light categories	
Aug	279 (3.4%)	pv68-M47_Vemund-14	492 (6.0%)	March	3566 (8.0%)	Day	10140 (22.8%)
Sep	576 (7.0%)			April	2500 (5.6%)	Dusk	3013 (6.8%)
Oct	372 (4.5%)			May	2445 (5.5%)	Night	28251 (63.6%)
				June	1389 (3.1%)	Dawn	2997 (6.7%)
				July	481 (1.1%)	Lunar phase	
				Location		FM	1493 (3.4%)
				Porsanger_2009_2013	34829 (78.4%)	FQ	1469 (3.3%)
				Vesteralen_2008	9572 (21.6%)	LQ	1536 (3.5%)
						Middling	38412 (86.5%)
						NM	1491 (3.4%)

Table 6. Months divided in percent representation of each light category, and subsequent mean percent haul-out for each level per month. Skagerrak and northern Norway data sets are represented, respectively. Skagerrak months run from August to March, and northern Norway months from September to July (August). The polar night in the north ensures mainly night-level observations from November through January, and northern midnight sun ensures a dominance of day-level observations from May through July. Months are pooled (Skagerrak 2017 - 2020, northern Norway 2007 - 2013).

	Skagerrak 2017 -2020 (N = 8225)				**Northern Norway 2007 - 2013 (N = 44401)**			
Month	Night (perc.)	Day (perc.)	Dawn (perc.)	Dusk (perc)	Night (perc.)	Day (perc.)	Dawn (perc.)	Dusk (perc)
September	**33**	**56**	**5**	**6**	**27**	**52**	**10**	**10**
Hauled out (mean)	30.5	23.9	27.2	29.5	14.4	14.9	9.1	15
October	**43**	**42**	**7**	**8**	**44**	**38**	**9**	**9**
Hauled out (mean)	40.5	3.2	27	20	22	11.6	10	11.8
November	**59**	**26**	**8**	**7**	**67**	**13**	**10**	**10**
Hauled out (mean)	19.5	9.3	12.1	6.6	18.7	9.9	8.5	9.1
December	**58**	**25**	**0.4**	**8**	**99.6**	**0.0008**	**0.002**	**0.002**
Hauled out (mean)	20.2	12.3	11.3	12	15.1	30.8	7.8	15.5
January	**57**	**28**	**8**	**6**	**84**	**5**	**5**	**6**
Hauled out (mean)	16.5	12	12.4	7	15	11.7	16.7	12.3
February	**49**	**38**	**5**	**8**	**50**	**29**	**10**	**10**
Hauled out (mean)	16.9	13.6	9.8	11.2	10.4	9.7	12.8	9.1
March	**40**	**48**	**8**	**4**	**32**	**49**	**10**	**10**
Hauled out (mean)	14.6	25.8	22.2	5.7	13.8	9.8	11.8	6.9
April	**-**	**-**	**-**	**-**	**3**	**90**	**4**	**3**
Hauled out (mean)	-	-	-	-	10.5	8.8	16.4	8.6
May	**-**	**-**	**-**	**-**	**-**	**100**	**-**	**-**
Hauled out (mean)	-	-	-	-	-	11.2	-	-
June	**-**	**-**	**-**	**-**	**-**	**100**	**-**	**-**
Hauled out (mean)	-	-	-	-	-	17.4	-	-
July	**-**	**-**	**-**	**-**	**-**	**100**	**-**	**-**
Hauled out (mean)	-	-	-	-	-	36.9	-	-
August	**24**	**60**	**8**	**8**	**-**	**-**	**-**	**-**
Hauled out (mean)	68.6	41.9	69.8	41.4	-	-	-	-

Table 7. Months divided in percent representation of each gender, and subsequent average percent haul-out for each sex per month. Skagerrak and northern Norway data sets are represented, respectively. Skagerrak months run from August to March, and northern Norway months from September to July (August). Month are pooled (Skagerrak 2017 - 2020, northern Norway 2007 - 2013).

	Skagerrak 2017 - 2020 (N = 8225)		**Northern Norway 2007 - 2013 (N = 44401)**	
Month	Male (perc.)	Female (perc.)	Male (perc.)	Female (perc)
September	**34**	**66**	**53**	**47**
Hauled out (mean)	41.3	18.8	12.7	15.8
October	**-**	**100**	**54**	**46**
Hauled out (mean)	-	22.3	15.5	16.2
November	**44**	**56**	**52**	**48**
Hauled out (mean)	15.3	15.4	15.3	15.8
December	**48**	**52**	**51**	**49**
Hauled out (mean)	21.2	12.6	14.7	15.5
January	**50**	**50**	**46**	**54**
Hauled out (mean)	15.5	13	14.7	14.8
February	**49**	**51**	**33**	**67**
Hauled out (mean)	14.9	14.8	10.3	10.3
March	**20**	**80**	**41**	**59**
Hauled out (mean)	27.4	18.5	10.8	11.1
April	**-**	**-**	**43**	**57**
Hauled out (mean)	-	-	9.8	8.6
May	**-**	**-**	**46**	**54**
Hauled out (mean)	-	-	10.3	11.9
June	**-**	**-**	**68**	**32**
Hauled out (mean)	-	-	16.4	19.6
July	**-**	**-**	**98**	**2**
Hauled out (mean)	-	-	37.4	13.6
August	**58**	**42**	**-**	**-**
Hauled out (mean)	51	49.5	-	-

Table 8. Months divided in percent representation of each moon phase category, and subsequent mean percent haul-out for each level per month. Only the northern Norway data set is represented. Months run from September to July (August). Months are pooled in the time period 2007 - 2013.

	Moon Categories in Northern Norway 2007 - 2013 (N = 44401)				
Month	Full Moon (perc.)	First Quarter (perc.)	Last Quarter (perc.)	Middling (perc)	New Moon (perc.)
September	**3**	**3**	**4**	**86**	**3**
Hauled out (mean)	5.9	7.2	20	14.7	7.9
October	**3**	**3**	**3**	**87**	**3**
Hauled out (mean)	8	9.1	13.7	16.3	12.2
November	**3**	**3**	**3**	**87**	**3**
Hauled out (mean)	11.6	21.6	25.5	15.1	15.4
December	**4**	**3**	**4**	**85**	**3**
Hauled out (mean)	16.9	6.8	37.2	14.5	7.9
January	**3**	**3**	**3**	**87**	**4**
Hauled out (mean)	10.3	29.9	2.3	14.2	25.9
February	**3**	**4**	**3**	**86**	**3**
Hauled out (mean)	9.5	6.1	6.1	10.5	13.7
March	**3**	**3**	**3**	**88**	**3**
Hauled out (mean)	0.2	5.9	2	11.2	29.3
April	**3**	**3**	**3**	**87**	**3**
Hauled out (mean)	6.1	9.3	24.9	9	0
May	**3**	**3**	**3**	**85**	**5**
Hauled out (mean)	8.1	7.9	7.9	11.3	15.7
June	**3**	**3**	**3**	**88**	**2**
Hauled out (mean)	19.1	23	6.8	17.7	10.1
July	**2**	**2**	**5**	**88**	**2**
Hauled out (mean)	12.1	41.6	5.4	37.4	100
August	**-**	**-**	**-**	**-**	**-**
Hauled out (mean)	-	-	-	-	-

3.1.2 Summary statistics on the response variables

The distribution of the response variable (proportion of time hauled out) was important to understand, due to its non-normal properties. Central tendencies of proportion of time hauled (behavioral response) for Skagerrak were: mean = 0.181, SD = 0.362, mode = 4.738×10^{-5}, median = 4.74×10^{-5}, and for northern Norway: mean = 0.142, SD = 0.311, mode = 1.113×10^{-5}, median = 1.11×10^{-5}. These values indicate highly positively skewed distributions, with many very low values. As another measure of symmetry, the Skagerrak response had a skewdness of 1.643 (SE = 0.003) and a kurtosis of 3.87 (SE = 3.053), and the northern Norway response had a skewdness of 2.014 (SE = 0.012) and a kurtosis of 5.442, indicating similar distributions, but a larger skew towards zero and higher peaks here than found in the Skagerrak response.

Predictions of how to best model the distribution based on skewness and kurtosis by 500 bootstrap samples in a Cullen and Frey graph (see Figure 29 in the Appendix), suggested that the response fell within a theoretical beta distribution. This is visualized in the two times two density graphs in Figure 5, which show obvious and significant positive skewdness with medians (red vertical lines) (and modes) very close to zero (see also Figure 29 in Appendix).

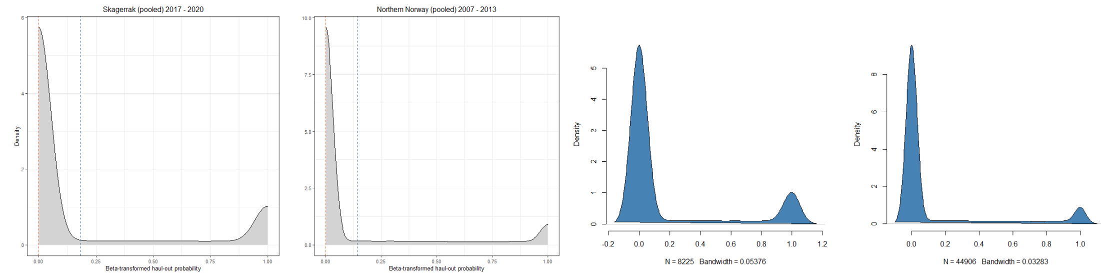

Figure 5. Two visualizations of density graphs of the response variable (proportion of haul-out time) for Skagerrak and northern Norway. The blue vertical lines in the first two graphs represent mean values, and the red vertical lines represent median values of the distribution of the response. Notice the significant positive skewdness and clear kurtosis of the distributions, with all mean values being greater than the median values. N is the number of summaries (observations) of the responses.

The response variable (where one observation was the proportion of time hauled out between a time interval of 2 hours, with an interval range of (0, 1)) was thus considered to have a beta distribution. The shape parameters α and β for the Skagerrak response, with known μ (0.265) and σ^2 (0.1614), and the northern Norway response, with known μ (0.1417) and σ^2 (0.0966), were calculated by the algebraic formulas in Equations 3.1 and 3.2. The shape parameters for the Skagerrak response was $\alpha = 0.055$ and $\beta = 0.1521$.

$$\alpha = (\frac{1-\mu}{\sigma^2} - \frac{1}{\mu})\mu^2 \tag{3.1}$$

$$\beta = \alpha(\frac{1}{\mu} - 1) \tag{3.2}$$

The process of validating the parameters was done by solving for μ (Equation 3.3) and σ^2 (Equation 3.4).

$$\mu = \frac{\alpha}{\alpha + \beta} \tag{3.3}$$

$$\sigma^2 = \frac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)} \tag{3.4}$$

3.1.3 Summary statistics of the study animals

Skagerrak. Five seals (three males and two females) were tagged at the **Bolærne islands** and skerries (Færder National park) in the middle of the outer Oslo fjord November 14, 2019 (Table 2 and Figure 3). One individual, a male (“Vemund”), stopped transmitting on December 25, after 41 days. Another male (“Einar”) stopped transmitting February 27 the next year (105 days). The third male (“Pedro”) and the two females (“Karin” and Iris") transmitted until March 12, 21 and 28, 2020 (119, 128 and 135 days, respectively). Six seals were tagged around **Jomfruland National Park** between August 25 and August 29, 2017. See Figure 3 for location. The transmitting days for three of these individuals (male 04, male 08, and male 09) did not extend further than 6 days. Two of the individuals (male 06 and female 10) transmitted for 22 and 23 days respectively. One individual, female 05, transmitted for 128 days with the last record on December 31, 2017.

The mean weight of the 11 study animals in Skagerrak was 51.877 kg (SD = 9.612), and the mean length was found to be 123.694 cm (SD = 9.811) The gender distribution was 57% females and 43% males.

Individuals tagged in **Porsangerfjorden** represented the northernmost area of this study. See Table 3 for more details and Figure 3 for location. Two males (pv35-01 and pv35-02) were tagged in September 2012, where one transmitted for 484 days, and the other for 49 days. One male (pv35-03) tagged the year before, in August 2011, transmitted for 51 days. Three males tagged in September 2010 (pv30-02, pv30-08 and pv30-10) transmitted for 112, 287, and 22 days, respectively. Two females (pv30-09 and pv30-13) were also tagged in September 2010, and they transmitted for 311 and 254 days, respectively. One male (pv30-03) was tagged in August 2010, and transmitted for 152 days. In October 2009, one male (pv30-07) was tagged, and transmitted for 99 days. In September 2009, three males (pv30-01, pv30-05, and pv30-12) and two females (pv30-06 and pv30-11) were tagged, and they transmitted for 311, 207, 102, 268 and 274 days, respectively. For more details about the harbor seals tagged in Porsangerfjorden, please see Ramasco, Biuw, and Nilssen (2014) and Ramasco (2015). In **Vesterålen** (Øksnes/Stø), five juvenile female harbor seals were tagged in August 2007 (gp10-641, -655, -683, -684, and -685). They transmitted data for 215, 95, 196, 209, and 170 days, respectively. See Table. 3 for details, and Figure 3 for location along the coast. The biological data of these seals listed in Table 3 were retrieved from Ramasco (2008).

The mean weight of the 16 study animals in northern Norway was approx 27.376 kg (SD = 5.318), and the mean length was found to be 98.807 (SD = 9.259) The two genders were approx equally distributed, with 50% males and 50% females.

Figures 26 to 29 in the Appendix portrays haul-out time line profiles for individual harbor seals in this study.

3.1.4 Visual presentation of the covariates

Figure 6. Waterlevel observations (cm) for tracking events in Skagerrak 2017-20 (left) and northern Norway 2007-13 (right), respectively. A red smoothing line was added in order to highligh trends.

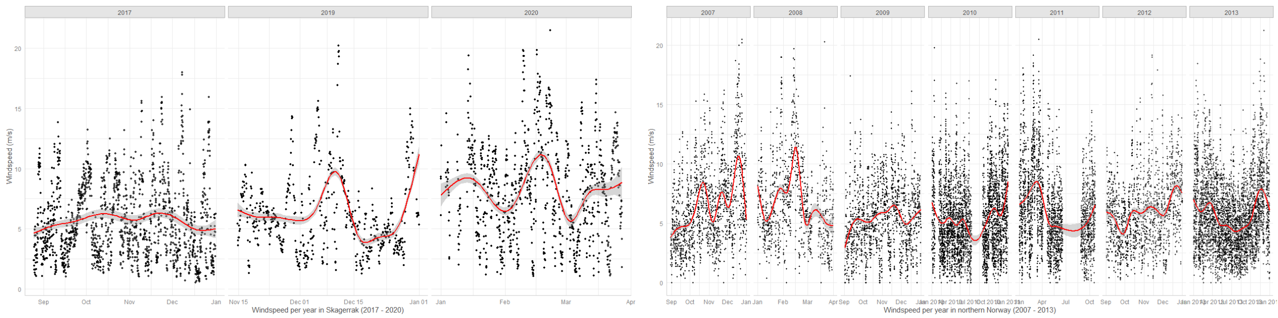

Figure 7. Windspeed measurements (m/s) for tracking events in Skagerrak 2017-20 (left) and northern Norway 2007-13 (right), respectively. A red smoothing line was added in order to highligh trends.

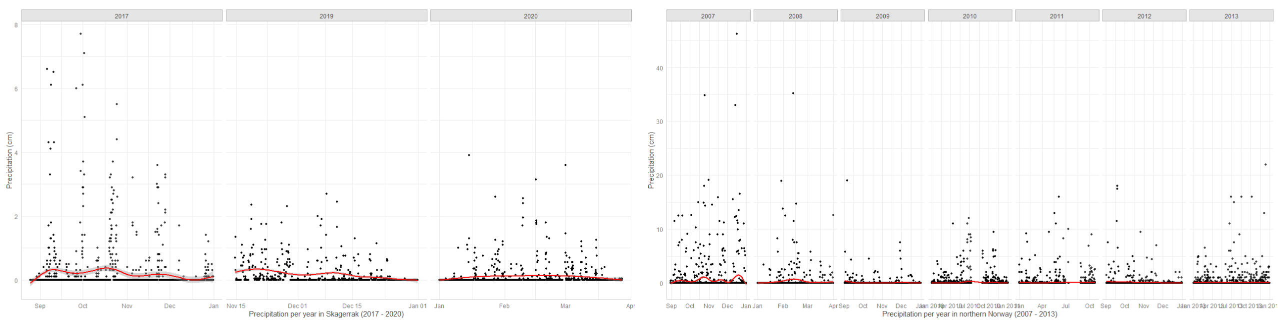

Figure 8. Precipitation statistics (cm) for tracking events in Skagerrak 2017-20 (left) and northern Norway 2007-13 (right), respectively. A red smoothing line was added in order to highligh trends.

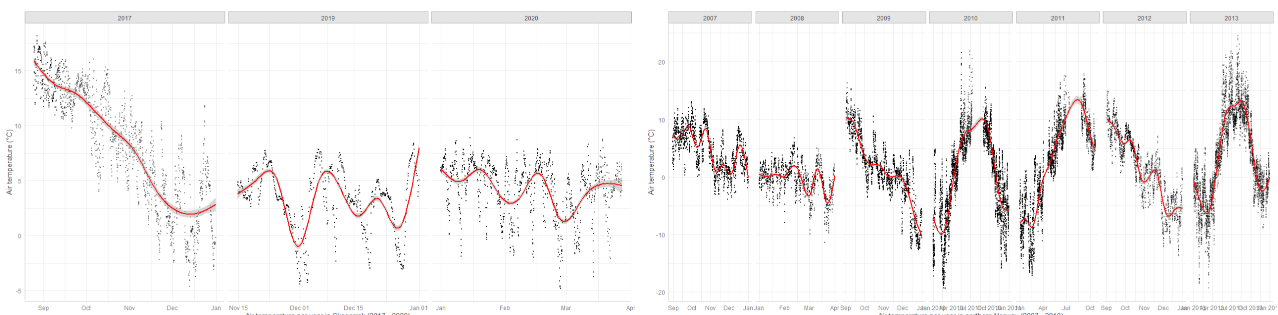

Figure 9. Air temperature measurements (°C) for tracking events in Skagerrak 2017-20 (left) and northern Norway 2007-13 (right), respectively. A red smoothing line was added in order to highligh trends.

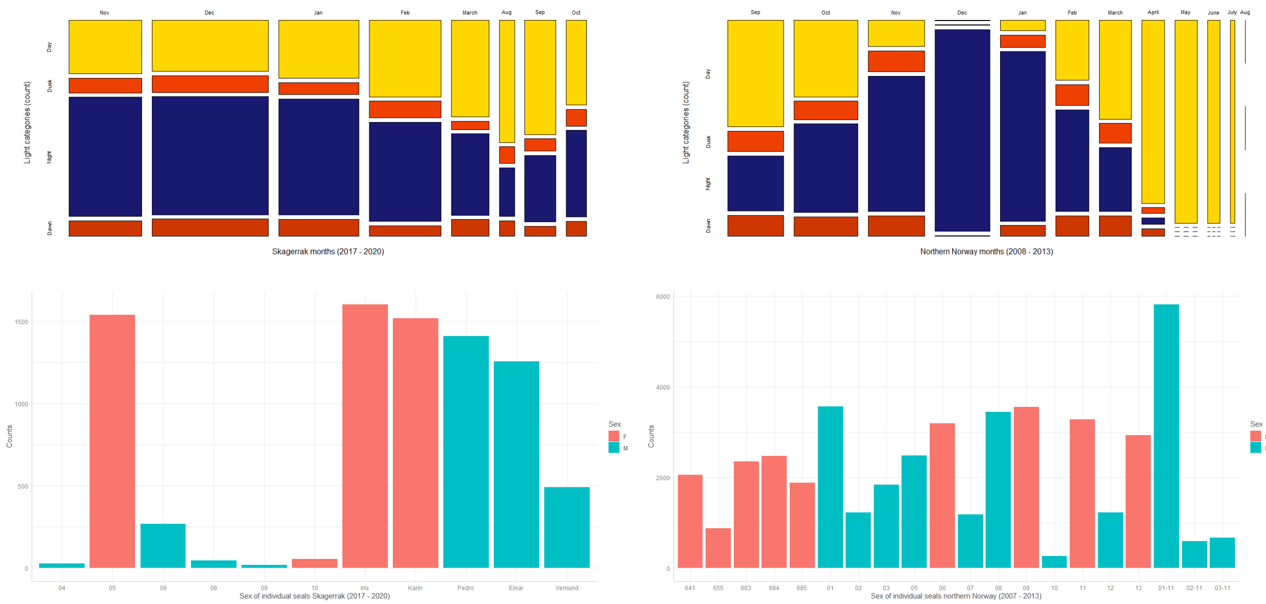

Figure 10. Upper mosaic plots depict light categories for each month of tracking events in Skagerrak (left) and northern Norway (right), respectively. From bottom: dawn, night, dusk, and day. Lower barcharts depict sex and observation counts of each individual seal for tracking events in Skagerrak (left) and northern Norway (right), respectively.

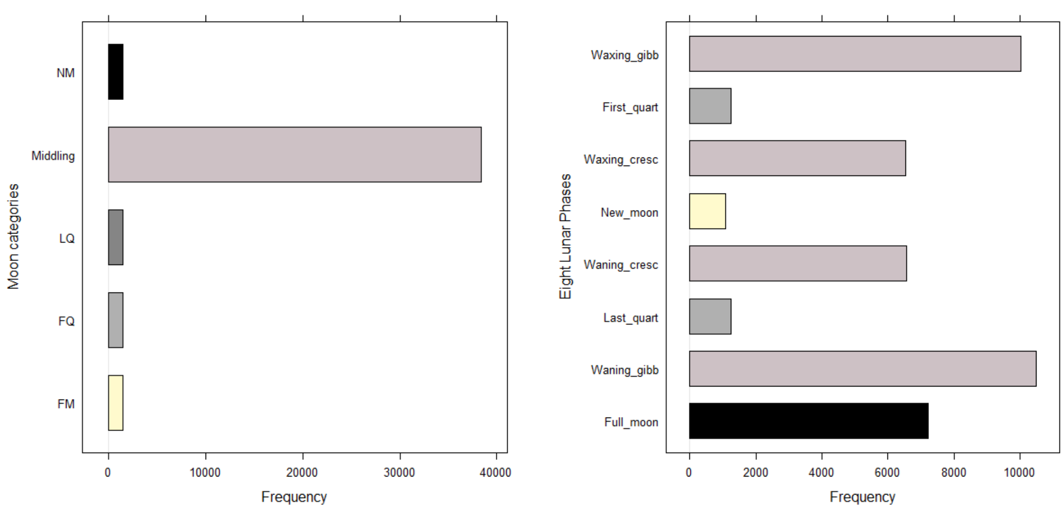

Figure 11. Frequency of the five moon categories used in this study (left), and the four additional middle-phases (right) pooled in the Middling category to the left. Both areas in the study are represented, since lunar phases change systematically throughout the synodic month (every 29.53 days, see nineplanets.org (n.d.)). From the bottom left: full moon (FM), first quarter (FQ), last quarter (LQ), middling (the four phases in between, pooled together), and new moon (NM). See figure for further reference.

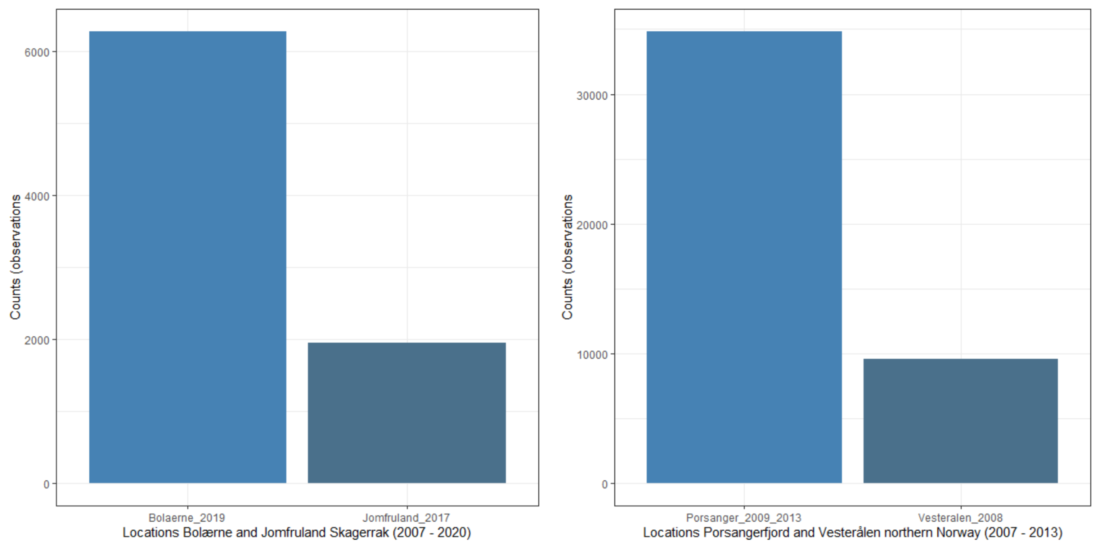

Figure 12. Observation counts from the two locations in the Skagerrak (left). The locations were Jomfruland and Bolærne in Vestfold and Telemark County, respectively. Observation counts from the two locations in northern Norway (right). The locations were Porsangerfjord in Troms and Finnmark county and Vesterålen in Nordland County, respectively.

3.2 Model formulas

3.2.1 Skagerrak model formula

The final model formula fitted to the Skagerrak data set (Equation 3.5):

$$\begin{aligned} &transform\_HAUL.TM \sim fMonth + sAir\_Temperature + Light\_cat + Sex + sWaterlevel + \\ &sWindspeed + sAir\_Temperature \times sWindspeed + sAir\_Temperature \times sWaterlevel + \\ &sWaterlevel \times sWindspeed + (1|REF) \end{aligned} \tag{3.5}$$

3.2.2 Northern Norway model formula

The final model formula fitted to the northern Norway data set (Equation 3.6):

$$\begin{aligned} &transform\_HAUL.TM \sim sAir\_Temperature + sWaterlevel + sWindspeed + fMonth + \\ &Light\_cat + Moon\_cat + sAir\_Temperature \times sWindspeed + sWaterlevel \times sWindspeed + \\ &sAir\_Temperature \times sWindspeed + (1|REF) \end{aligned} \tag{3.6}$$

3.3 Model estimates

The following two sub-chapters, including Tables 9 and 10, are reports of the estimates, standard errors, and 95% confidence intervals (CI's) of my findings. The estimates with significant terms and CI's not including 0 effect are highlighted in bold font and reported in the following paragraphs. Due to the logistic link between the response and covariates, coefficients are interpreted as log-odds, having a *multiplicative* effect, and converted to probabilities and odd ratios to make interpretations more intuitive.

3.3.1 Skagerrak beta GLMM

Table 9 lists coefficients, their standard errors, confidence intervals, p-values, probabilities and odds ratios from the Skagerrak model. A brief description of the results are presented below.

On the categorical predictor **Month**, the coefficients for conditions **January**, **February**, **March**, **August**, **September** and **October**, respectively, represented the differences in log-odds between cases with conditions of the mention months, and the case with condition **November** (the reference month, i.e., base level). On the categorical predictor **Light**, the coefficient of condition **Night** represented the difference in log-odds between the case with **Night**, and the case with condition **Day** (the reference light category, i.e., base level).

Table 9. Table of coefficients, standard error, 95 percent confidence interval, z- and p values, calculated probabilities, and odds ratios of the Skagerrak GLMM model predictions with beta distributed response, a logit link function, and a random intercept. Significant terms according to p values and confidence intervals are highlighted in bold. Intercept probability and odds is the value if all predictors had zero effect

	Coefficient	SE	CI low (95 perc.)	CI high (95 perc.)	z value	p value	Probability (perc.)	Odds ratio
Intercept	**-1.150**	**0.084**	**-1.314**	**-0.985**	**-13.678**	**<0.001**	**24.1**	**0.317**
December	0.017	0.049	-0.08	0.114	0.342	0.732	24.4	0.322
January	**0.170**	**0.059**	**0.054**	**0.287**	**2.868**	**0.004**	**27.3**	**0.376**
February	**0.178**	**0.059**	**0.063**	**0.293**	**3.029**	**0.002**	**27.4**	**0.378**
March	**0.253**	**0.066**	**0.124**	**0.382**	**3.831**	**<0.001**	**29**	**0.408**
August	**0.996**	**0.155**	**0.692**	**1.301**	**6.42**	**<0.001**	**46.2**	**0.858**
September	**0.332**	**0.116**	**0.104**	**0.559**	**2.854**	**0.004**	**30.6**	**0.441**
October	**0.303**	**0.095**	**0.116**	**0.49**	**3.176**	**0.001**	**30**	**0.429**
Air temperature	-0.058	0.034	-0.125	0.009	-1.702	0.089	23	0.299
Dusk	-0.035	0.06	-0.152	0.083	-0.578	0.563	23.4	0.306
Night	**0.169**	**0.033**	**0.104**	**0.234**	**5.062**	**<0.001**	**27.3**	**0.375**
Dawn	0.017	0.06	-0.101	0.135	0.286	0.775	24.4	0.322
Sex (male)	0.147	0.09	-0.029	0.323	1.638	0.101	26.8	0.367
Waterlevel	-0.021	0.019	-0.058	0.017	-1.086	0.278	23.7	0.205
Windspeed	**-0.233**	**0.021**	**-0.273**	**-0.193**	**-11.359**	**<0.001**	**20.1**	**0.251**
Air Temperature x Waterlevel	-0.041	0.024	-0.089	0.006	-1.704	0.088	23.3	0.304
Air Temperature x Windspeed	**0.057**	**0.021**	**0.016**	**0.097**	**2.714**	**0.007**	**25.1**	**0.335**
Waterlevel x Windspeed	**0.044**	**0.015**	**0.015**	**0.073**	**3.014**	**0.003**	**24.9**	**0.331**
SD (Random intercept)	0.111	-	-	-	-	-	-	-

Intercept (the probability of hauling out by females during day time in November), with factor -1.15 (SE = 0.084, 95% CI = [-1.314, -0.985], P = 24.1%, odds = 1/3.15), when all predictors were held at zero. In other words, β_0 was the baseline log-odds of hauling out during conditions **Female**, **Day**, and **November**.

Haul-out time was significantly higher in **August** (P = 22.1%), **September** (P = 6.5%), **October** (P = 5.9%), **December** (P = 0.3%), **January** (P = 3.2%), **February** (P = 3.3%), and **March** (P = 4.9%), compared to reference condition **November**.

Haul-out time was significantly higher under condition **Night** (P = 3.2%), compared to condition **Day**.

Under condition **Windspeed**, the log-odds of hauling out significantly decreased by factor -0.233 (SE = 0.021, 95% CI = [-0.273, -0.193], P = 20.1%, odds = 1/3.98). P = (-24.1 + 20.1) % = -4% for every unit increase in **Windspeed**.

Under condition **Air temperature interacting with Windspeed**, the log-odds of hauling out significantly increased by factor 0.057 (SE = 0.021, 95% CI = [0.016, 0.097]). P = (-24 +25) % = 1%, odds = 1/2.99, compared to hauling out during daytime in November. For every increase of a combined effect of unites of temperature and windspeed, P = 1%.

Under condition **Waterlevel interacting with Windspeed**, the log-odds of hauling out significantly increased by factor 0.044 (SE = 0.015, 95% CI = [0.015, 0.073]), P = (-24.1 +25.1) % = 1%, odds = 1/3.02, compared to hauling out during daytime in November. For every increase of combined effect of units of waterlevel and windspeed, the probability of hauling out increased by P = 1%.

3.3.2 Northern Norway beta GLM

Table 10 lists coefficients, their standard errors, confidence intervals, p-values, probabilities and odds ratios from the northern Norway model. Results derived from the estimates are explained.

On the categorical predictor **Month**, the coefficients for conditions **October**, **November**, **December**, **January**, **February**, **March**, **June** and **July**, respectively, represented the differences in log-odds between cases with conditions of these months, and the case with condition **September** (the reference month, i.e., base level). On the categorical predictor **Light categories**, the coefficient of condition **Night** represented the difference in log-odds between the case with **Night**, and the case with condition **Day** (the reference light category, i.e., base level). On the categorical predictor **Moon phase**, the coefficient for condition **Last quarter** represented the difference in log-odds between the case with **Last quarter**, and the case with condition **Full moon** (the reference moon phase).

Intercept (the probability of hauling out during day time under full moon in September), with factor -1.453 (SE = 0.041, 95% CI = [-1.533, -1.374], P = 24.1%, odds = 1/5.10), when all predictors were held at zero.

Haul-out time was significantly higher in **October** (P = 2.2%), **November** (P = 3%), **December** (P = 3.2%), **January** (P = 3.1%), **February** (P = 3%), **March** (P = 2.7%), **June** (P = 1.5%), and **July** (P = 11.1%), compared to the reference condition **September**.

Haul-out time was significantly higher under condition **Night** (P = 2.2%), compared to condition **Day**.

Under condition **Windspeed**, the log-odds of hauling out significantly decreased by factor -0.134 (SE = 0.007, 95% CI = [-0.147, -0.121], P = 17%, odds = 1/4.90). P = (-18.9 + 17) % = -1.9% hauling out for every unit increase in **Windspeed**.

Under condition **Air temperature**, the log-odds of hauling out significantly increased by factor 0.11 (SE = 0.011, 95% CI = [0.09, 0.131], P = 20.7%, odds = 1/4.29). P = (-18.9 + 20.7) % = 1.8% for every unit increase in **Air temperature**.

Under condition **Waterlevel**, the log-odds of hauling out significantly decreased by factor -0.124 (SE = 0.006, 95% CI = [-0.136, -0.112]), P = 17.1%, odds = 1/3.83. P = (-18.9 + 17.1) % = -1.8% hauling out for every unit increase in **Waterlevel**.

Haul-out time was significantly higher under condition **Last quarter** (P = 2.4%), compared to reference condition **Full moon**.

Table 10. Table of coefficients, standard error, 95 percent confidence interval, z- and p values, calculated probabilities, and odds ratios of the northern Norway GLM model predictions with beta distributed response and a logit link function. Significant terms according to p values and confidence intervals are highlighted in bold. Intercept probability and odds is the value if all predictors had zero effect

Parameter	Coefficient	SE	CI low (95 perc.)	CI high (95 perc.)	z value	p value	Probability (perc.)	Odds ratio
Intercept	**-1.453**	**0.041**	**-1.533**	**-1.374**	**-35.703**	**<0.001**	**18.9**	**0.196**
Air temperature	**0.110**	**0.011**	**0.09**	**0.131**	**10.471**	**<0.001**	**20.7**	**0.233**
Waterlevel	**-0.124**	**0.006**	**-0.136**	**-0.112**	**-19.985**	**<0.001**	**17.1**	**0.261**
Windspeed	**-0.134**	**0.007**	**-0.147**	**-0.121**	**-20.332**	**<0.001**	**17**	**0.204**
October	**0.134**	**0.023**	**0.088**	**0.179**	**5.755**	**<0.001**	**21.1**	**0.267**
November	**0.183**	**0.028**	**0.128**	**0.237**	**6.59**	**<0.001**	**21.9**	**0.281**
December	**0.191**	**0.031**	**0.13**	**0.253**	**6.104**	**<0.001**	**22.1**	**0.283**
January	**0.189**	**0.035**	**0.121**	**0.257**	**5.434**	**<0.001**	**22**	**0.282**
February	**0.182**	**0.036**	**0.112**	**0.253**	**5.085**	**<0.001**	**21.9**	**0.28**
March	**0.167**	**0.034**	**0.101**	**0.234**	**4.928**	**<0.001**	**21.6**	**0.276**
April	0.058	0.035	-0.011	0.127	1.659	0.097	19.9	0.248
May	-0.027	0.033	-0.092	0.038	-0.824	0.41	18.5	0.228
June	**0.093**	**0.041**	**0.012**	**0.173**	**2.259**	**0.024**	**20.4**	**0.257**
July	**0.603**	**0.068**	**0.47**	**0.736**	**8.879**	**<0.001**	**30**	**0.427**
Dusk	0.002	0.027	-0.05	0.054	0.087	0.931	19	0.234
Night	**0.135**	**0.018**	**0.1**	**0.17**	**7.569**	**<0.001**	**21.1**	**0.268**
Dawn	-0.026	0.026	-0.077	0.026	-0.967	0.334	18.6	0.228
First quarter	0.055	0.047	-0.037	0.147	1.179	0.238	19.8	0.247
Last quarter	**0.149**	**0.046**	**0.058**	**0.24**	**3.214**	**0.001**	**21.3**	**0.271**
Middling	0.061	0.033	-0.004	0.126	1.826	0.068	19.9	0.249
New moon	0.009	0.046	-0.082	0.099	0.188	0.851	19.1	0.236
Air temperature x Windspeed	**0.016**	**0.006**	**0.003**	**0.029**	**2.49**	**0.013**	**19.2**	**0.238**
Waterlevel x Windspeed	**0.042**	**0.006**	**0.03**	**0.054**	**6.799**	**<0.001**	**19.6**	**0.244**
SD (Random intercept)	0.054	-	-	-	-	-	-	-

Under condition **Air temperature interacting with Windspeed**, the log-odds of hauling out significantly increased by factor 0.016 (SE = 0.006, 95% CI = [0.003, 0.029] P = 19.2%, odds = 1/4.20). For every increase of combined effect of units of air temperature and windspeed, the probability of hauling out increased by P = 0.3%.

Under condition **Waterlevel interacting with Windspeed**, the log-odds of hauling out significantly increased by factor 0.042 (SE = 0.006, 95% CI = [0.03, 0.054], P = 19.6%, odd = 1/4.10). For every increase of combined effect of units of water level and windspeed, the probability of hauling out increased by $P = 0.7\%$.

3.3.3 Forest plots of coefficient estimates

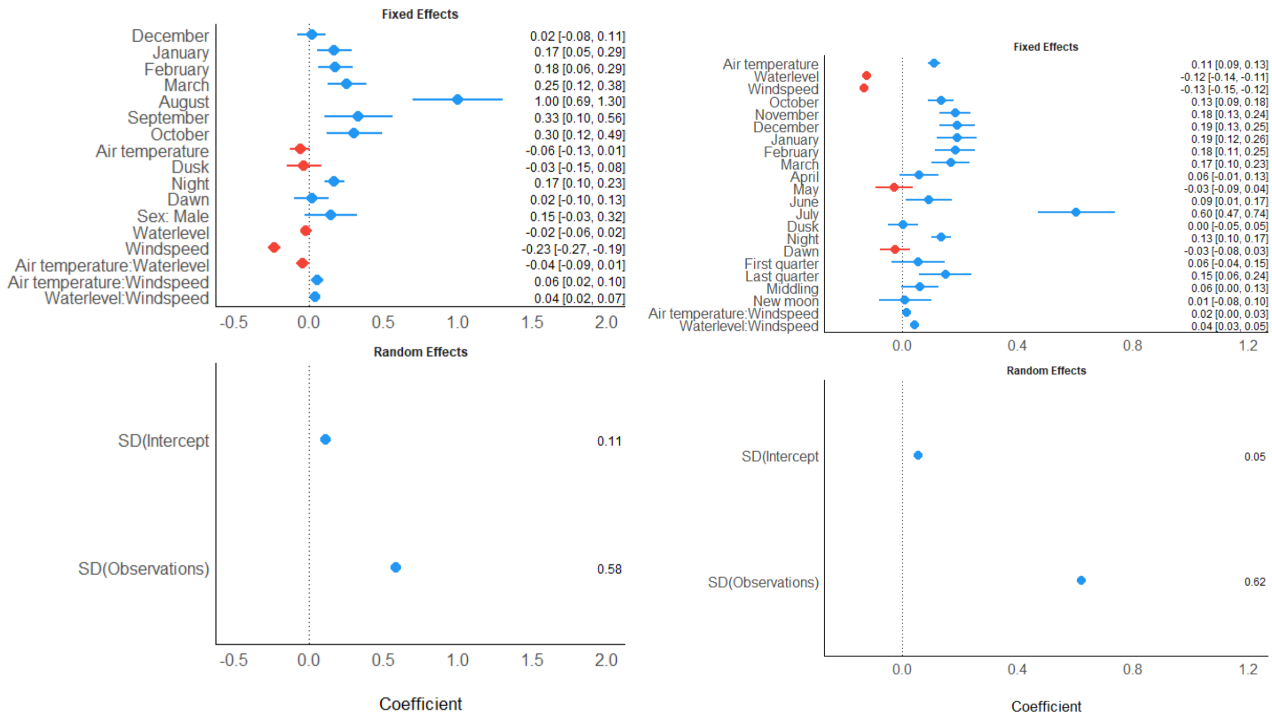

Figure 13. Forest plots of fixed and random effects estimated from the Skagerrak GLMM and the northern Norway GLM, both with a beta distributed response. Random effects have undergone shrinkage, and the point estimates represent the standard deviations calculated by the model by use of the Laplace approximation.

3.3.4 Random effect

Individual seals were added as random effect to account for pseudo-replication. Random effects assume normal (Gaussian) distribution, i.e., $Skagerrak_{REF} \sim N(0, \tau)$ and $North_{REF} \sim N(0, \sigma)$. The following two times two plots show ordered caterpillar plots and a probabilistic normal distribution of the samples of individual seals. The Skagerrak model's random effect is portrayed above, and the norther Norway model's random effect is portrayed below.

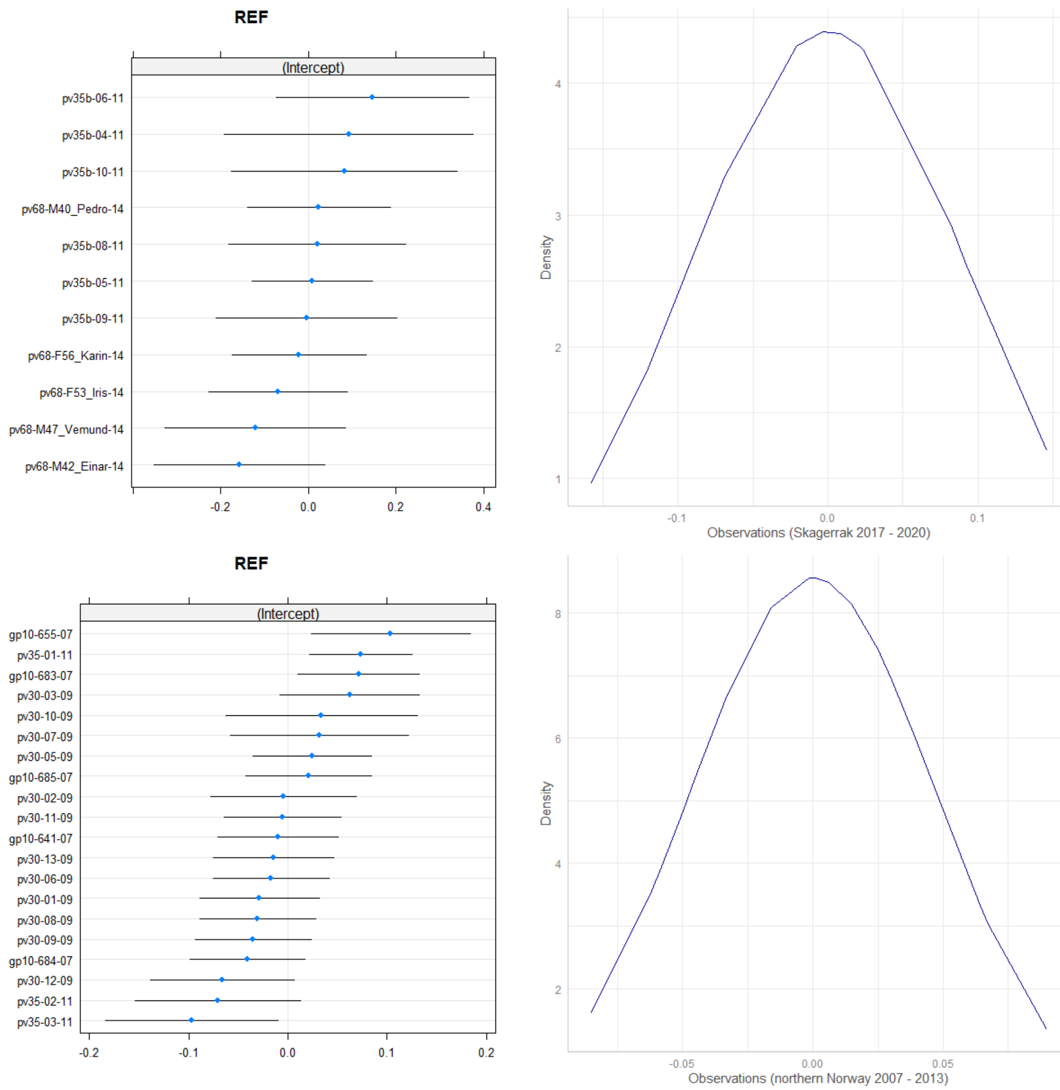

Figure 14. Upper left: Caterpillar plots (left) and density plots (right) of estimates of the random effect of the Skagerrak GLMM, ordered by magnitude. The random effect was assumed to be multivariately Gaussian (normally distributed), by the Laplace approximation, with mean 0 and standard deviation 0.111.

3.3.5 Effect plots of fixed effects

The following graphs show predicted effect plots of all significant fixed effects in the Skagerrak and northern Norway models.

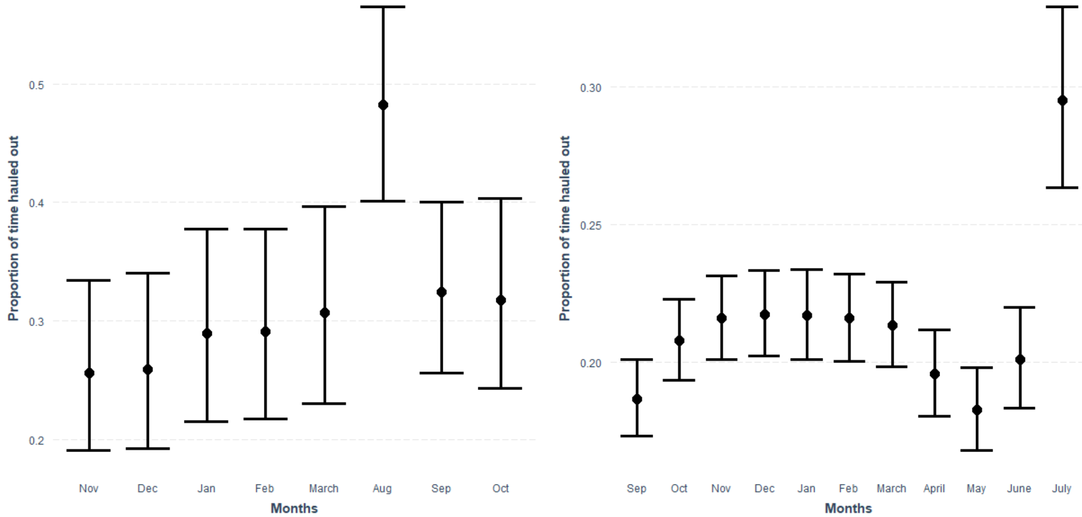

Figure 15. Predicted effect plots of months, estimated from the Skagerrak GLMM (left) and northern Norway GLMM (right), respectively.

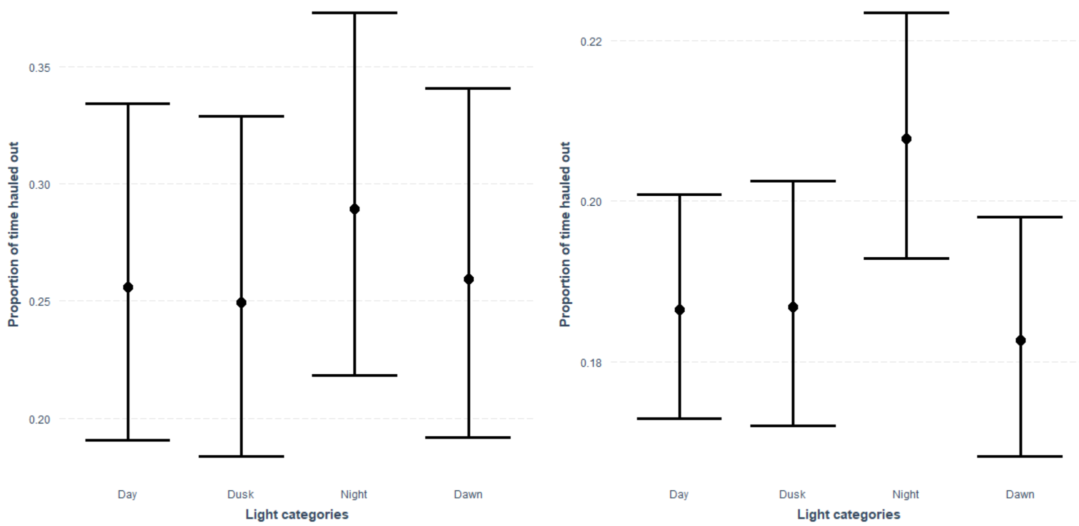

Figure 16. Predicted effect plots of light categories, estimated from the Skagerrak GLMM (left) and northern Norway GLMM (right), respectively.

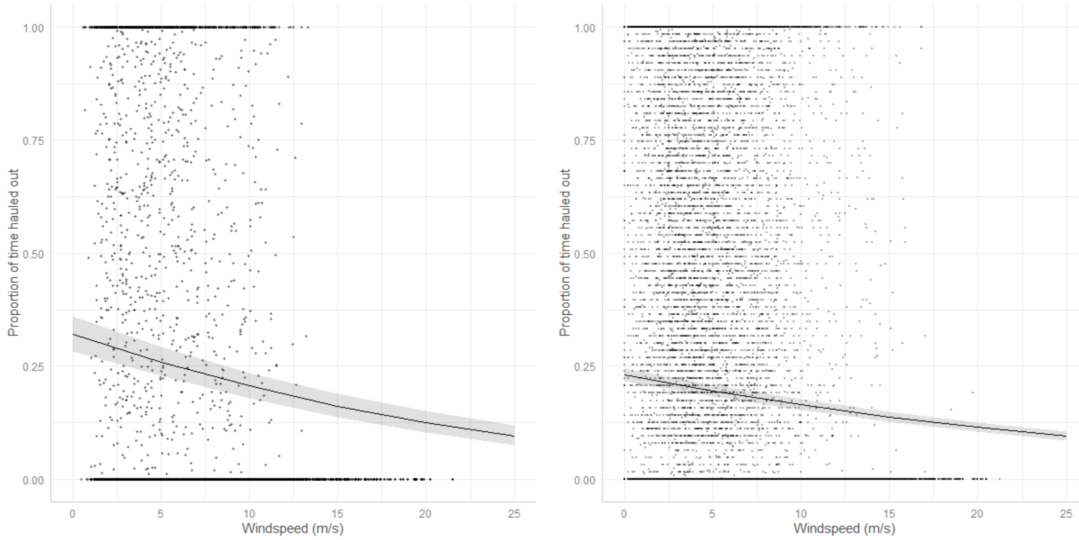

Figure 17. Predicted effect plots of windspeed (m/s), estimated from the Skagerrak GLMM (left) and northern Norway GLMM (right), respectively.

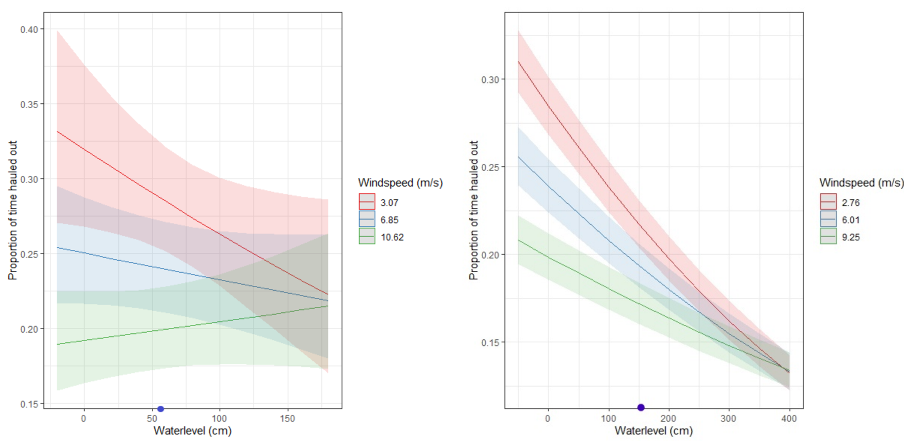

Figure 18. Predicted interaction effect plots of waterlevel (mm) x windspeed (m/s), estimated from the Skagerrak GLMM (left) and northern Norway GLMM (right), respectively. The graphs show differences in single slopes of Windspeed with varying values and how these change by cm increase in Waterlevel. The indigo points on the x-axes are the mean values of nautical chart zeros in Skagerrak (55.95 cm) and northern Norway (150.55 cm), respectively.

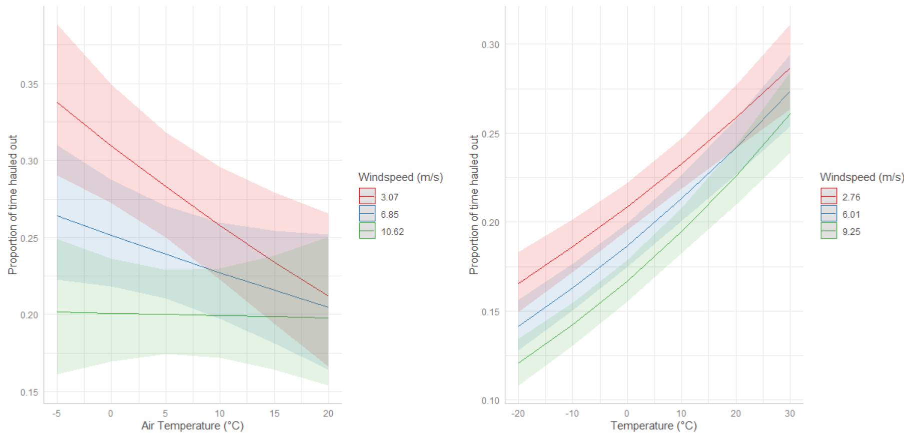

Figure 19. Predicted interaction effects plot of air temperature and windspeed, estimated from the Skagerrak GLMM (left) and the northern Norway GLMM (right), respectively. The graphs show differences in single slopes of Windspeed with varying values and how these change by degrees Celsius increase.

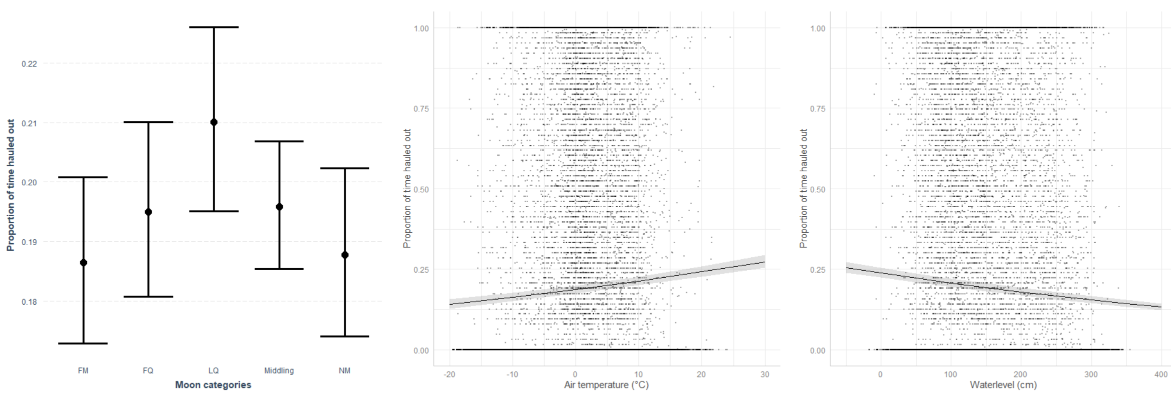

Figure 20. Predicted effect plots from estimates of Northern Norway GLMM; moon categories, temperature, and waterlevel, respectively. Full moon (FM) was the reference moon phase. Probability of hauling out was predicted to increase with increasing air temperature and decrease with increasing windspeed intensity.

3.4 Model validations

3.4.1 Nakagawa's R-squared

The variance explained by conditional R^2 for the Skagerrak beta GLMM (the whole model) was 0.194, and the marginal R^2 (only fixed effects) was 0.171.

The variance explained by conditional R^2 for the northern Norway beta GLMM (the whole model) was 0.048, and the marginal R^2 (only fixed effects) was 0.045.

3.4.2 Residual diagnostics

Figure 21 shows residual diagnostic plots of the Skagerrak GLMM and norther Norway GLMM, respectively.

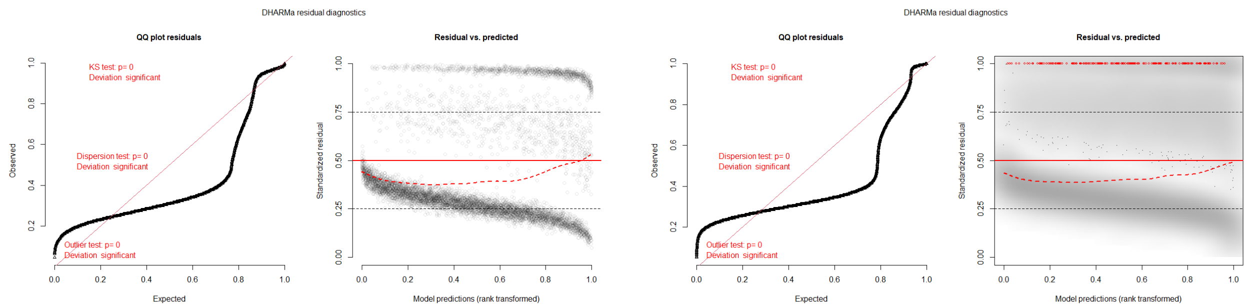

Figure 21. Residual diagnostics for the Skagerrak beta GLMM (left) and the northern Norway beta GLMM (right), respectively. An algorithm (Hartig 2021) has standardized the residuals to values between 0 and 1, and simulated new response data from the fitted models. QQ-plots show more residuals between 0 and 1, indicative of more residuals in the tails than would be expected, i.e., many simulated values are larger than the observed (overdispersion). The residuals versus Predicted plots, where the simulated outliers (red points) indicate many more observations were the simulations are lesser than the observed values.

3.4.3 Simulations

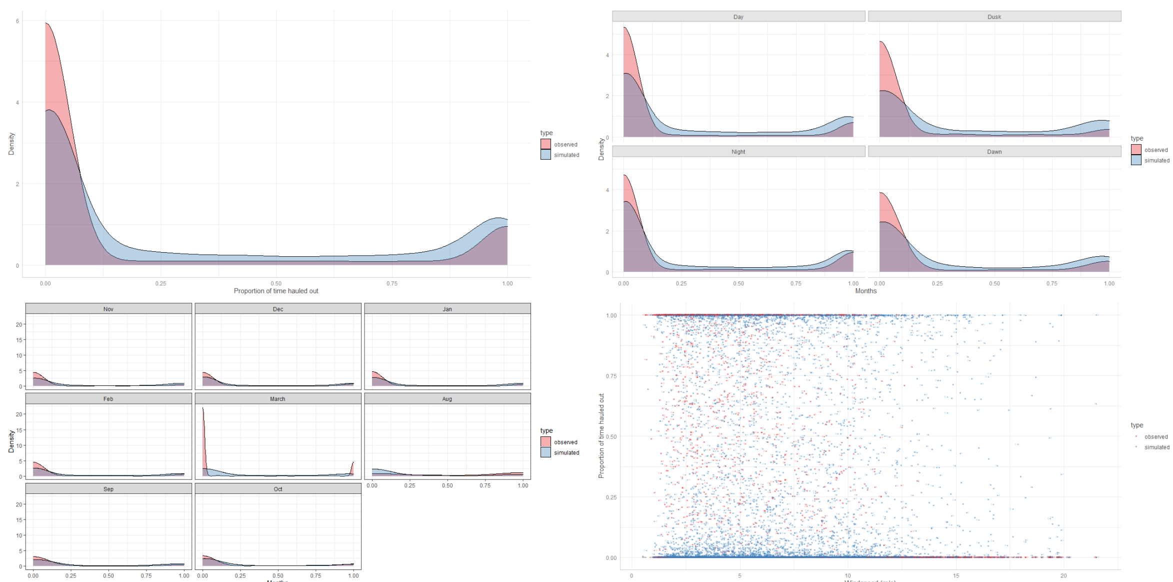

Figure 22. The Skagerrak model estimated and simulated values for the proportion of time hauled out (response), and for the fixed covariates light, months, and windspeed. Only significant effects were simulated. The simulation was performed with the R-package 'glmmTMB' (Mollie et al. 2017).

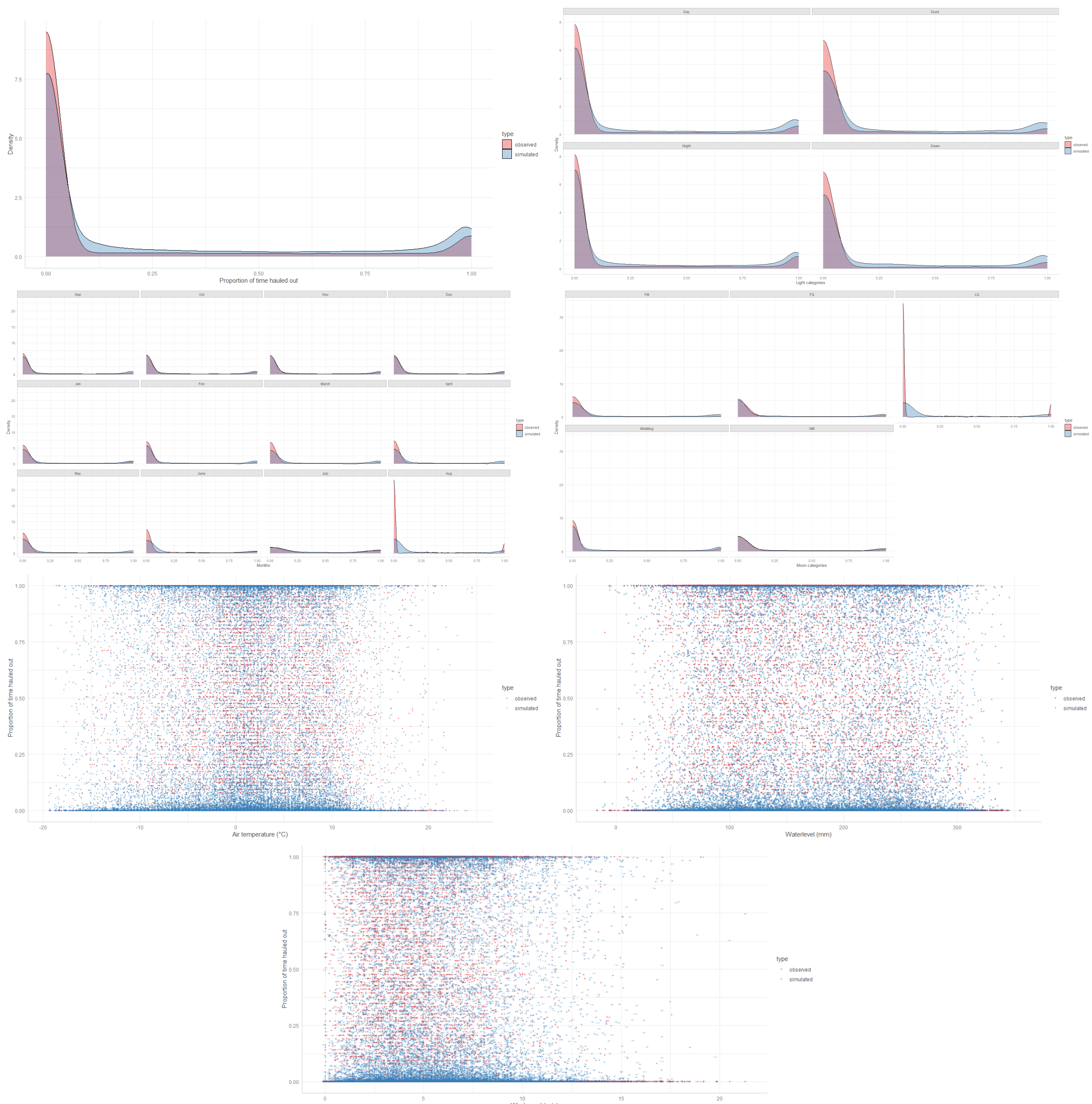

Figure 23. The northern Norway model estimated and simulated values for the proportion of time hauled out (response), and for the fixed covariates light, months, lunar phase, air temperature, waterlevel and windspeed. Only significant effects were The simulation was performed with the R-package 'glmmTMB' (Mollie et al. 2017).

4 Discussion

This study is based on synoptic data from transmitter records from a total of 31 harbor seals deployed with GPS phone tags in Skagerrak, Vesterålen and Porsangerfjorden from 2007 to 2020. The findings presented here accentuate previous findings of haul-out behavior of harbor seals in relation to temporal and environmental factors (Pauli and Terhune 1987; Grellier, Thompson, and Corpe 1996; Simpkins et al. 2003; Patterson and Acevedo-Gutiérrez 2008; Hamilton et al. 2014; Granquist and Hauksson 2016; Rosing-Asvid et al. 2020).

4.1 Main findings

In this study I uncovered a difference in the probability of hauling out between the two areas, with a generally lower probability in northern Norway than in Skagerrak. The seasonal patterns also differed between the areas (Figure 15). In Skagerrak, seals steadily hauled out more from November until March. In norther Norway, haul-outs increased from September until December, but from January until June I saw a low but distinct decrease in haul-out probability. Furthermore, I found that progressively increasing windspeed intensities had a significantly negative effect on haul-out probability in both areas (Figure 17). Water levels and air temperatures affected haul-outs in northern Norway, with a decrease in probability of hauling out with increasing water levels and an increase in probability with rising air temperatures (Figure 20). Interestingly I found that harbor seals in northern Norway hauled out significantly less at full moon than during half-moon on the last quarter (Figure 20). An unambiguous circadian pattern was difficult to detect, due to the lack of observations during summer months. This led to a predominance of observations at night (Figure 16), and it was not corrected for in the model. Even though, I argue that in both locations nighttime rest took precedence over diurnal haul-outs. In Skagerrak, I found that March was the only month with a higher probability of haul-outs during day compared with night, but I did detect a larger preference towards hauling out at dawn than at dusk (Tables 2 and 6). In both areas, a significant interaction effect of air temperature and windspeed was found to affect haul-out behavior (Figure 19). High windspeed intensities acted as a buffer on temperature's effect on haul-out probabilities. I have reason to believe that the temperature predictor in the Skagerrak model was unbalanced (see e.g., Figure 9), making the southern interaction effect unreliable. A significant interaction effect of water level and windspeed in both areas was also detected, and here high windspeed intensities acted as a buffer on the effect of rising water levels on haul-out behavior (Figure 18). I did not find a significant effect of precipitation in neither of the two areas, but see Figure 8. Furthermore, variation between sexes was not detected in neither Skagerrak nor northern Norway (Figure 10 and Table 7), but the sex-effect was retained as a non-significant term in the Skagerrak-model and might thus have included information to improve the model fit (Table 9).

These findings strengthen pre-existing knowledge about geographical difference in haul-out behavior, and also implicate differences in haul-out patterns with respect to environmental factors and circadian patterns (Van Parijs, Hastie, and Thompson 2000; Simpkins et al. 2003; Cunningham et al. 2009; Hamilton et al. 2014; Rosing-Asvid et al. 2020).

4.2 Seasonal and general haul-out probabilities

Months with observations in the Skagerrak model went from late August until the end of March. In northern Norway, all 12 months of the year was represented, except August. In Skagerrak, the observations in August, September and October were few and were represented exclusively by the six seals tagged right after the end of molting at Jomfruland (August 25, 2017), see Table 5, also Figure 25 and Table 11 in the Appendix. August had thus only seven days of data transmission, and this might have created a bias in the high haul-out probability found this month. April - July was represented in northern Norway, but only June and July were estimated to be significant (Tables 5 and 10).

In Skagerrak, the overall probability of hauling out was larger than in northern Norway. When averaging on all months in the models, I found that the overall probability of hauling out in Skagerrak was $\sim 29.9\%$, compared to $\sim 21.7\%$ in northern Norway, with a difference of $\sim 8.2\%$. The overall average when removing non-significant months from the calculations, was $\sim 30.7\%$ probability in Skagerrak, compared to $\sim 22.8\%$ in northern Norway, with a difference of $\sim 7.9\%$ in favor of Skagerrak. When only looking at the winter months (November - February), the difference was less ($\sim 3.8\%$), but still a significantly higher probability of observing haul-outs in Skagerrak than in northern Norway.

When looking at common months in the models, the largest difference was found in September, with $\sim 11\%$ higher probability of hauling out in Skagerrak than in northern Norway. A reasonably large difference was also found in October, where Skagerrak seals hauled out $\sim 8.9\%$ more than seals in northern Norway. The difference in haul-out probability was found to be lowest in November and December ($\sim 2.2\%$) but increased again in January and February ($\sim 5.3 - 5.5\%$), and further still in March ($\sim 7.4\%$).

In Skagerrak, haul-outs decreased from September until the end of November by $\sim 6.5\%$ and increased again by $\sim 2.9 - 3.0\%$ in January and February, with a further increase by $\sim 1.6\%$ in March. In Skagerrak, November was the month with lowest probability of hauling out. In northern Norway, September was estimated to have the lowest haul-out probability.

In northern Norway, haul-outs increased from September until the end of December by $\sim 3.2\%$, and then progressively decreased again from the end of December to the end of March by $\sim 0.6\%$. There were no data from April (onset of spring) to end of July (high summer) in Skagerrak. In northern Norway, April and May were estimated by the model to be non-significant, but the overall probability of hauling out decreased further from March, until July. July had a steep increase in haul-outs and the highest probability of hauling out of all the months (overall $\sim 30\%$, with an increase of $\sim 9.6\%$ from the previous month). Female harbor seals usually give birth to their first pup between the age of 4 and 5 (Härkönen, Harding, and Lunneryd 1999), and since all animals tagged in northern Norway were juveniles, pupping was not the reason. Härkönen, Harding, and Lunneryd (1999) found that juveniles hauled out more than older individuals, and this can thus partly explain the increase of haul-outs during the the summer months (see Figures 27-29 in the Appendix for haul-out profiles). If tags are still attached, they will fall off by the onset of the molting period in late July, and two animals in the north, a male (pv30-01-09) and a female (pv30-09-09), transmitted data until radio silence July

9th, 2010 and July 11th, 2011, respectively. One male (pv35-01-11), tagged in Børselv/Porsangerfjorden September 1st, 2012, evidently did not lose his tag during the molting period in 2013. His tag transmitted data for 484 days until December 31st, 2013. Even so, July had very few observations compared with all other months represented in the northern Norway data.

Tidal amplitudes have been thoroughly documented to have a strong effect on haul-out behavior (Boulva and McLaren 1979; Cronin et al. 2009; Hamilton et al. 2014), and the difference between low- and high tides in northern Norway are much greater than in Skagerrak (see Figure 6, also Table 12 in the Appendix). The results of this study confirmed the negative effect of rising water levels on the northern Norway harbor seals. The overall lower probability of hauling out in the north compared with the probability found for their southern conspecifics could be (partly) assigned to the water level effect. Furthermore, temporal differences were found between the two areas, with varying haul-out patterns across the months represented in this study. The largest difference was found during late fall and in the early spring, but there was also a marked difference during the winter months, with less haul-outs in northern Norway compared with Skagerrak (Figure 15).

Worth to have in mind is that seasonal patterns vary between years and along the line of time, such that care should be taken when drawing inference from only a few years of data (Cordes et al. 2011).

4.3 Circadian patterns in the haul-out probabilities

In both areas, seals were found to haul out less during daylight hours than night hours, with no significant effect detected on the behavior during twilight hours (Figures 10 and 17). A large part of the explanation for the high haul-out probability during night hours was that the tracking records did not include the summer months in the south. In Skagerrak, nighttime constituted of $\sim 51.5\%$ of the observations and daytime of $\sim 34\%$. In northern Norway, the difference was even larger with $\sim 63.6\%$ nightly observations and $\sim 22.8\%$ observations during daytime. This can be attributed to the large amount of observations during winter months in the north, relative to summer months, and to the polar night.

Overall, I found that it was $\sim 3.2\%$ more likely for seals to haul out at night than at day in Skagerrak. Compared with norther Norway, where it was a $\sim 2.2\%$ larger probability to haul out at night than day, it was 1% more likely overall for the southern harbor seals to haul out during night compared with day.

In northern Norway, I found that seals hauled out most at day in September, December, and from May to July (Arctic summer). All other months, including March, showed a higher proportion of haul-outs at night, expect in January where most haul-outs were recorded at dawn - closely followed by nightly haul-outs (Table 6). Above the Arctic circle, the sun starts coming back after the polar night around medio January, which might explain the high preference for hauling out during lighter hours this time of year. As I also found a positive correlation between haul-outs and air temperature in the northern model, one explanation for the higher probability of hauling out during dawn than during night in January could be related to temperature. I found that the mean winter temperature (January - February) in northern Norway was $-5°C$ (SD = 6.056), compared with $4.47°C$ (SD = 2.530) in Skagerrak. I also detected a temperature difference in the north between night and dawn in January. Average temperature during night in January was $-4.73°C$ (SD = 5.380), and during dawn it was $-1.50°C$ (SD = 3.364). It was thus on average $3.36°C$ warmer at dawn than at night i January.

There was no discernible difference in preference between the twilight periods in northern Norway, which differed from what I discovered in Skagerrak.

In Skagerrak, the model predicted a more consistent nightly haul-out pattern throughout the year than in northern Norway, which was interesting. At these latitudes, daylight hours are progressively getting shorter from the middle of August. The Skagerrak data did not show a large difference in observations between night and day in August - October (Table 6). The largest probability of hauling out in August was at dawn ($\sim$ 69.9%) and at night ($\sim$ 68.6%). Even in October and November, most haul-outs were recorded at night. March was the only month in Skagerrak where a clear preference for hauling out during day was observed. Dawn and dusk were not significant in the Skagerrak model, but from the data set I found that seals hauled out more at dawn ($\sim$ 23.7%) than at dusk ($\sim$ 16.7%). I could not detect a correlation between dawn and low tides, and it could thus indicate that other factors affected the Skagerrak seals' preference for hauling out at dawn compared to dusk.

According to previous research, harbor seals have been found to haul out most during daytime (at low tide) (Boulva and McLaren 1979; Thompson 1989), but Ramasco (2015) investigated forage patterns of the Porsangerfjorden-seals (the same individuals as in this study) - and she found that these individuals hauled out more at night, especially during spring and fall. Ramasco (2015) argued further that this pattern most likely resulted from behavioral patterns of harbor seal prey species. Due to the high haul-out probability at night in Skagerrak, I speculate that a similar pattern could be present among Skagerrak-seals in this study. It is a possibility, and it would be interesting to investigate further. Sørlie et al. (2020) studied and thoroughly documented harbor seal diet in Skagerrak based on otoliths found in seal feces, and further research on harbor seal behavior in relation to behavioral and migration studies of prey species and trophic relationships therein could be of importance for increasing the knowledge base and future conservation and management of harbor seals, and ultimately of Norwegian coastal ecosystems.

Also a major factor found to impact harbor seals' haul-out pattern (but not included in this study) is the amount of human disturbance in areas of central haul-out sites (S. M. Andersen et al. 2012; London et al. 2012; Jansen et al. 2015). Harbor seals have been observed to habituate to repeated disturbances (which is not necessarily a good thing, see Olson and Acevedo-Gutierrez (2017)), and London et al. (2012) revealed a dynamic haul-out pattern of a population of harbor seals in the Hood Canal region of Washington State in the United States. They found a pattern between the presence of human disturbance and preference for rest at night, and a change to daily haul-outs when the tourist season was over. The Skagerrak is heavily trafficked, especially through the port of Oslo and in Oslofjorden in Norway, the port of Gothenburg in Sweden and through Kattegat into the Baltic (Andersson et al. 2006). Tourism associated with coastal recreational activities is also heavy along the Norwegian Skagerrak coastline. It could thus be of importance to investigate if the relationship I found between a higher proportion of haul-outs at night compared to day during the fall and winter months in Skagerrak related to an adaptive pattern due to human activities.

4.4 Environmental factors and effects on haul-out probability

Windspeed intensities showed to have a negative effect on haul-out behavior in both areas (Figures 7 and 18), and a larger negative effect was detected in Skagerrak (for every unit increase, the probability of hauling out went down by $\sim 4\%$) compared with northern Norway ($\sim 1.9\%$). See Tables 9 and 10. The negative effect of windspeed in the north was marginally greater than the negative effect of water level ($\sim 0.1\%$). The windspeed effect found in the northern Norway model might have been moderated by the negative effect of water level (water level effect reduced probability of hauling out by $\sim 1.8\%$), and also by the positive effect of air temperature (air temperature effect increased haul-out probability by $\sim 1.8\%$). Windspeed was the only single environmental factor to prove significant in Skagerrak, but both water level and air temperature estimates were retained as non-significant effects in the Skagerrak GLMM. Temperature and water level estimates were thus interpreted as having value for the overall model fit and note the possible unreliability of the temperature estimate. Additionally, water level and air temperature were given significant effects when moderated by (high) windspeeds in both Skagerrak and northern Norway.

Even though air temperature as a single predictor did not prove significant in the Skagerrak model, rising temperatures had a negative effect on haul-out probability in Skagerrak, contrary to the temperature effect in northern Norway and contrary to previously documented temperature effects on the behavior (Pauli and Terhune 1987; Reder et al. 2003; Simpkins et al. 2003; Mogren et al. 2010; Granquist and Hauksson 2016). A probable explanation for the negative effect of temperature found on haul-out probability in Skagerrak was that the highest temperature measurements were recorded in August and September (Figure 9). August in Skagerrak had a very high haul-out probability ($\sim 46.2\%$), but very few observations ($\sim 3.4\%$). Six seals were tagged at Jomfruland, August 25, and summary records only spanned the seven last days of this month. Two of the tags stopped transmitting after 1-2 days, and a third stopped transmitting after 6 days of transmission (Table 2). The haul-out probability for August as a level in the categorical Month-factor was thus not representative for the whole month and is probably unreliable.

The Skagerrak data consisted of observations from two locations (Jomfruland and Bolærne, respectively). Bolærne is in outer Oslofjord and is a generally more exposed area than Jomfruland, but both locations have access to in-shore and protected sites (Figure 3 and Table 1). Most of the very high windspeeds (91% of 1000 highest wind observations) recorded in the Skagerrak data set were measured around Ytre Oslofjord (11.27 - 21.50 m/s, i.e., strong breeze - strong gale). Harbor seals usually choose the protected side of a haul-out site when winds are strong (K.T. Nilssen, personal communication, November 17th, 2021). Granquist and Hauksson (2016) found evidence for the effect of wind direction, and due to the distances between weather stations and the local topographic variations in the areas of this study, I believe that by adding direction to the windspeeds (e.g., by use of wireless weather stations, see Herstrøm (2013)), it could have improved the precision and increased the information of the windspeed effect.

The single effect of water level, i.e., tidal state, did not show to significantly affect haul-out behavior in Skagerrak, but it was retained in the model and interpreted as having value for the overall model fit (Figure 6 and Table 9). Additionally, water level was given a significant effect when moderated by (high) windspeeds. There is also growing evidence that it is not always the tide that best predicts harbor seal haul-out behavior, but rather complex interactions between different influences (Hastie et al. 2016).

4.5 Lunar effects on haul-out probability in northern Norway

The results also revealed a significant moon phase-effect on the haul-out probability in northern Norway. Here I found that seals tended to haul out less during full moon than during the last quarter (i.e., half-moon moving towards new moon). See the effect plot in Figure 20, and percent representation of each lunar phase in Figure 11. Prior to fitting the model, I performed a thorough data exploration of the chosen variables, and the generalized variance inflation factor (GVIF) was used to detect possible collinearity (Ieno and Zuur 2015). I found no collinearity between the categorical moon phase factor and the continuous water level predictor, but the tide cycle is irrefutably linked to the lunar cycle and the results must therefore be interpreted in the light of this connection. The difference from lowest astronomical tide (LAT) to highest (HAT) in Skagerrak is 60 cm and decidedly less severe than in northern Norway (Table 12 in Appendix). In the north, the difference between LAT and HAT (averaged between Vesterålen and Porsangerfjorden) is 319.5 cm (derived from Sjødivisjonen 2020). Since high tides are one of the major factors influencing haul-out behavior where seals haul out on sites that become submerged during the tidal cycle (Thompson 1989; Hauksson and Einarsson 2010; London et al. 2012), it is reasonable to interpret the haul-out pattern in the north to be heavily affected by the influence of rising and sinking water levels. Nevertheless, recent research is shedding light on the complex ecosystem patterns that exist between external factors (such as light conditions) and the behavior of vertically migrating prey, and the meso- and top predators hunting them (Espeland et al. 2010; Owen et al. 2019).

No significant effect was found on the other moon phases, but looking at probability values alone, the overall lowest haul-out probability was found during full moon. The moon effect was not retained in the Skagerrak model, but see Table 8 for a description of the moon phase categories and how they were distributed in both Skagerrak and norther Norway.

4.6 Interaction effects between environmental factors on haul-out probabilities

I found that the effect of air temperature on haul-out probabilities was modified by windspeed in both Skagerrak and northern Norway (Figure 19). The negative effect of air temperature found on the behavior in Skagerrak was assumed to have a degree of unreliability attached to the estimate. In the south, high windspeeds canceled the negative effect of air temperature to an approx. zero effect. Low windspeeds produced a steep negative slope along the increasing temperature gradient, while medium windspeeds (~ 6.85 m/s, i.e., moderate breeze), had a less steep negative slope. In northern Norway, I found that as temperatures increased from approx. $0°C$, all windspeed intensities increased the probability of hauling out more than by temperature alone, but the slope was steepest at high windspeeds (~ 9.25 m/s, i.e., fresh breeze). In other words, when northern harbor seals were exposed to temperatures above $0°C$, high windspeeds would add to the positive temperature effect and further increase the probability of hauling out. Below $0°C$, an additional effect of windspeed was not found to affect haul-out probability.

This study also revealed that the effect of water level on haul-out probabilities was buffered by windspeed in both areas (Figure 18). High windspeed effects surpassed the water level effect, and much more markedly in Skagerrak than in northern Norway. In Skagerrak, haul-out probability decreased with rising water levels at low to medium windspeeds ($\sim 3.07 - 6.85$ m/s, i.e., gentle to moderate breeze). At high windspeeds (~ 10.62 m/s, i.e., fresh breeze), the probability of hauling out started to increase with rising water levels. In other words, at high windspeeds the wind effect canceled the negative effect of rising water levels. This interaction effect found in the Skagerrak model could partly be explained by the high haul-out probability found in February. The highest windspeed and water level measurements were found to coincide during two periods in February 2020, and the probability of hauling out this month was estimated to be highest between November and February. High windspeeds could also create a lot of wave action and difficult feeding conditions. I speculate that sheltered, in-shore haul-out sites were used during these harsh conditions. In northern Norway, the effect of windspeed on water level was much less obvious, and was only found to be effective at extremely high water levels (~ 380 cm, i.e., approx. 229 cm above nautical chart zero and predictions above actual observations (max ~ 355 cm).

On the background of these interpretations, I do not feel confident about attempting to draw inference from either of the interaction terms in the two models. With caution, these results indicate that windspeed could be part of more complex interactions of environmental variables.

4.7 Precipitation

I did not find a significant effect of precipitation on variation in haul-out probability in neither Skagerrak nor the north. Others have found both weak and significant negative effects of precipitation on haul-out behavior (Pauli and Terhune 1987; Grellier, Thompson, and Corpe 1996; Simpkins et al. 2003; Cronin et al. 2009; London et al. 2012). Granquist and Hauksson (2016) did not detect an effect of precipitation in their study. Of importance regarding the precipitation data in this study is that the density of weather stations with pluviometers (rain gauges) was low, especially in northern Norway. In Vesterålen, only one weather station situated in the inner skerries of Sortland had precipitation data. Also, in Porsangerfjorden all precipitation data came from one single weather station (Banak). The precipitation observations were recorded every 12 hours in northern Norway. In Skagerrak, the precipitation observations were hourly measures. All of five weather stations used from 2019 to 2020 had rain gauges, but during the 2017-event only one station situated in the center of Arendal city had precipitation observations.

4.8 Limitations and implications for future research

4.8.1 Limitations

Haul-out behavior has been found to vary between ages and sexes, and care must be taken in extrapolating results disclosed from animals sampled in a non-random manner (Thompson et al. 1998; Härkönen, Harding, and Lunneryd 1999). This is highly relatable to my study since the capture methods in northern Norway targeted only juveniles. Furthermore, the five juveniles captured and tagged in Vesterålen were all females (see Figure 12 and Table 3). It is unlikely that the sample from Skagerrak is representative of the population with records from 11 animals, and some which did not transmit data for more than a few days. Weight and length of animals were not included as biological factors in the models for this reason.

The weather data was retrieved from stations with varying distance to the areas where GPS locations of the seals were recorded. The arithmetic averaging of weather data between stations could have been greatly refined by applying the inverse variance weighted average method to account for the relative importance of the effect sizes of the weather predictors. Also, harbor seals exhibit highly individual movement-, travel- and foraging patterns that can vary a great deal (Thompson and Miller 1990; Bjørge et al. 2002; Cunningham et al. 2009). This can lead to imprecise weather characteristics representation of haul-out sites.

It is not straightforward to validate beta GLMMs, as there is no single appropriate statistical method to quantify uncertainly found in such models (Bolker et al. 2009; Bono, Alarcón, and Blanca 2021). I was not able to identify a parametric bootstrap function that could handle a glmmTMB-object (Brooks et al. 2017). When attempting to predict from the model estimates, the memory (8 GB RAM) of my computer could not handle the large variance-covariance matrix. I thus simulated the model with a `newdata` argument, from a computer-generated random distribution, and I was satisfied with the results as the simulations validated the models' performance and predictive abilities reasonably well. Figure 22 shows simulations of the Skagerrak model, and it is evident that the model systematically underestimated predictions $< 13\%$, and overestimated prediction above this. In northern Norway (Figure 23), the model underestimated predictions $< 6\%$ haul-out probability, and overestimated predictions above.

The pattern found in the simulations indicated both over- and underdispersion (see Figure 21 for simulated residual diagnostic plots). Overdispersion is a common phenomenon in models that handle non-normal (Bolker et al. 2009). Interpretation of estimates were thus done with caution, as overdispersion usually produces confidence intervals that are too narrow. See the forest plots of the models in Figure 13, where it is evident that estimates of the environmental factors fall between pretty narrow confidence intervals. This can lead to inflated type I errors. A large data set can alleviate some of the troubles, as in this study. But large data sets can also be extremely sensitive to outliers or influential high or low data point, and data exploration prior to model fitting revealed several high and low values. I did not remove them, due to the highly skewed and non-normal distributions and because I believed them to have information important to investigate. The high proportion of extreme values of ones and zeros in the response variable in this study is clearly a source of the overdispersed variation between these extremes. In conclusion, there is a great deal of uncertainty in the ability to draw inference from the models in this study, but with caution there is information in the results.

Further, it was not easy to find a justified method to be able to report explained variance. I chose to apply Nakagawa's R^2 in both models (Nakagawa and Schielzeth 2013), since this method is able to handle random intercept models, and since my main focus was to be able to explain the total variance of the models. The formula was systematically tested by LaHuis et al. (2014), and they found justification for using it on random intercept models. The strengths of the models were weak and only explained some of the variance in the data. Nakagawa's R^2 values calculated for the whole Skagerrak model was 0.194, and for the northern Norway model the R^2 value was 0.048. Individual seals were used as random effects, and this increased the R^2 of the Skagerrak GLMM by 0.023. In the northern Norway GLMM, the random effect increased the R^2 by as little as 0.003.

The convergence issues of the northern Norway GLMM, that I by-passed by dredging a model selection table, is also important to highlight as a severe limitation towards inference. Optimizing the data set to be able to converge within the algorithm used on the data set in the `buildmer` package should have been done, and thus draw inference from the estimates with a possible higher degree of certainty.

4.8.2 Implications for future research

Surveys on harbor seal numbers are being performed under locally ideal conditions at preferred haul-out sites during the molting season along the Norwegian coast (e.g., Boveng et al. 2003; North Atlantic Marine Mammal Commission 2021). The analyses in this study do not include the molting season, since the GPS phone tags do not stay on the seals during this period. Still, I allow myself to suggest that the results can be of practical use, in the sense that I found general differences in probabilities, as well as differences in how clearly environmental factors influenced the behavior. I do not think that the results can be extrapolated, but I did find evidence for differences between the areas. It may seem that it is easier to predict a clearer pattern of haul-out behavior in relation to environmental factors in the north, compared to the Skagerrak. Further, I suggest more fine-scaled investigations and modeling of possibly influential factors such as wind direction, wind chills, air pressure, cloud cover, and anthropogenic influence. Accounting for foraging patterns in relation to prey species behavior could also reveal new information and add precision in predictions of fine-scale harbor seal behavior.

If future capture and mark studies of harbor seals manage to get behavioral profiles of individuals during the summer months pre-molt in Skagerrak, it will be possible to get a more complete seasonal haul-out pattern. A larger sample size would also be advantageous, as it would produce a more balanced representation of the population. Capture methods have been upgraded from the first deployments in northern Norway to the last ones in Skagerrak and are now better able to capture a more balanced portion of the population. This method assumes that the proportion on land versus in the water does not vary by sex and age, and this has has been found to vary (Thompson et al. 1998; Härkönen, Harding, and Lunneryd 1999; Cronin et al. 2009).

Amount of human disturbance and effect on haul-out behavior and pattern was not tested in this study. By comparing haul-out patterns during weekends and holidays compared with weekdays in areas highly affected by recreational activities, it could be possible to reveal potential correlations between behavior and disturbance.

Precipitation was not found to affect haul-out behavior in this study. There were a low numbers of precipitation measurement from both areas. When investigating haul-out behavior in the future, I suggest the use of strategically placed wireless weather stations with rain gauges to add precision to existing weather stations in the areas of study.

5 Conclusion

Harbor seals are parts of the sensitive, highly variable and heavily utilized ecosystems along the Norwegian coast (Field, Hempe, and Summerhayes 2002; Andersson et al. 2006; Ramasco 2015; North Atlantic Marine Mammal Commission 2021). Optimal conservation and sound management is dependent on scientific knowledge. This research adds to the increasing knowledge pool of environmental effects and the spatial and temporal variation in harbor seal haul-out patterns along the Norwegian coastline.

My research found that seals in northern Norway in general hauled out less than their conspecifics in Skagerrak. This pattern of less haul-outs of harbor seals in northern populations from fall to spring has been observed and documented for the isolated population on Svalbard (Hamilton et al. 2014). I found that harbor seals in both study areas showed a seasonal pattern, and that patterns varied between Skagerrak and northern Norway. Seasonal variation has been thoroughly documented for other harbor seal populations, and differences have been detected between northern and southern populations (Huber et al. 2001; Thompson et al. 1996; Cordes et al. 2011; Hamilton et al. 2014; Rosing-Asvid et al. 2020). Circadian patterns indicated a preference towards hauling out at night, with a more pronounced pattern in Skagerrak than in northern Norway, and this adds to previous studies that have found variation under which light conditions seals prefer to haul out (Boulva and McLaren 1979; Ramasco 2015). Tidal amplitudes vary between areas, as in my study, and it has been found to be highly predictive on haul-out behavior in areas with large differences between flood and ebb and more difficult to predict from in areas where the difference is smaller and other factors become more prominent (Patterson and Acevedo-Gutiérrez 2008; London et al. 2012; Hamilton et al. 2014; Hastie et al. 2016). High and low tides clearly affected the northern animals in this study, and the effect was more ambiguous in Skagerrak as it only showed an effect when interacting with windspeed. Northern harbor seals also showed a marked increase in going on land with rising air temperatures. Windspeed was the only environmental predictor that the two areas had i common, and thus negatively affected the probability of hauling out. Interestingly, the negative effect was more severe in Skagerrak. Northern Norway seals were found to be more in the water during full moon than any of the other lunar phases, with a significant difference between half-full moon on the last quarter. I would like to see more research on the lunar phases in relation to harbor seal behavioral ecology.

To my knowledge, a comparative study between northern and southern harbor seal populations in Norway have not previously been done, and I hope the results and inference from analyses performed in my work adds information to the research of harbor seal behavior along the Norwegian coast.

6 References

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7 Appendices

7.1 Appendix A: additional tables

Table 11. The amount of time hauled out by each individual seal expressed as a percent of the total sum of haul-outs, expressed in percent. Skagerrak- and northern Norway, respectively

ID (Skagerrak)	Observations (%)	ID (NN)	Observations (%)
pv35b-04-11	0.744	gp10-641-07	5.000
pv35b-05-11	11.658	gp10-655-07	3.050
pv35b-06-11	4.063	gp10-683-07	7.222
pv35b-08-11	0.768	gp10-684-07	5.597
pv35b-09-11	0.308	gp10-685-07	5.095
pv35b-10-11	0.964	pv30-01-09	6.025
pv68-F53__Iris-14	6.824	pv30-02-09	2.614
pv68-F56__Karin-14	8.034	pv30-03-09	4.547
pv68-M40__Pedro-14	11.373	pv30-05-09	5.295
pv68-M42__Einar-14	5.867	pv30-06-09	5.498
pv68-M47__Vemund-14	2.755	pv30-07-09	4.060
pv74-F46__Olivia-20	10.156	pv30-08-09	6.990
pv74-M62__Gamle-Erik-20	14.093	pv30-09-09	6.884
pv74-M70__Osito-20	8.707	pv30-10-09	0.737
pv74-M86__Bjorn-20	5.33	pv30-11-09	6.028
pv74-M88__Diego-20	8.357	pv30-12-09	2.144
TOTAL	100	pv30-13-09	5.507
	_	pv35-01-11	15.729
	_	pv35-02-11	1.010
	_	pv35-03-11	0.966
	_	TOTAL	100.000

Table 12. Water levels and extreme values in cm above Chart Zero for ports of Helgeroa, Honningsvåg, and Tromsø, respectively.

Tide level	Helgeroa	Honningsvåg	Tromsø
High tide with 1 year repetition interval	140	335	337
HAT (Highest Astronomical Tide)	80	321	318
MHWS (Mean High Water Springs)	64	277	274
MHW (Mean High Water)	61	251	247
NN1954 (Normal zero 1954)	59	177	169
MHWN (Mean High Water Neaps)	58	226	219
NN2000 (Normal zero 2000)	56	186	180
MSL (1996-2014) (Mean Sea Level 1996-2014)	50	164	162
MLWN (Mean Low Water Neaps)	42	103	106
MLW (Mean Low Water)	39	78	51
MLWS (Mean Low Water Springs)	36	52	51
LAT (Lowest Astronomical Tide)	20	0	0
Low tide with 1 year repetition interval	-14	-7	-12

7.2 Appendix B: additional figures

Figure 24. Tagging of a male harbor seal in Tvedestrand September 29, 2021. The animal is sedated, the fur has been dried and defatted and the GPS phone tag is about to be attached to the neck by Martin Biuw. Michael Poltermann has prepared the tag with superglue. Carla Freitas is taking notes of the animal's vital signs, procured by veterinarian Diogo Marques who is closely monitoring heart rate and oxygen uptake.

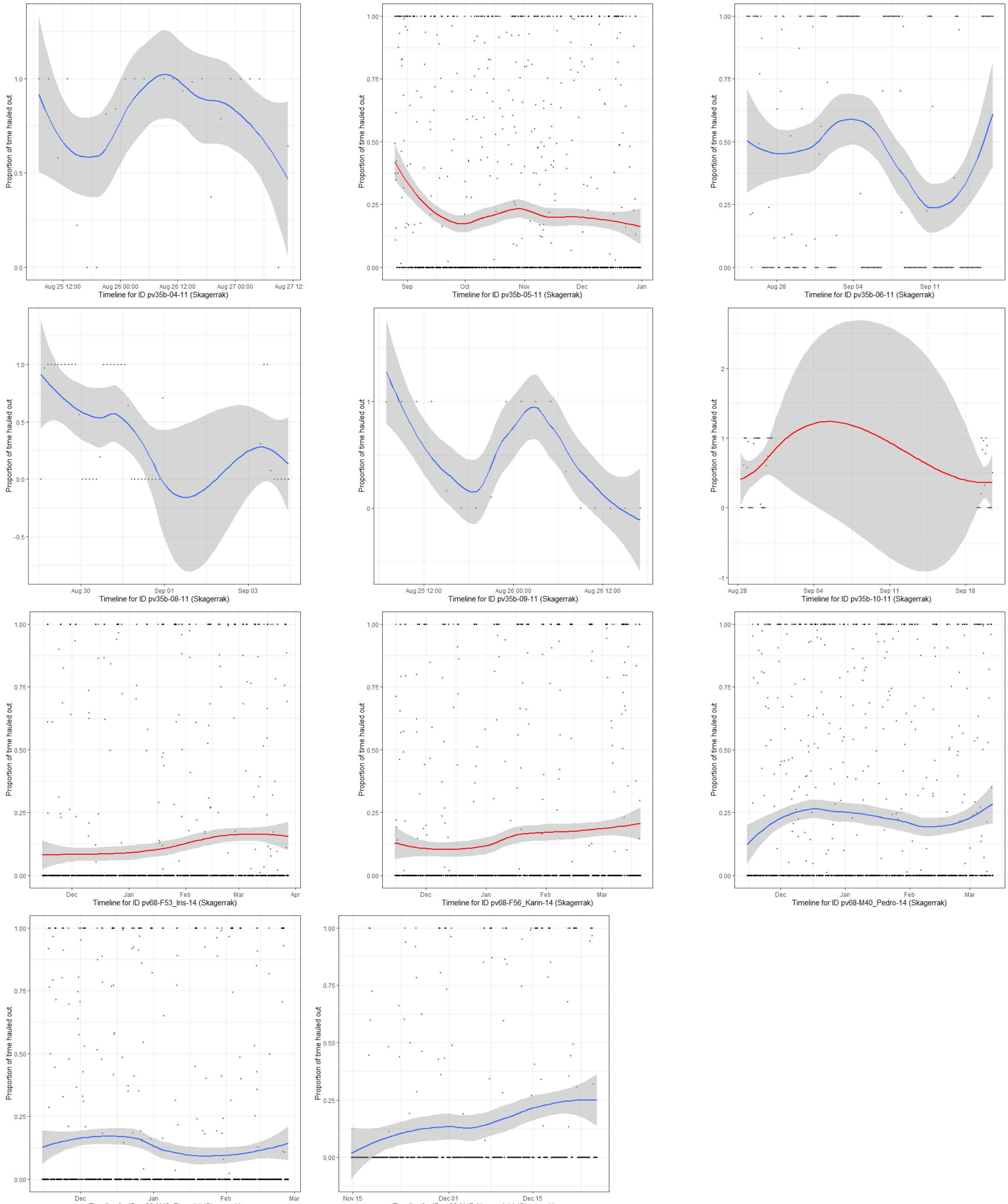

Figure 25. Skagerrak 2017 - 2020: Haul-out timeline profiles of the 11 individual seals included in the Skagerrak analysis. A loess line has been added to highlight the trend in behavior across time. Females are symbolized with a red line, and males with a blue line.

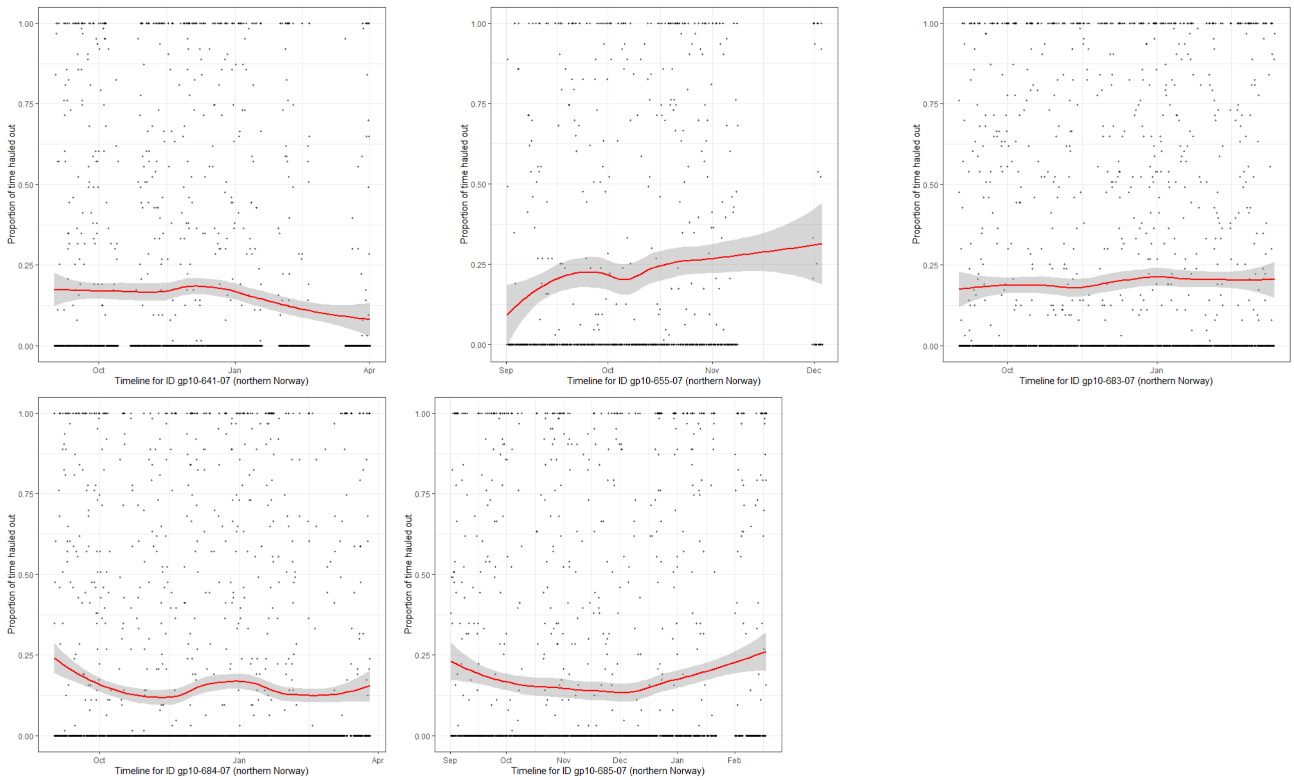

Figure 26. Vesterålen 2007-08: Haul-out timeline profiles of the five individual seals tracked in Vesterålen and included in the northern Norway analysis. A loess line (red indicating females) has been added to highlight the trend in behavior across time. All individuals were juvenile females.

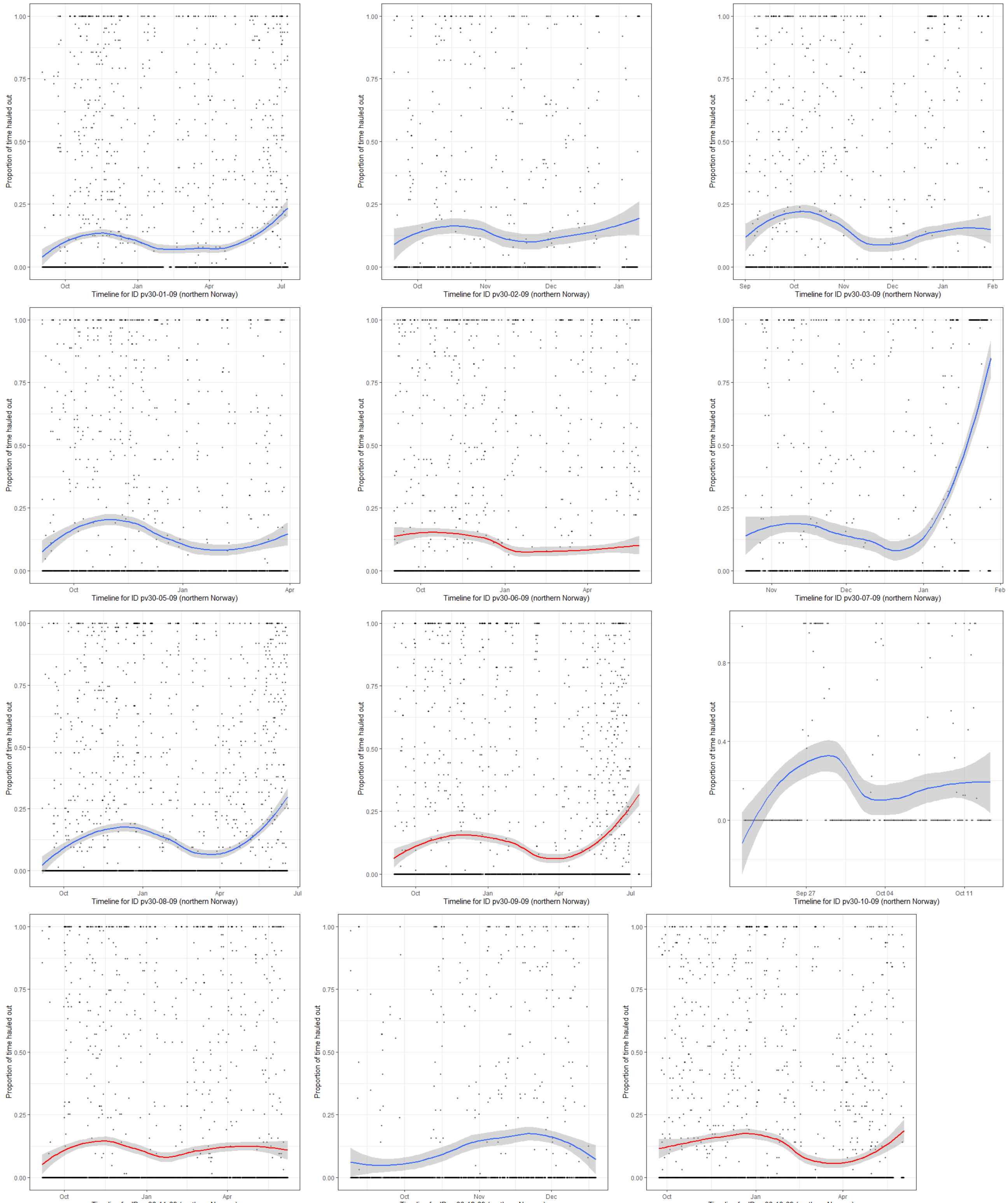

Figure 27. Porsangerfjorden 2009-2011: Haul-out timeline profiles of the 12 individual seals tracked in Porsangerfjorden and included in the northern Norway analysis. A loess line has been added to highlight the trend in behavior across time. Females are symbolized with a red line, and males with a blue line.

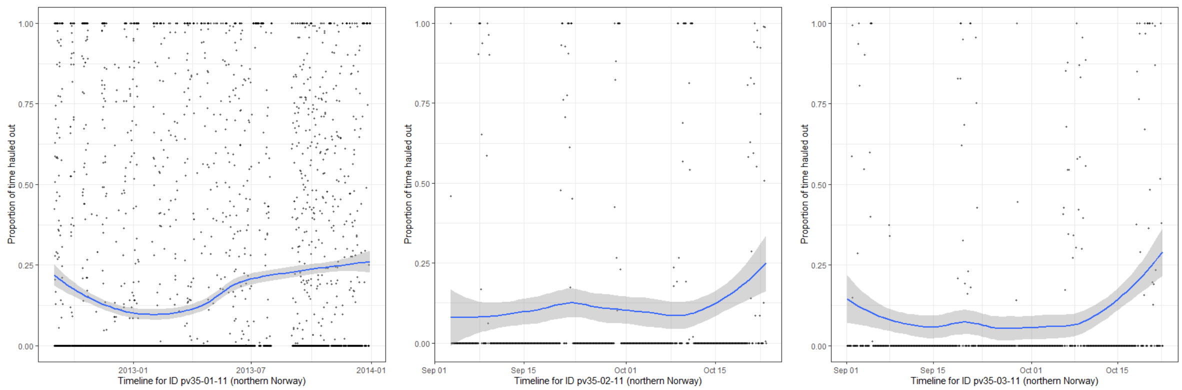

Figure 28. Porsangerfjorden 2011-2013: Haul-out timeline profiles of the three individual seals tracked in Porsangerfjorden and included in the northern Norway analysis. A loess line has been added to highlight the trend in behavior across time. Females are symbolized with a red line, and males with a blue line.

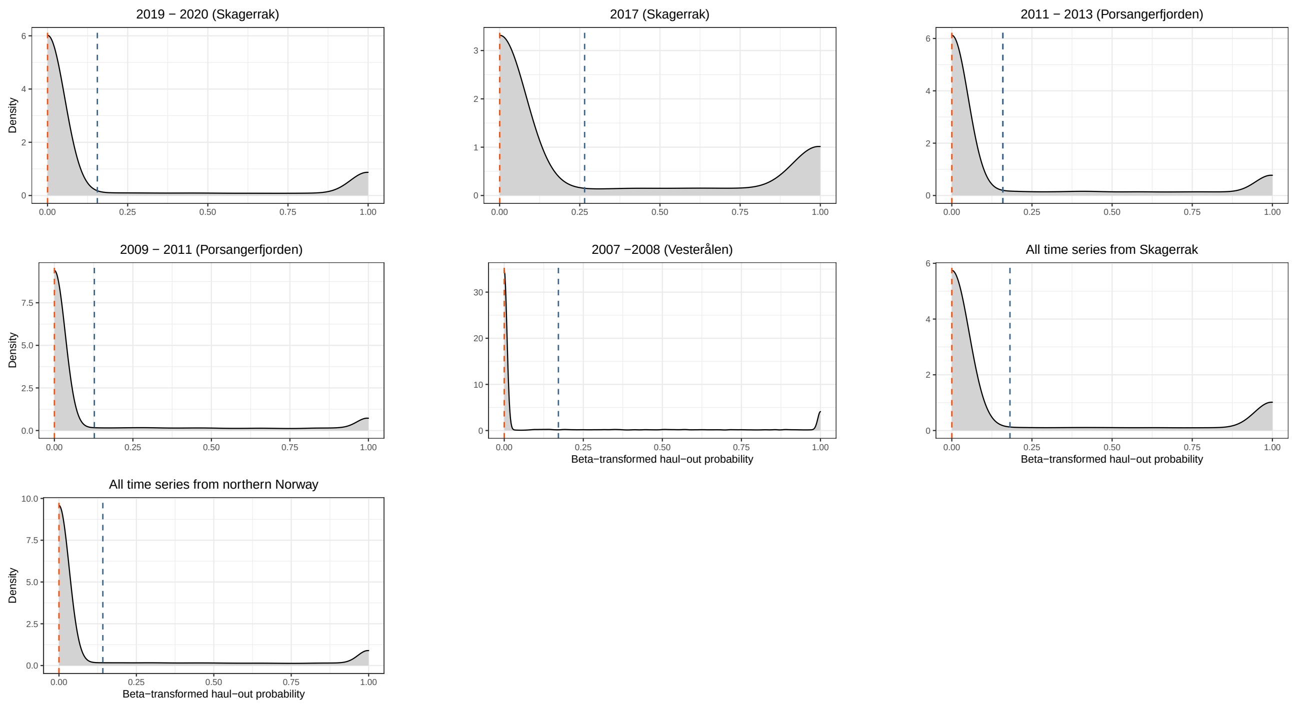

Figure 29. Density plots of the response variable (proportion of haul-out time) in each location in Skagerrak, in each location in northern Norway, and for all locations pooled together. The blue veritcal lines represent mean values, and the red vertical lines represent median values of the distribution of the response. Notice the significant positive skewdness of the distribution, with all mean values being greater than the median values.

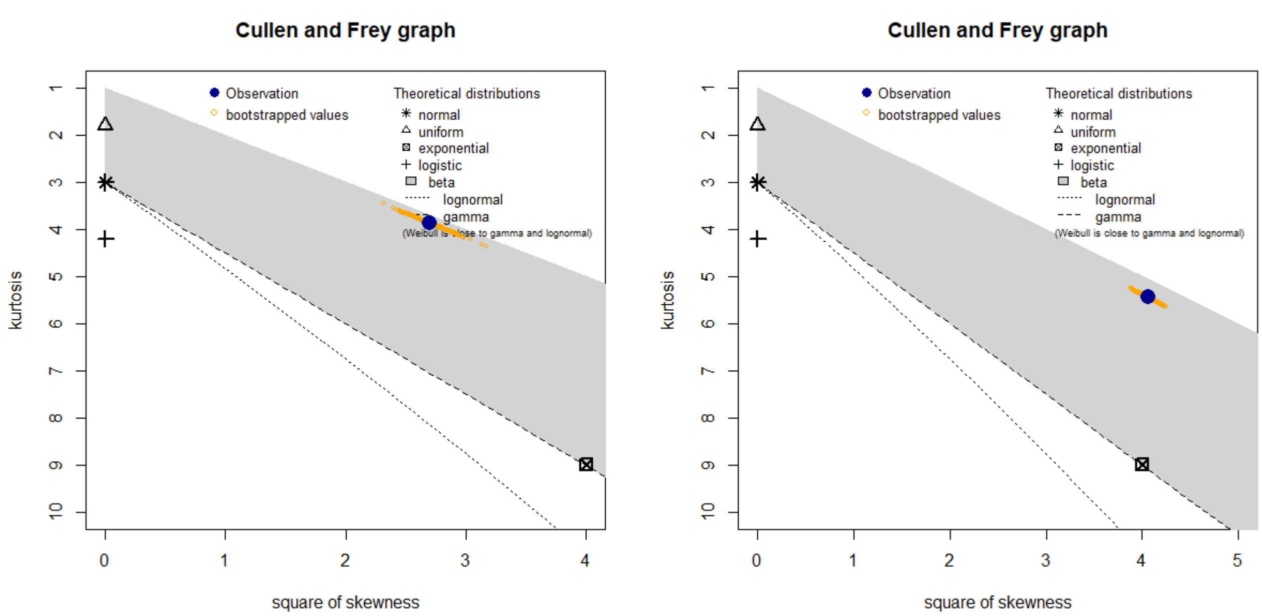

Figure 30. Skewness and kurtosis (Cullen and Frey) graphs plotted from bootstrap samples (500). The graphs show that both the observations and the bootstrap samples fall within a theoretical beta distribution.

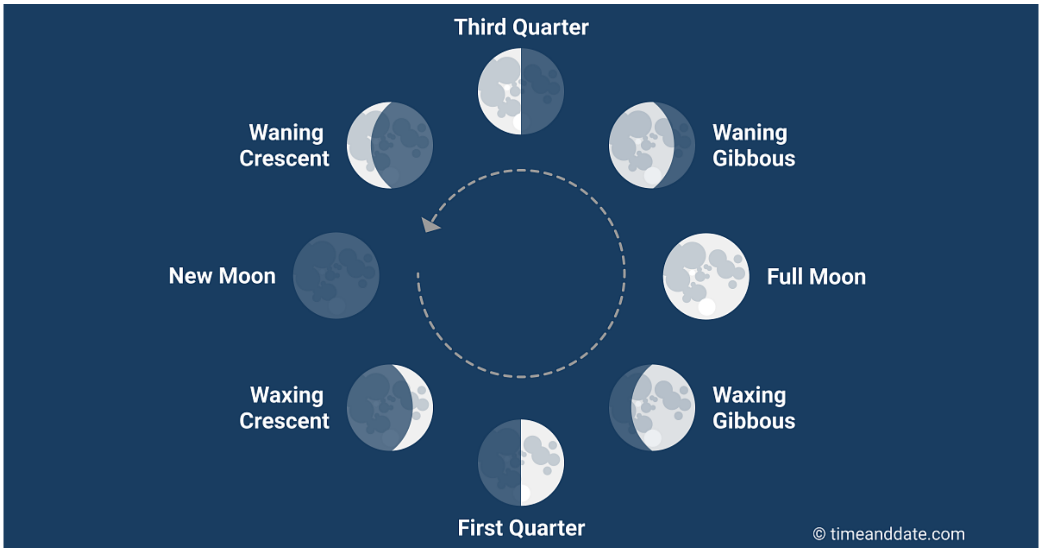

Figure 31. The eight lunar phases. The categorical moon phase variable in the model consisted of four of these (full moon (FM), first quarter (FQ), new moon (NM) and third- or last quarter (LQ)). The fifth level in the variable, Middling, consisted of the periods in between the former (waning/waxing gibbous, and waning/waxing crescent).

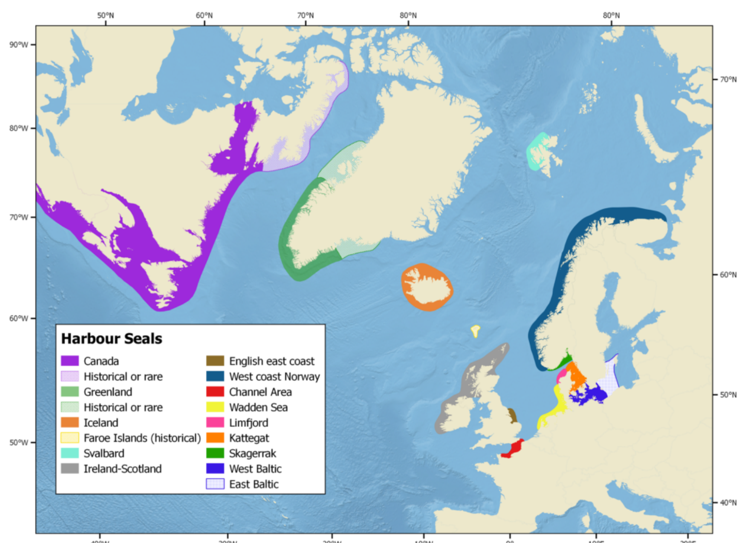

Figure 32. Genetically differentiated North Atlantic harbor seal populations (Andersen and Olsen 2010, Andersen et al. 2011, NAMMCO 2021 (https://nammco.no/topics/harbour-seal/).