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Passive acoustic monitoring of cetaceans in the Norwegian Skagerrak

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Master

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ABSTRACT

Marine ecosystems have been under pressure for decades as a result of intensive human activity. Cetaceans have also been negatively affected by our actions, so to implement protection and conservation plans, it is crucial to know the current state of the populations. In the last decades, passive acoustic monitoring (PAM) has become an important tool to fulfil this purpose. This study, makes use of PAM to investigate the spatial and temporal occurrence of cetaceans in the Norwegian Skagerrak between March 2023 and February 2024. Two methods were used: i) Monthly transect ship surveys from Norway to Denmark using a towed hydrophone array; and ii) Moored Continuous Porpoise Detectors (CPODs, n = 6) deployed at the Norwegian coast to monitor the presence and the vocal activity of harbour porpoises (*Phocoena phocoena*). Towed hydrophone data were analysed using the PAM software PAMGuard to study the cetacean occurrence along the year. The CPOD data were used to investigate spatial, seasonal and diel patterns in porpoise presence and vocal activity, as well as how sea temperature and currents affect these. Ship surveys revealed the presence of harbour porpoises, northern bottlenose whales (*Hyperoodon ampullatus*), minke whales (*Balaenoptera acutorostrata*) and bottlenose dolphins (*Tursiops truncatus*) in the area. Generalized Additive Models, fitted to the CPOD data, showed spatial, seasonal and diel variations on harbour porpoise presence and vocal activity, while the effect of hydrographic conditions was less clear. Significantly higher harbour porpoise presence and vocal activity were registered during spring, especially in the northernmost areas of Raet National Park. Moreover, porpoise presence was significantly higher during the night, independently of the time of the year. Changes in prey availability, as well as porpoise calving and mating seasons, and prey migration may be behind these observations. This study was the first of its kind performed in the Norwegian Skagerrak, and it provided novel information about specially, the harbour porpoises in the Norwegian Skagerrak. However, important knowledge gaps must still be filled to properly manage them.

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PREFACE

I would like to express my gratitude to Carla for guiding and helping me through every step of the project, to Lars for helping me with the statistical analysis and the writing, and to Jonathan for teaching me how to identify and analyse acoustic recordings and for welcoming me into his home in Scotland. Special thanks also to Ane Timenes Laugen from UiA for her guidance in statistical analysis, to Jon Albretsen from IMR for providing oceanographic data for the models, to the G. M. Dannevig crew for welcoming me into the ship and providing assistance with anything I needed, and to the researchers in SMRU for letting me join their sampling in Wales and having the patience to show me how to work with passive acoustic data.

Kristiansand, 2024.05.14

Jon Mokoroa Alberdi

INTRODUCTION

Ocean ecosystems have been under pressure for decades, mainly due to human activity (Halpern et al., 2008, 2019). Human populations keep growing and migrating to the coasts, increasing human activity on the sea and aggravating the already poor state of the ecosystems (Halpern et al., 2008, 2019). Marine mammals have also been negatively affected by our actions. They are especially vulnerable to anthropogenic noise, different kinds of pollution, entanglement, fishery interactions, collisions, vessel harassment, hunting and climate change among others (de Vere et al., 2018). Therefore, a continuous monitorization of cetacean populations is needed in order to develop management programs.

Passive acoustic monitoring (PAM) has made this continuous monitorization easier. Cetaceans use different kinds of vocalizations to navigate, forage or communicate with each other (Zimmer, 2011; Dudzinski & Hill, 2022). Baleen whales, such as minke whales (*Balaenoptera acutorostrata*) or humpback whales (*Megaptera novaeangliae*), make low frequency vocalizations like moans and grunts mainly for navigation purposes, while they generally use high frequency vocalizations like whistles and songs for communication (Dudzinski & Hill, 2022). Alternatively, odontocetes such as porpoises and dolphins use narrow band high frequency (NBHF) sounds known as clicks primarily for close range echolocation, navigation, foraging and object identification (Koschinski et al., 2008; Zimmer, 2011; Dudzinski & Hill, 2022). Whistles, on the other hand, are used for communication and individual identification inside odontocete groups (Zimmer, 2011; Dudzinski & Hill, 2022). As some of these vocalizations are species specific, it is possible to use them to conduct population studies via PAM (Dudzinski & Hill, 2022).

In ecological studies, PAM consists on deploying acoustic sensors to record sounds from the environment. The recordings are then analysed to monitor one or several target species. For marine mammal investigation, these acoustic sensors are either moored to a buoy or towed by a ship (Mellinger et al., 2007). When moored, it is possible to collect continuous data from the study area; and when towed, wider areas can be covered by performing acoustic ship transects. Nowadays, self-contained underwater sound recorders like sound traps (Ocean Instruments NZ) and porpoise detectors (PODs) (Chelonia Ltd.) are the most common moored devices. PODs are specifically developed to monitor porpoises and do not store any sound, they only process data on potential cetacean tonal clicks, which allows them to use less memory and energy. Data analysis is more efficient. However, only NBHF cetaceans (i.e. porpoises and some dolphins) can be reliably studied (Treganza, 2014). Alternatively, underwater sound recorders and towed hydrophone arrays record and store every sound detected inside their effective frequency range, and therefore, collect more data than PODs. This allows more thorough research of the acoustic background, including the study of more species, but more data storage capacity, time and effort is needed to analyse the data. Many studies have reported advantages of using PAM (Ross et al., 2023). It has proved to be useful to perform uninterrupted data collection, to study areas and seasons of heightened inaccessibility, or to research especially elusive or cryptic animals such as beaked whales (family Ziphiidae) (MacLeod et al., 2006; Deichmann et al., 2017; Gottesman et al., 2021). However, some limitations have also been observed. For instance, while useful for occurrence studies, PAM struggles to determine true absences (Toth et al., 2022; Ross et al., 2023). A target individual may be present, but its sound could be masked by other noises, too quiet to detect, or the animal may have simply gone silent (Toth et al., 2022; Ross et al., 2023). This adds uncertainty to absence estimations. Abundance estimations can also be difficult, since it is challenging to tell if the sound comes from a single individual or more (Ross et al., 2023). Some species have shown seasonal variations in acoustic activity too, which makes abundance analysis even harder. It is worth noting that acoustic localisation techniques are improving, which could solve this issue. However, more research needs to be done to generalise the use of PAM for abundance estimations (Rhinehart et al., 2020; Verreycken et al., 2021; Ross et al., 2023).

Numerous surveys on cetacean abundance have been conducted in the European north Atlantic waters. One of the main projects, Small Cetaceans in European Atlantic Waters and the North Sea (SCANS), focused on investigating the populations of small cetaceans like the harbour porpoise (*Phocoena phocoena*) during the summer, approximately every 10 years since 1994 (Hammond et al. 2002; Hammond et al. 2013; Hammond et al. 2021; Gilles et al., 2023). This project was complemented by other studies such as Cetacean Offshore Distribution and Abundance in the European Atlantic (CODA) in July 2007 (Hammond et al., 2009) and ObSERVE in 2015 and 2016 (Berrow et al., 2018). CODA mainly focused on surveying habitats beyond the continental shelf of Europe during the summer, and ObSERVE surveyed the seas inside Ireland's Exclusive Economic Zone during the summers and winters of 2015 and 2016. With these studies, all European Atlantic shelf waters were covered either by aerial surveys or ship transects, and the large-scale distribution of several small and large cetaceans was established. Only the ObSERVE program combined visual surveys with PAM, and it was also the only project that sampled seasons other than summer, but it was restricted to Ireland. Apart from these studies, abundance studies for commercially important baleen whales are also recurrently carried out in Norway and Iceland. Norwegian studies focus on minke whales, while Icelandic studies focus on fin whales (*Balaenoptera physalus*). However, they also provide abundance estimations for other species. They are conducted only during the summer and they cover open sea areas such as, the North Sea, Norwegian Sea, Barents Sea or the Central North Atlantic area (Pike et al., 2019; Leonard & Øien, 2020; Solvang et al., 2021). Overall, year-round studies are needed, since little is known about the seasonal occurrence of cetaceans in European waters.

The Skagerrak Sea connects the North Sea to the Baltic Sea and therefore, it is one of the most traffic-busy seas in the world (Pratson, 2023). Cetacean population analysis, behavioural studies, researches on migration patterns and occurrence investigations must therefore be carried out to be able to develop adequate management programs. However, in the Skagerrak and adjacent seas, the harbour porpoise has been the only recurrently monitored species. The North Sea harbour porpoise population is estimated to be around 340 000 individuals, of which 30 050 individuals are estimated to live in the Skagerrak and the westernmost area of the North Sea adjacent to it (Gilles et al., 2023). The Baltic population is estimated to be as small as 491 (Amundin et al., 2022). Research performed in the western Baltic Sea, Belt Sea and Kattegat Sea estimated 40 475 harbour porpoise individuals in the area (Viquerat et al., 2014). In the Danish side of the Skagerrak, many PAM and telemetry studies on harbour porpoises have been conducted (Sveegaard et al., 2011; Kindt-Larsen et al., 2016; Stadler et al., 2020; Jørgensen et al., 2024; Scheidat et al., 2024). However, no similar research has been carried out in the Norwegian side up until now, and the information about the rest of cetaceans is also scarce. The main reason for this is the low number of studies performed on the topic in this area, but the elusive nature of species like the beaked whales also makes them harder to study (MacLeod et al., 2006; Deichmann et al., 2017; Gottesman et al., 2021). For instance, SCANS-IV surveys observed bottlenose dolphins (*Tursiops truncatus*), common dolphins (*Delphinus delphis*), white beaked dolphins (*Lagenorhynchus albirostris*) and minke whales in the North Sea-Skagerrak area (Gilles et al., 2023). Historical data and stranding records have shown that Sowerby's Beaked Whales (*Mesoplodon bidens*) (Stavenow et al., 2022), killer whales (*Orcinus orca*) and long-finned pilot whales (*Globicephala melas*) are also present in the region (Kinze et al., 2018).

In this study the occurrence of cetaceans in the Norwegian Skagerrak was monitored, using acoustic ship surveys and moored continuous porpoise detectors (CPODs) (Chelonia Ltd.). Ship surveys covered a transect across the Skagerrak strait on a monthly basis, while CPODs continuously monitored the occurrence of harbour porpoises along the Raet National Park and adjacent waters at the Norwegian coast. Both samplings were conducted from April 2023 to February 2024. The aims were:

i. To study cetacean occurrence across the Skagerrak strait and its temporal variation throughout the year.
ii. To study harbour porpoise presence and vocal activity along the Norwegian coast and its variation in space, time and with oceanographic conditions.

METHODOLOGY

- Study area, materials and methods

The Skagerrak is a 240 km long and 140 km wide sea, located between the south coast of Norway, and the Danish Jutland peninsula. It connects the North Sea to the west with the Baltic Sea to the east via the Kattegat strait. The Norwegian trench crosses the Skagerrak parallel to the Norwegian coast and it is 700 m deep at its deepest part (Rodhe, 1987; NOAA, 2022). This trench makes the Norwegian side of the strait much steeper than the Danish side (NOAA, 2022). In fact, most of the Danish side is less than 50 m deep, which makes half of the strait shallow and flat, and half of the strait deep and steep (NOAA, 2022). The surface water's temperature varies throughout the year between 2ºC and 20ºC. The major currents show a cyclonic circulation. The Atlantic water coming from the North Sea flows into the Danish side of the Skagerrak parallel to the coast. This water mass then connects to the water current coming from the Baltic Sea, and exits the Skagerrak from the Norwegian part of the sea, again parallel to the coast (Rodhe, 1987). The Skagerrak contains several different bottom types such as sandy seafloors, rocky reefs, and deep areas and as a consequence, a variety of ecosystems can be found (Rosenberg et al., 1996; Norderhaug et al., 2015; Trannum et al., 2018).

SHIP SURVEYS

Passive acoustic data were collected opportunistically onboard the research vessel G. M. Dannevig during passages in the Skagerrak using a towed hydrophone array. The ship conducted a monthly transect between Norway and Denmark. PAM was undertaken during the transit section of the survey, where no sampling stops were performed for the main purpose of the cruise. In total, PAM was conducted in 7 cruises, between April 2023 and February 2024. The first PAM transect crossed the Skagerrak from the Flødevigen Research Station (His, southern Norway) to the city of Hirtshals (northern Denmark) while the following transect covered the way back to Norway either to Flødevigen or to the city of Risør (Figure 1). The hydrophone was deployed as soon as possible and retrieved as late as possible in the transect, depending on the number of vessels in the surroundings. This decision was made by the captain.

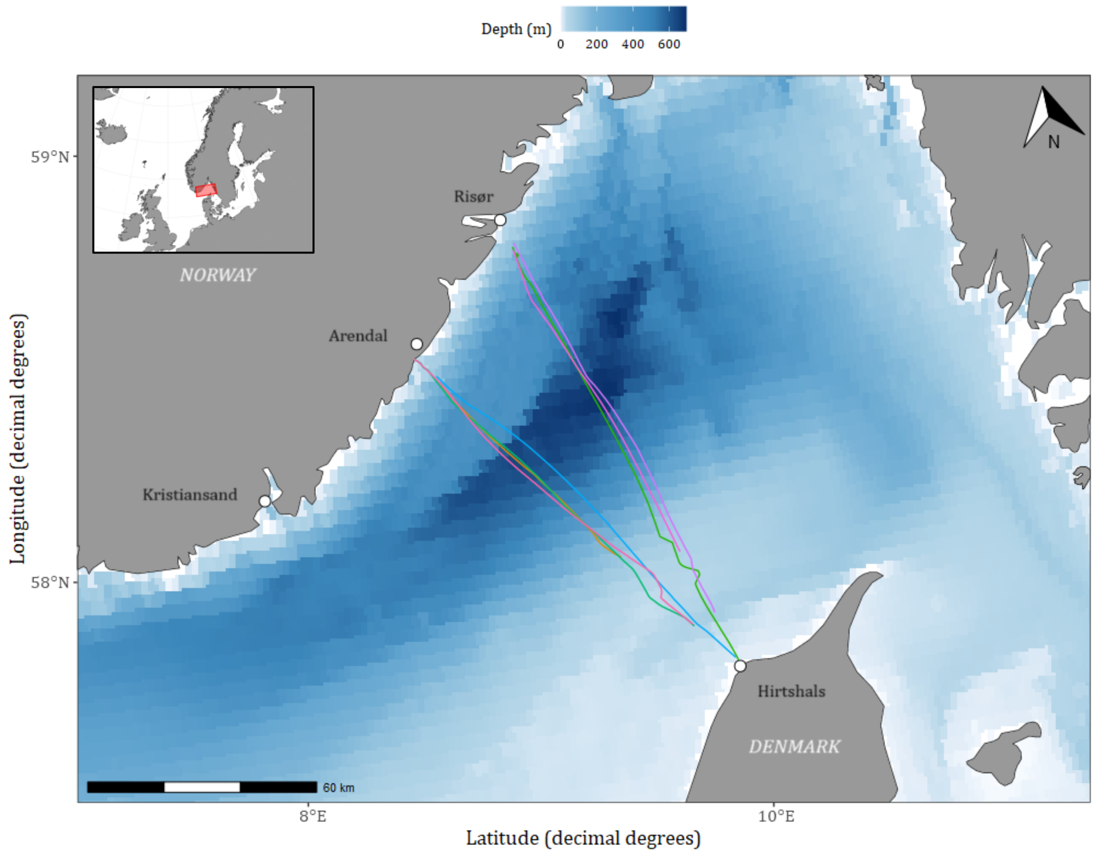

Figure 1. Map of the Skagerrak showing the acoustic transects performed in the cruise.

The hydrophone array used for this research consisted of 4 elements placed in series (one after the other) and installed inside an oil-filled polyurethane tube (Figure 2). The whole device was connected to the ship via a 350 m long Kevlar-strengthened multicore cable, coiled around a winch. The other end of the cable was connected to a PAMBox that contained a SAIL (St. Andrews Instruments Ltd.) acoustic conditioning and digital acquisition card. The first and last elements in the array (hydrophones 0 and 1, respectively) were two mid frequency hydrophone and preamplifier units, placed 3 m apart from each other (nominal best sensitivity with preamp -165 dB rel 1V/µPA) (Figure 2). These preamplifiers had a low-cut filter between 10-100 Hz. These units show a good frequency response to sounds between 10-100 Hz and 50 kHz. The second and third elements in the array (hydrophones 2 and 3, respectively) were two high frequency hydrophone and preamplifier units, placed 30 cm apart from each other (nominal best sensitivity with preamplifier -159 dB rel 1V/µPA) (Figure 2). Each unit consisted of a spherical hydrophone element feeding a broadband Magrec HP/02 preamplifier. These preamplifiers had a low-cut filter set at 2 kHz, and the units have a good frequency response to sounds between 2 kHz and 150 kHz. The array had a pressure sensor located in the tube close to the connection to the cable. The other end of the array had a rope tail that made the device more stable in the water while being towed (Figure 2).

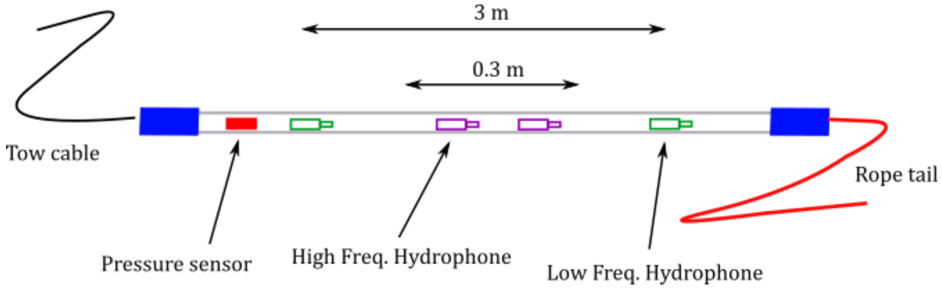

Figure 2. Layout of the elements in the hydrophone array.

Complementarily, visual surveys were performed during the transects. The visual survey was opportunistic, using either one or two observers. Observers were stationed at the bridge surveying the front 180º field of vision. When 2 observers were present, one observer took care of the port 90º and the other surveyed the starboard 90º. Time of observation, species, confidence on the identification (definite, possible, low), number of individuals and geographic coordinates were noted for each sighting. Besides this, Beaufort wind force (0-12), speed of the vessel, visibility and surrounding vessels were also noted every hour.

The cruises were performed in April, July, September, October, November and December in 2023 and in February in 2024. Some months were skipped either because of bad weather conditions or due to issues related to the cruise's main research. The hydrophone malfunctioned at the beginning of the transect in July, when only 32 minutes were properly recorded. This malfunction was fixed for the next cruise.

MOORED CPODS

Six CPODs were deployed in Raet National Park and adjacent waters, between the villages of Homborsund and Lyngør in southern Norway (Figure 3). The CPODs were placed around 1 km from the shore and around 5 km from each other, at areas that were around 50 m deep. The chosen stations were – from south to north – Homborsund, Fevik, Torungen, Trømoy, Møkkalasset and Askerøy.

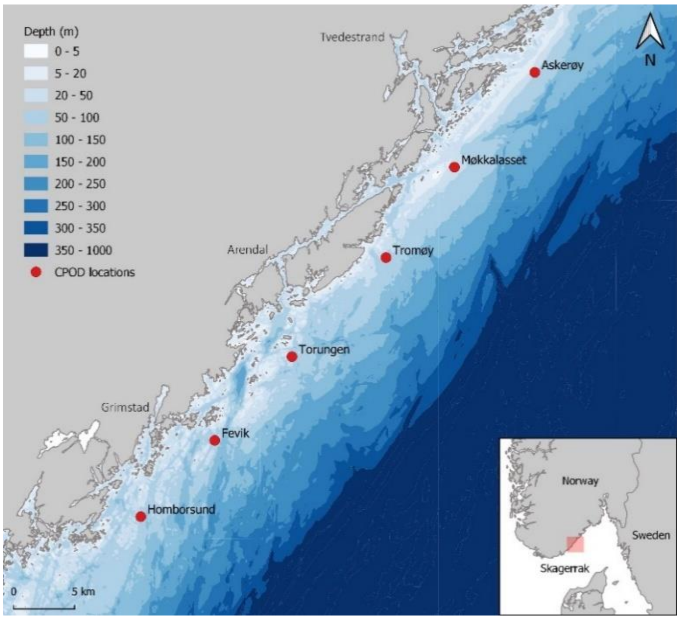

Figure 3. Map of the CPOD sampling area. The red dots indicate the sampling sites. From south to north: Hombrosund, Fevik, Torungen, Trømoy, Møkkalasset and Askerøy.

A 4 m rope was tied to a surface buoy and to an underwater buoy. A 6 m rope was used to tie the underwater buoy and the CPOD. Therefore, the CPODs were placed at around 10 m deep. Finally, the CPOD was tied to a weight with a 40m long rope. This weight was also tied to a heavier weight by a 20 m long rope (Figure 4). In total, the whole device was prepared to be deployed at areas less than 50 m deep.

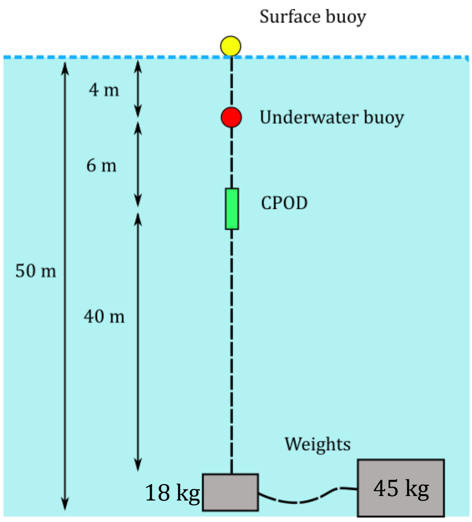

Figure 4. Layout of the structure that consists of a surface buoy, an underwater buoy, the CPOD and the weights.

The CPODs were deployed the 27th of March 2023 at all stations except in Askerøy, where it was deployed the 09th of May 2023. All stations were retrieved at the end of February 2024. During the deployment period, each memory card and battery was changed every 3 to 8 months. No data were recorded by some CPODs during certain periods due to battery drainage or memory usage. The CPOD in Trømoy malfunctioned for the entirety of September and part of October.

- Data analysis

SHIP SURVEYS

The data collected with the towed hydrophone array were analysed using the PAMGuard open-source software (v2.02.09; Gillespie et al., 2009). Species identification was carried out based on odontocete clicks. No other sounds were analysed, including sounds from mysticetes. Specific click classifiers for harbour porpoise and beaked whale were used to identify these species. The main target inside the beaked whales' family was the Sowerby's beaked whale. However, the click parameter and classifier specifications were broadened in order to cover other beaked whale species, such as the Cuvier's beaked whale (*Ziphius cavirostris*). The digital pre-filter used a IIR Butterworth filter type with a band pass ranging from 5 kHz to 200 kHz and a filter order of 4. The filter type for the digital trigger filter was specified to be IIR Chebyshev, with a band pass between 10 kHz and 150 kHz. A filter order of 4 and a pass band ripple of 2 were applied. In order to improve accuracy, 2 different click detection parameters were used, one for each target. A high pass filter of 100 kHz was applied for harbour porpoise click parameters, while a band pass filter between 20 kHz and 80 kHz was applied for beaked whales. The energy test bands for the harbour porpoise classifier were set at 100 kHz and 150 kHz, while the control bands were set at 40-90 kHz and at 160-190 kHz. The thresholds of both control bands were set at 6 dB. The peak and mean frequency search and integration range was set at 40-240 kHz. The peak frequency range was set at 100 kHz and 150 kHz. Click length was limited to a range between 0.01 ms and 0.22 ms, with a threshold of 6 dB below maximum. For the beaked whale classifier, the energy test bands were set at 24 kHz and 80 kHz. The lower control band was set at 12-24 kHz, while the upper control band was set at 80-150 kHz. The thresholds for both control bands were set at 3 dB. The peak and mean frequency search and integration range was set at 10 kHz and 96 kHz. The range for the peak frequency was established at 25 - 80kHz, as well as the range for the mean frequency. Furthermore, visual displays included in PAMGuard such as frequency spectrograms and click detectors were also used to manually analyse both automatically classified click trains and unclassified click-trains. Only click-trains containing more than 5 clicks were considered when classifying events for the study. Each acoustic detection was classified depending on the subjective confidence on the identification as definitive, possible or low. Acoustic events and sightings from the visual surveys were mapped using R Statistical Software (v4.2.1; R Core Team, 2022), and its IDE RStudio (v2023.6.1.524; Posit Team, 2023), and the *ggplot* (v3.5.1; Wickham, 2016) and *ggOceanMaps* packages (v2.2.0; Vihtakari, 2024). Bottom depth of the event locations was also obtained using the *ggOceanMaps* package.

MOORED CPODS

Data processing

The potential cetacean clicks logged by the CPODs were run through the "KERNO" classifier included in the CPOD.exe software (Chelonia Ltd.). This classifier looks for clicks and inter click intervals from a click-train that are similar to the previous and subsequent ones. At least 5 clicks are required for KERNO to classify a sequence of clicks as a train. Then the click-trains are given a confidence class and assigned a source or species. Only Hi and Mod quality NBHF (porpoise) trains were analysed. The detected harbour porpoise trains were extracted as clicks per hour and wrangled and analysed in RStudio using the *tidyverse* package collection (v.2.0.0; Wickham et al., 2019). Every hour in which the CPOD had been on for less than 45 minutes was deleted in order to avoid bias. Oceanographic data were retrieved from Institute of Marine Research's (IMR) main hydrodynamical model system for Norwegian fjords. The model system is similar to the system described in Dalsøren et al. (2020). Time series were extracted for the six locations where CPODs had been deployed. Hourly data were extracted for each location from March 2023 to December 2023, and interpolated vertically to depths of 0 m, 20 m and 35 m. No data for 2024 were available. Because of this, CPOD data collected in January and February 2024 were not included in the models. The oceanographic data consisted on 3 water temperature values and 3 sea current speed values (SC) for each hour. The first values corresponded to conditions at 0 m depth (T0 and SC0). The second values corresponded to conditions at 20 m depth (T20 and SC20). The third values corresponded to conditions at 35 m depth (T35 and SC35). These data were added to the dataset in order to build models later on. Solar elevation data were also added using the *Maptools* package for RStudio (v1.1-6; Bivand & Lewin-Koh, 2022). Solar elevation represented the angle between the sun and the horizon at each hour of data, where 0º corresponded the horizon and 90º the most perpendicular point the Sun can take from the surface. These data were calculated based on the coordinates of the CPODs, the time of the year and the time of the day. The angles were then transformed into a categorical variable called “Period of the day” by classifying every angle above 0º as “Day”, angles between 0º and -12º as “Twilight” (based on Nautical Twilight), and angles below -12º as “Night”.

Data exploration

Data exploration was performed following the protocol described by Zuur et al. (2010), in order to find out how the data were distributed, what issues they had, how the variables were correlated and what would be the best structure for the models.

As expected, a tight correlation was found between sea temperature (at all three depths) and the months variable. A remarkable correlation between the Tº variables was also observed; specially between T0 and T20, and T20 and T35. SC variables showed the same correlation. Therefore, the Tº variables and SC20 were discarded. No substantial correlation was observed between any other variables. The number of hours with positive detections (number of detected clicks > 0, n = 2945) supposed the 9.5% of the hours with 0 clicks (n = 30 893). However, the difference between the first mode (hours with 0 clicks = 30 893) and the second mode (hours with 6 clicks = 292) was much bigger. This hinted a zero-inflation problem.

Statistical analysis

As one of the main aims was the analysis of time series data, non-linear relations, as well as non-normal data distribution were expected. This led to the decision of using two Generalized Additive Models (GAMs) to test whether the time of the day, time of the year, location or sea currents had an effect on (i) harbour porpoise presence and (ii) vocal activity (number of porpoise-clicks per hour). This allowed to investigate the presence and the vocal activity separately for each moment and condition. The presence data were analysed with a logistic model (GAM1), while the count data were analysed with a log-linear model (GAM2). However, later tests revealed that dispersion parameters were far from optimal for GAM2 (Figure S3). Therefore, a quasi-Poisson approach was taken to correct the Standard Errors (SE). The models were built using the *mgcv* package (v.1.8-40; Wood, 2010) for RStudio.

Both models included the continuous Month, SC0 and SC35 variables, as well as the categorical variables Site and Period of the day. The Autocorrelation Function (ACF) showed a temporal autocorrelation of the data of lag 2 (Figure S1). Therefore, an autoregressive process of order 1 (corAR1) (see Zuur et al., 2009 for more details) based on Julian hours and differentiated by site was added to both models. The formulae of GAM1 and GAM2 were, respectively, as follows:

$$logit(p_i) = \alpha + f1(Month) + f2(SC0_i, k = 5) + f3(SC35_i, k = 5) + \beta 1Site + \beta 2SolarElev_i$$

$$log(Clicks_i) = \alpha + f1(Month) + f2(SC0_i, k = 5) + f3(SC35_i, k = 5) + \beta 1Site + \beta 2SolarElev_i$$

Where p_i indicates the probability of detecting a harbour porpoise during hour *i*. $Clicks_i$ represents the average number of harbour porpoise clicks detected during hour *i*. The f in the continuous variables of Month, SC0 and SC35 indicates a smooth function. The number of basis-functions in each smooth (k) was specified to be the default k = 10 for the month variables and k = 5 for the SC variables in order to reduce computational effort and overfitting. The default k value was used for the Month variables in order to get a more detailed display of the temporal variation. The β next to the categorical variables Site and Solar Elevation states their slope.

Model selection

The full models were fitted first, and backwards model selection was conducted afterwards based on the Akaike Information Criteria (AIC). The best binomial model included variables Month and SC35 modelled as smooth functions and variables Site and Solar elevation as categorical variables (Table S1). The best count model included the variables Month, SC0 and SC35 modelled as smooth functions and variables Site and Solar elevation as categorical variables (Table S1).

Model validation

Model validation was performed as described in Zuur & Ieno (2016). A residual simulation was performed for each model, using the *DHARMa* package for RStudio (v.0.4.6; Hartig, 2022). The fitted residuals were then plotted. The plots showed that the residuals were very similar to the fitted residuals for the binomial GAM1 model, indicating no dispersion issues (dispersion = 0.998, p-value = 0.9) (Figure S2). However, Poisson distribution GAM2 fitted residuals showed significantly lower values than expected, which indicated under-dispersion (dispersion = 441.51, p-value < 0.001) (Figure S3). To solve this, the quasi-Poisson approach was taken, which allowed to obtain more robust SE and more reliable inferences were estimated. In the end, the formulae of the final binomial and count models looked as follows, respectively:

$$logit(p_i) = \alpha + f(Month) + f(SC35_i, k = 5) + \beta Site + \beta SolarElev_i$$

$$log(Clicks_i) = \alpha + f(Month) + f(SC0_i, k = 5) + f(SC35_i, k = 5) + \beta Site + \beta SolarElev_i$$

Models were then plotted using the *ggplot2* package.

RESULTS

SHIP SURVEYS

Approximately 40 hours of four channel acoustic data were collected during seven ship transects across the Skagerrak strait. This resulted in 450 GB of raw recordings. Overall, 17 acoustic events of two different species were recorded, 12 harbour porpoise events and five northern bottlenose whale (*Hyperoodon ampullatus*) events (Table S2, Figure 5, Figure 6).

Acoustic events happened every month except in July and September (Table S2). Harbour porpoise events were detected in all the remaining months. Two in April, one in October, four in November, two in December and three in February. Additionally, four northern bottlenose whale events happened in October and one in December. When it comes to the visual sightings, six harbour porpoise events were observed with a total of ten individuals, all of them in July (Table S2). A minke whale was seen also in July and a bottlenose dolphin in December (Table S2). Most harbour porpoise events were detected in waters less than 300 m deep (n = 12), either in the Norwegian side or in the Danish side of the Skagerrak. Six events happened over the Norwegian Trench, in waters more than 300 m deep (Table S2, Figure 6). Every northern bottlenose whale detection was made close to the Norwegian trench, in areas that were over 400 m deep (Table S2, Figure 6). The minke whale was observed in the Danish side and the bottlenose dolphin sighting occurred very close to the harbour in Hirtshals (Denmark) (Figure 6). Acoustic detections were made under Beaufort 0 to 5, while every sighting occurred when wind conditions were favourable (Beaufort 0 or 1). Most visual observation happened when two observers were on effort. None of the sightings happened while acoustic data were being recorded. The sightings in July occurred either before deploying the hydrophone array, or when the device malfunctioned. The sighting in December also occurred before deployment.

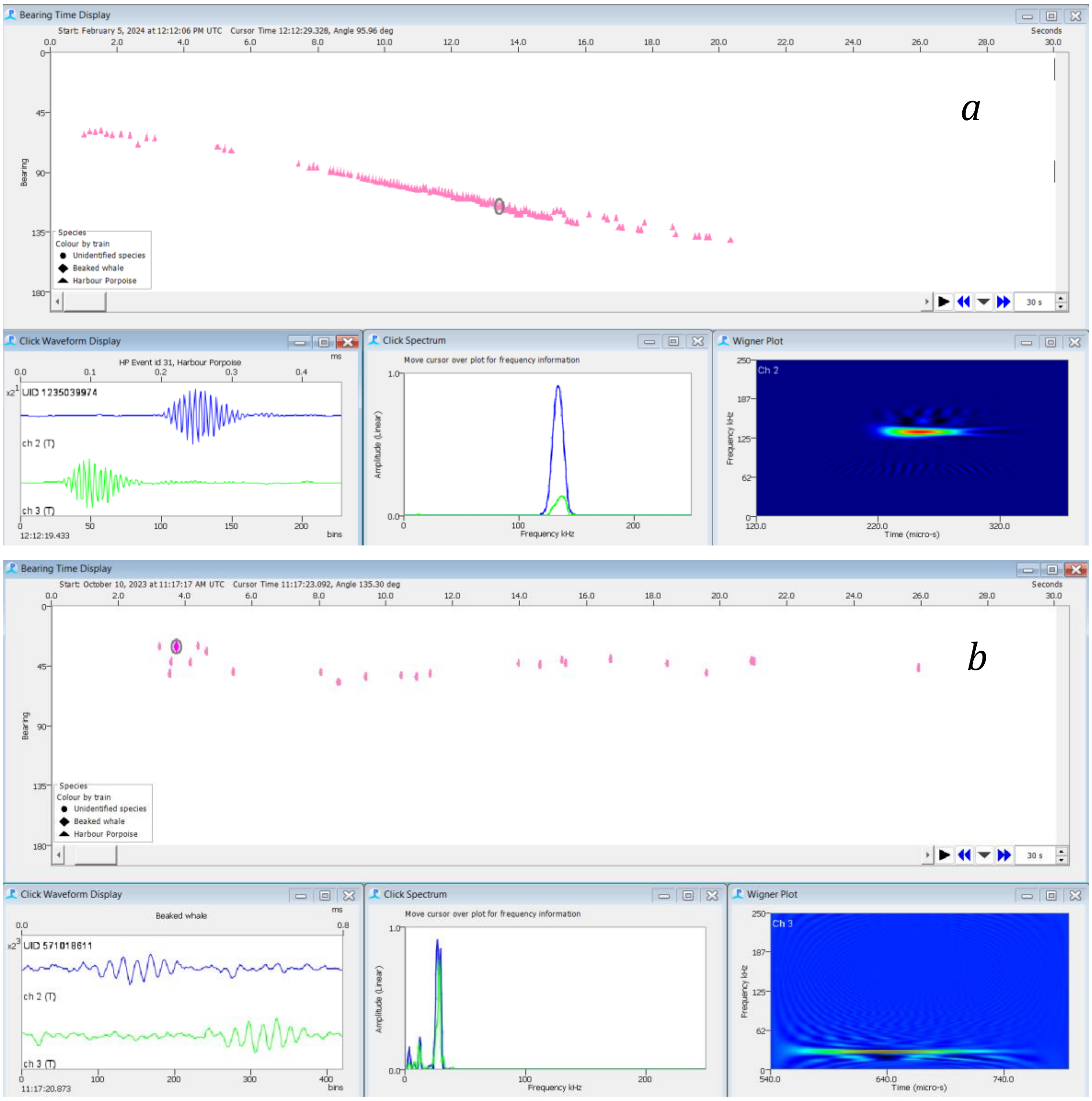

Figure 5. Display of the PAMGuard click detector module screen with an example of a harbour porpoise event on the top (a) and an example of a possible northern bottlenose whale event on the bottom (b). Every other click was removed from the displays. Top plots: x-axis shows time in seconds, y-axis shows the bearing from the hydrophone array. Pink points show harbour porpoise or northern bottlenose whale clicks. Bottom-left plots: the waveform-display of the selected click. Bottom-middle plots: spectrum of the selected click. x-axis represents the frequency (kHz), y-axis represents amplitude (linear). Bottom-right plots: Wagner plot of the selected click. x-axis represents time (ms), y-axis represents frequency (kHz). Colours indicate amplitude.

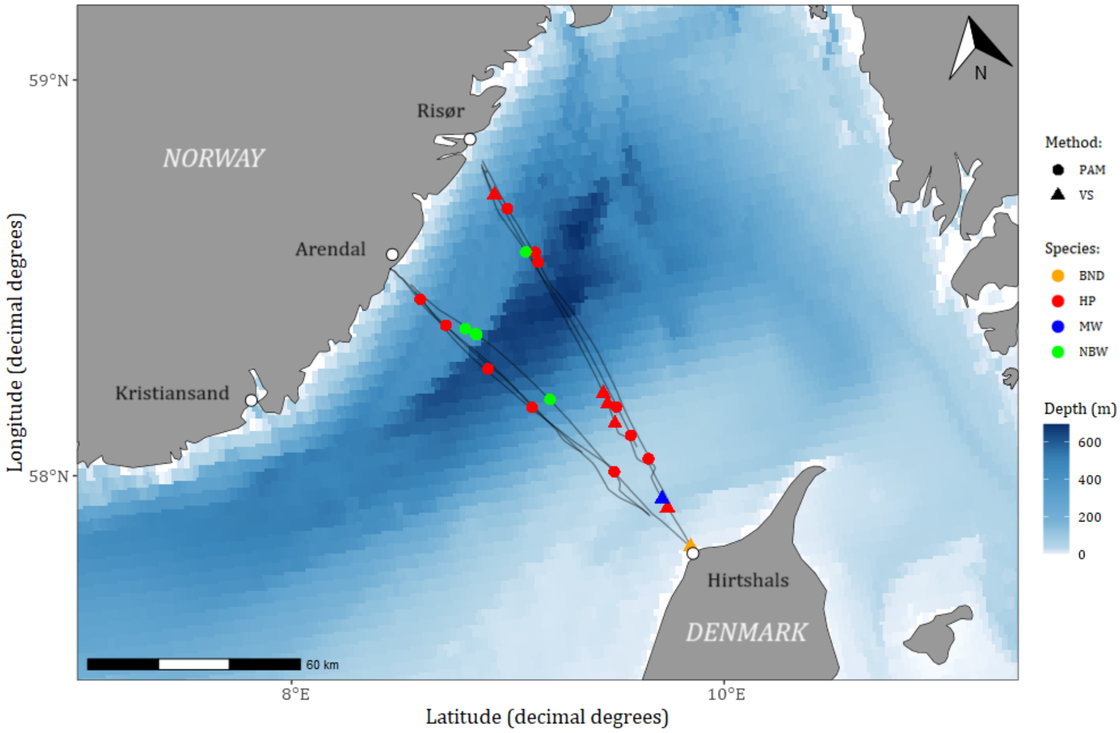

Figure 6. Map of the Skagerrak strait with bathymetry. Lines indicate the acoustic transects. Colours indicate species: bottlenose dolphin (BND), harbour porpoise (HP), minke whale (MW), northern bottlenose whale (NBW). Symbols indicate detection method: passive acoustic monitoring (PAM) and visual survey (VS).

MOORED CPODS

A total of 38 542 hours of harbour porpoise click data were collected between the end of March 2023 and February 2024. Overall, 228 046 porpoise clicks were detected throughout 11 months and 6 sites. Harbour porpoise presence showed significant diel and seasonal variations (Table 1, Figure 7, Figure 8). Sea currents; however, seemed to have no effect on harbour porpoise presence (Table 1, Figure 9). Porpoise vocal activity varied in similar fashion daily and seasonally (Table 2, Figure 11). Higher vocal activity was observed for sea current values close to 1 m/s (Table 2, Figure 12, Figure 13).

Clear diel patterns were observed in harbour porpoise occurrence. Porpoises were more present during the night and twilight than during the day, and this pattern was observed at almost every month (Table 1, Figure 7). The highest peaks were observed between 16:00 and 21:00 every month except in March, May and July (peaks at 14:00, 00:00 and 13:00 respectively) (Figure 7).

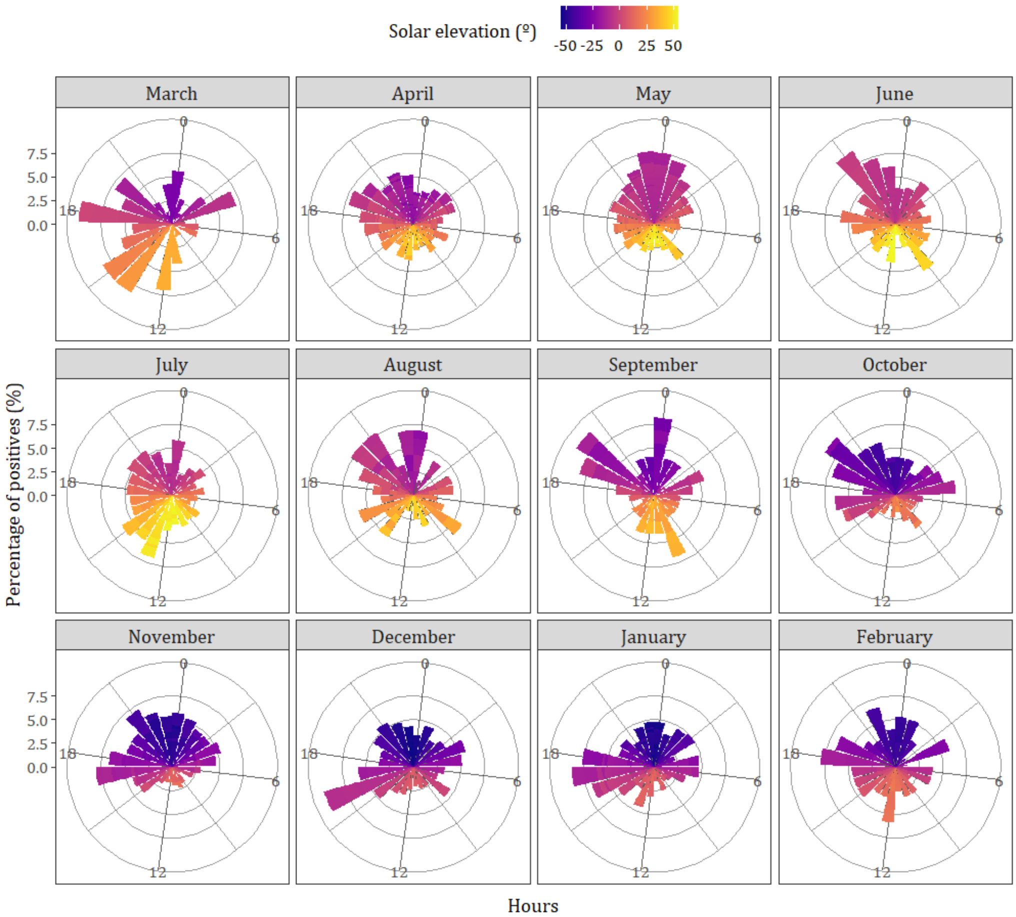

Figure 7. Percentage of hours with harbour porpoise detections (percentage of positives) as a function of period of the day observed between March 2023 and February 2024 at all sites. The x-axis (circular, resembling a clock) indicates hours and is divided in 24 segments from 0 h to 23 h. The bars represent what percentage of the total positive hours correspond to a specific hour, sorted by months. The top of the circles is midnight (00:00) and the bottom of the circles is noon (12:00). The colour represents the angle between the sun and the horizon in degrees (º), from 50º below the horizon (blue) to 50º over the horizon (yellow).

The binomial GAM showed that diel differences were statistically significant and consistent throughout the year and in all sites. Pronouncedly less presence was detected during the day than during the twilight or night (p-value < 0.001), but no significant difference on harbour porpoise presence was observed between night and twilight (p-value = 0.824) (Table 1, Figure 8). The model showed a presence peak around the end of April, and it progressively decreased until it reached the lowest point around the end of August (Figure 8). The highest value of the spring peak was recorded in Trømoy, where around 40% of the hours during the night and twilight were estimated to have porpoise presence. The lowest proportion was observed during the day in September, when the proportion of positive hours was below 0.05 at every sampled station. The model showed an increase in the proportion of positive hours around October at all stations (Figure 8). Two groups of stations were observed. The two northernmost stations, Askerøy and Møkkalasset, showed no difference between them, but they were different from the rest of the stations (Table 1). Specifically, Trømoy had significantly more porpoise presence than any other station, and the three southernmost stations had a significantly lower porpoise occurrence.

Table 1. Linear and smooth terms of the binomial GAM, used to analyse the harbour porpoise presence. Explanatory variables were Site and Period of the day as linear terms, and Month and sea currents at 35 m deep as smooth terms. Intercept represents statistics for the site Askerøy at twilight.

Outcome variable	**Linear term**	**β**	**SE**	***Z***	***p***	**Smooth term**	**edf**	**Ref.df**	**Chi.sq**	***p***
Presence	**Intercept**	-2.19	0.064	-33.90	<0.001	**s(Month)**	8.359	8.873	672.31	<0.001
	Møkkal.	0.10	0.067	1.47	0.14	**s(SC35)**	1.799	2.211	5.86	0.0742
	Trømoy	0.76	0.065	11.68	<0.001					
	Torungen	-0.49	0.083	-5.92	<0.001					
	Fevik	-0.27	0.072	-3.85	<0.001					
	Hombor.	-1.15	0.01	-11.57	<0.001					
	Day	-0.55	0.050	-11.08	<0.001					
	Night	-0.01	0.062	-0.22	0.824					

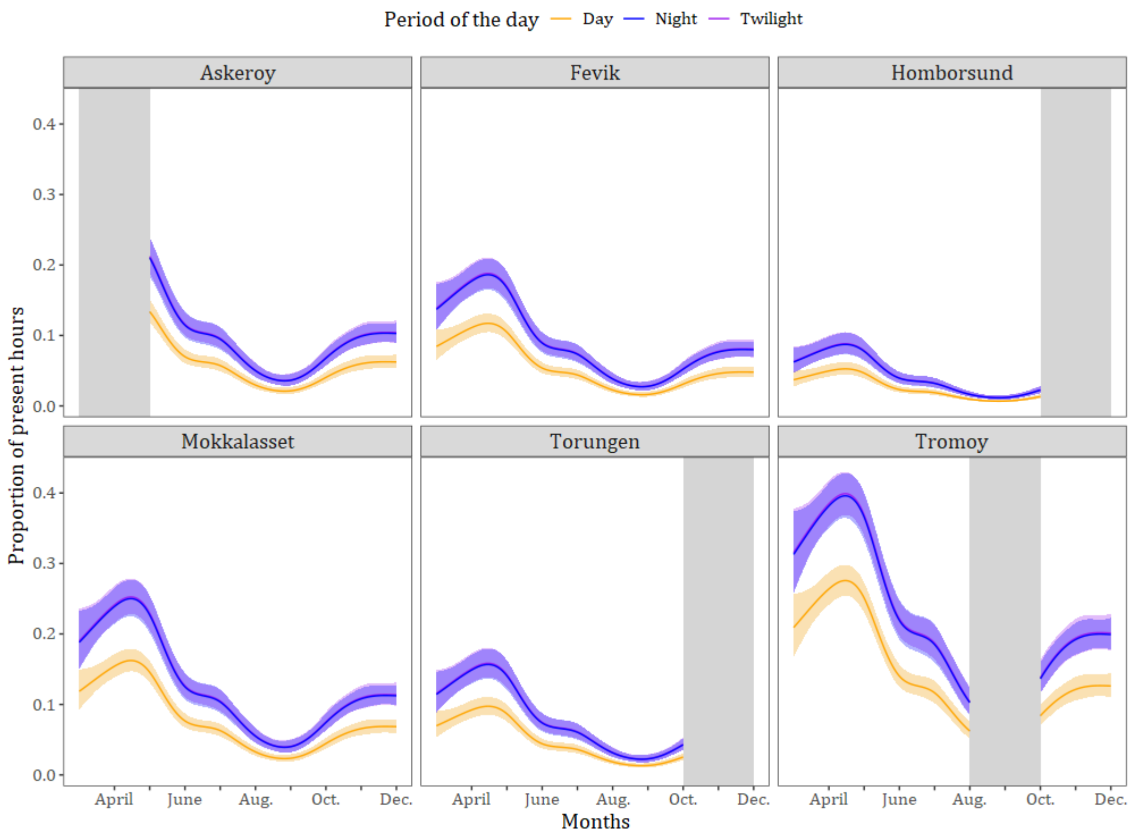

Figure 8. Probability of detecting a porpoise during the day, twilight and night at each station, as a function of months. Predicted from the binomial GAM. Yellow = Day; Purple = Twilight; Blue = Night. Coloured shades represent the standard error of the lines of the same colour. Grey areas indicate periods of no data. Notice that in this plot night and twilight data overlap each other. For this plot, SC values were kept constant at SC35 = 0.2 m/s.

The model showed that sea currents had no significant effect on the presence of harbour porpoises (p-value = 0.0742) (Table 1, Figure 9).

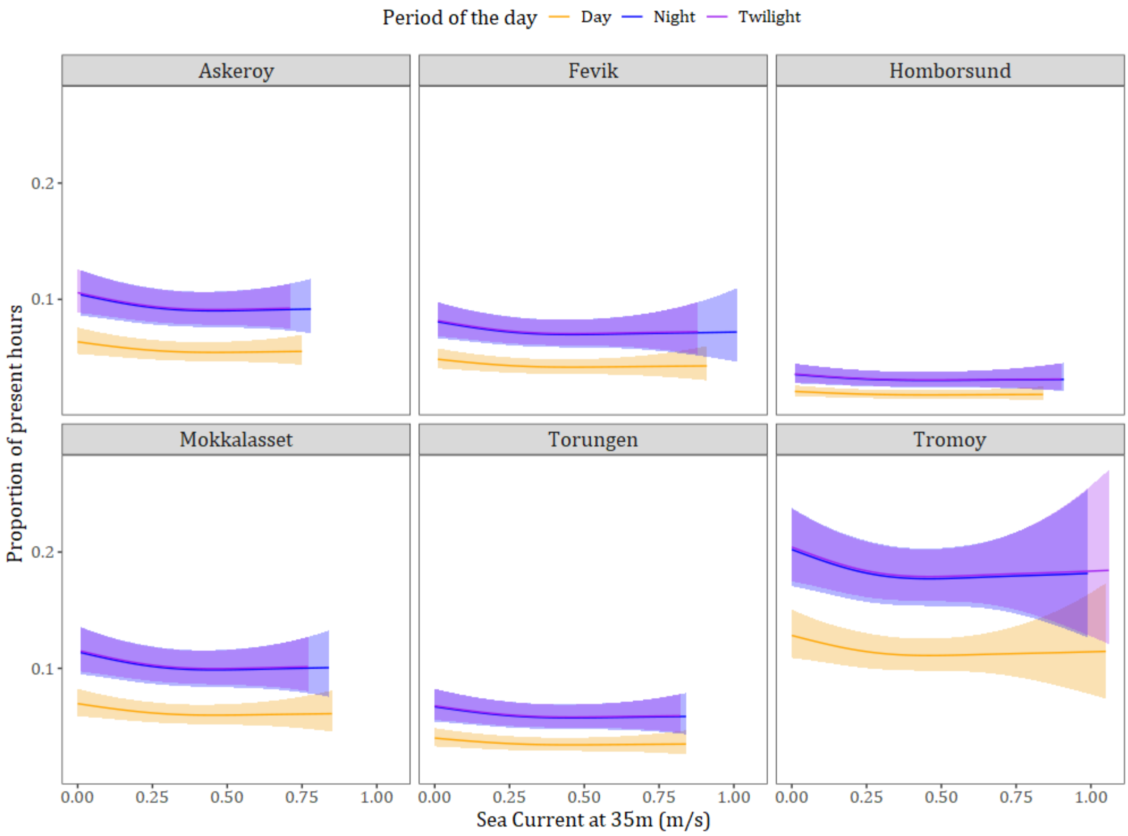

Figure 9. Probability of detecting a harbour porpoise during the day, twilight and night at each station, as a function of sea current speed at 35 m depth. Predicted from the binomial GAM. Yellow = Day; Purple = Twilight; Blue = Night. Coloured shades represent the standard error of the lines of the same colour. Notice that in this plot night and twilight data overlap each other. The month variable was kept constant at the month of July.

Regarding vocal activity, more porpoise clicks were detected in the northernmost stations than in the stations in the south. The station with the highest number of clicks was Trømoy with a total of 127 648 clicks. Møkkalasset, Fevik, Askerøy and Troungen followed and Homborsund was the station with the lowest number, 5030 clicks (Figure 10). The months with the highest click number were April, May and July, while the lowest quantity was detected in the months of August, September and October without including March, since only 4 days were sampled that month. January was 4th even though only the CPODs of Trømoy and Møkkalasset worked the whole month, due to the CPODs in Askerøy and Fevik stopping half way. February was 8th with just 2 CPODs that only lasted until the 14th of February (Figure 10).

Figure 10. Number of clicks detected per day by the Continuous Porpoise Detectors (CPODs) at six sites along the Norwegian Skagerrak coast. Grey areas indicate periods of no data. Values over 1000 clicks per day are not shown (n = 342).

The count GAM showed seasonal, diel and spatial variations on harbour porpoise vocal activity (Table 2, Figure 11). The model revealed a peak on vocal activity around the end of April and beginning of May. A slight decrease was detected in the month of June, but the vocal activity increased again around the first weeks of July. The vocal activity then decreased, and reached its lowest values around the end of August and begining of September. The model displayed a small recovery around the end of October and begining of November (Figure 11). Less clicks per hour were counted during the day than during the night or twilight (p-value < 0.001), and a small difference was observed between twilight and night (p-value = 0.012) (Table 2). Slightly more clicks per hour were recorded during the night at every station, and the biggest variation on the vocal activity was also observed during the night, while the variation during the day was the lowest (Figure 11). The highest click number per hour mean was estimated in Trømoy, around 100 clicks per hour (Figure 11). The two northernmost stations, Askerøy and Møkkalasset, and Fevik showed a smaller difference between them than with the rest of the sations (Table 2).

Table 2. Linear and smooth terms of the count GAM used to analyse the vocal activity of harbour porpoises. Explanatory variables were Site and Period of the day as linear terms, and Month, sea currents at 0 m and sea currents at 35 m as smooth terms. Intercept represents statistics for the site Askerøy at twilight.

Outcome variable	Linear term	β	SE	*t*	*p*	Smooth term	edf	Ref.df	Chi.sq	*p*
Number of clicks per hour	**Intercept**	1.596	0.122	13.105	<0.001	**s(Month)**	8.858	8.992	32.826	<0.001
	Møkkal.	0.3	0.132	2.268	0.0233	**s(SC0)**	3.942	3.997	2.967	0.018
	Trømoy	1.482	0.122	12.155	<0.001	**s(SC35)**	3.967	3.999	4.972	<0.001
	Torungen	-0.63	0.174	-3.633	0.001					
	Fevik	-0.35	0.151	-2.316	0.0206					
	Hombor.	-1.45	0.229	-6.327	0.001					
	Day	-1.05	0.081	-12.87	<0.001					
	Night	0.232	0.093	2.51	0.012					

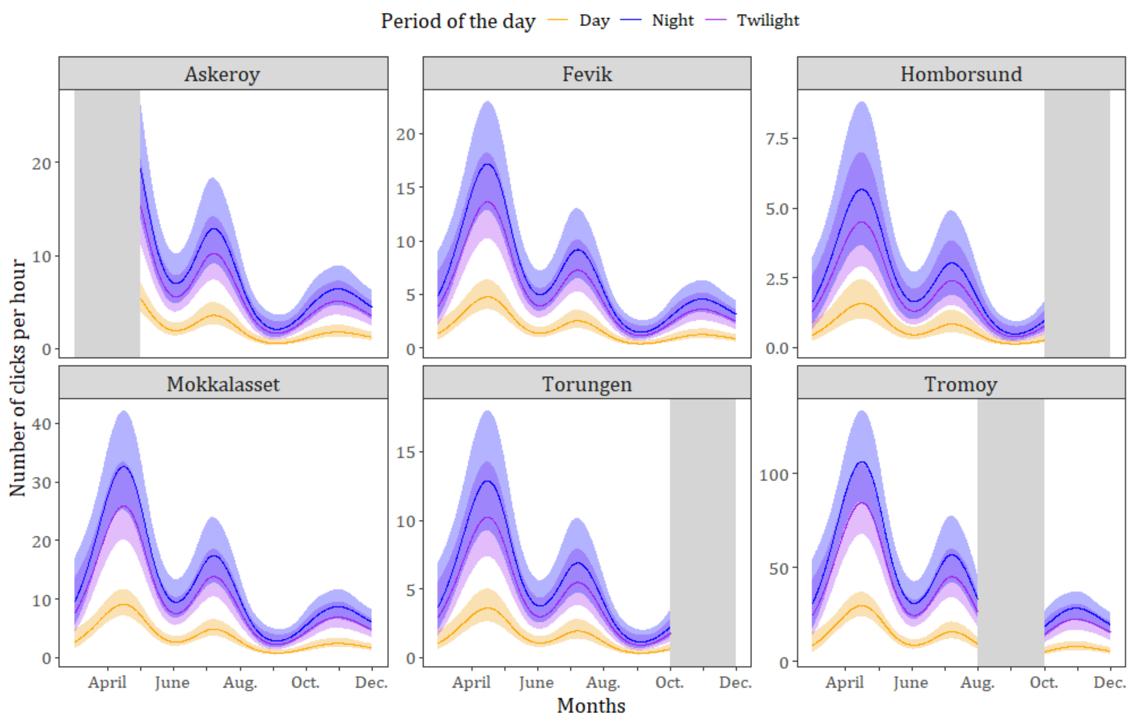

Figure 11. The mean number of clicks per hour during the day, twilight and night at each station, as a function of months. Predicted from the count GAM. Yellow = Day; Purple = Twilight; Blue = Night. Coloured shades represent the standard error of the lines of the same colour. Grey areas indicate periods of no data. For this plot, SC values were kept constant at SC0 = 0.3 m/s and SC35 = 0.2 m/s. Notice that each plot has its own y-axis scale.

The count model showed that vocal activity was significantly affected by surface and bottom currents (Table 2), with a general increased activity when surface currents were around either 0 m/s and 1 m/s (Figure 12). The lowest click number values were observed for SC0 speed of around 0.5 m/s and 1.5 m/s (Figure 12). An increase on SE was observed for SC0 values over 1.2 m/s. After 1.2 m/s a continuous increase on SE was also measured (Figure 12), due to a decrease on number of samples. During the day, significantly less clicks were counted compared to the number of clicks per hour during the twilight or during the night (Table 2). The latter two periods showed a slight difference on the click number between them. Night showed the highest variation on click number, and day showed the lowest (Figure 12).

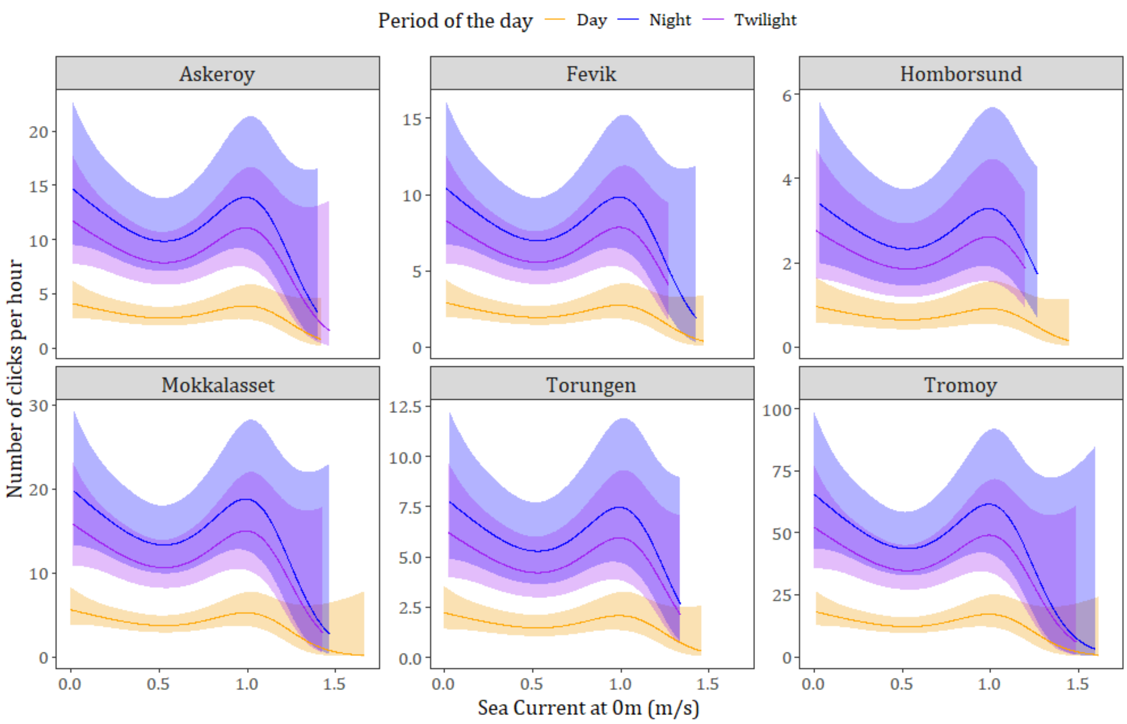

Figure 12. The mean number of clicks per hour during the day, twilight and night at each station, as a function of sea current speed at 0 m depth. Predicted from the count GAM. Yellow = Day; Purple = Twilight; Blue = Night. Coloured shades represent the standard error of the lines of the same colour. For this plot, the month variable was kept constant at the month of July, and a value of SC35 = 0.2 m/s was used. Notice that each plot has its own y-axis scale.

Finally, the model showed a peak in the mean number of clicks per hour when bottom currents were around 0.8 m/s, while the lowest prediction was estimated for when SC35 showed values around 0 m/s and around 0.5 m/s (Figure 13). Highest peak was observed in Trømoy during the night with around 100 clicks per hour when SC35 = 0.8 m/s, whereas Homborsund showed the lowest value (0.5 clicks per hour) when SC35 = 0.5 m/s (Figure 13). An increase on SE was observed for higher SC35 values due to a decrease on number of samples (Figure 13). Overall, night showed the highest variation on clicks while day showed the lowest.

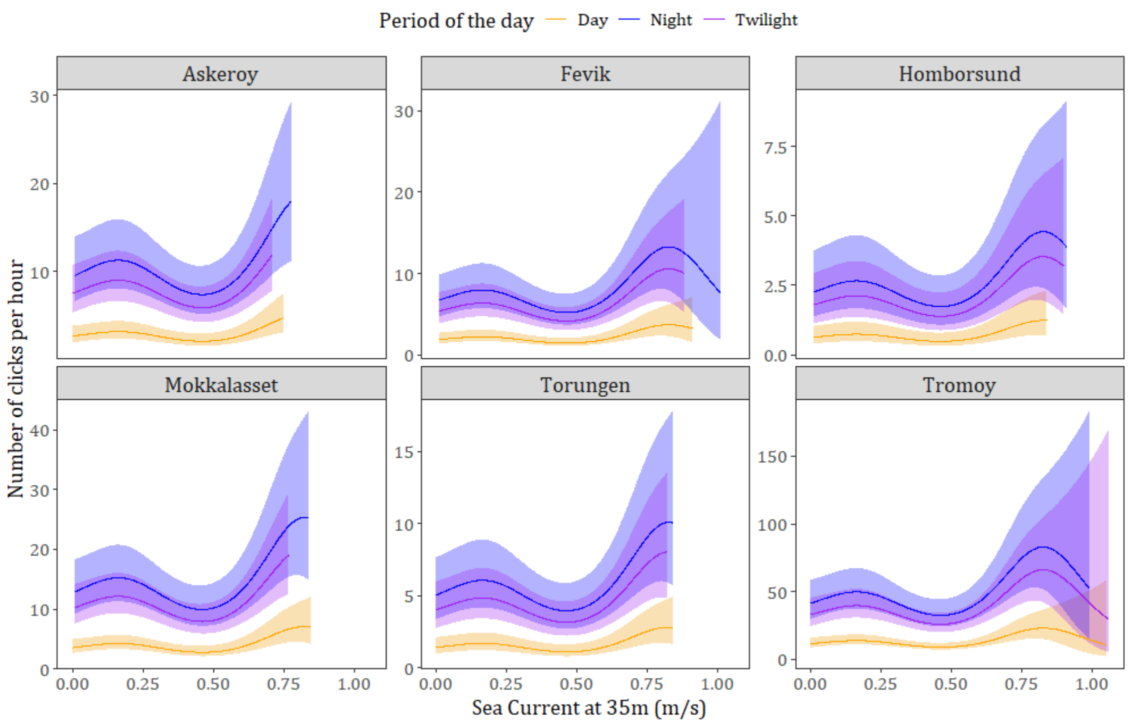

Figure 13. The mean number of clicks per hour at each station, as a function of sea current speed at 35 m depth. Predicted from the count GAM. Yellow = Day; Purple = Twilight; Blue = Night. Coloured shades represent the standard error of the lines of the same colour. For this plot, the month variable was kept constant at the month of July, and a value of SC0 = 0.3 m/s was used. Notice that each plot has its own y-axis scale.

DISCUSSION

The objectives of this study were to investigate the cetacean occurrence in the Skagerrak, as well as to examine how the presence and vocal activity of the harbour porpoises along the coast changed during the day, seasonally, spatially and with oceanographic conditions. Harbour porpoises, northern bottlenose whales, minke whales and bottlenose dolphins were detected during ship surveys. Porpoises showed temporal presence and vocal activity variations with the most prominent peaks during spring. Sea currents did not have any effect on porpoise presence, but indications of higher vocal activity were found for stronger currents.

SHIP SURVEYS

The towed hydrophone array was able to detect and locate odontocetes. It was also able to record odontocete clicks during rough weather and sea conditions too (Beaufort > 3), when it was not possible to see them. Most harbour porpoises were detected in shallower areas while every northern bottlenose whale detection was made at deeper areas. This coincides with the species' ecology, as northern bottlenose whales are known for performing long and deep dives, and harbour porpoises tend to habit shallower waters for the most part of the year (MacLeod et al., 2006; Booth et al., 2013).

Overall, 25 events with between 29 and 32 individuals were counted with the combination of acoustic and visual methods. The hydrophone array detected most events (n = 17), and three of them showed click trains that could correspond to two individuals, even though this was not possible to confirm. The fact that the hydrophone array was able to detect odontocetes at almost every month highlighted one of the advantages of PAM, which is the capacity to correctly function even when conditions are adverse. Acoustic detections were made even when Beaufort scale values were above three, while sightings only happened when Beaufort scale values were either zero or one. PAM also proved to be useful to detect normally elusive species such as the northern beaked whale. Beaked whales in general are known for taking long and deep dives (MacLeod et al., 2006), which makes them hard to detect. This coincides with what was observed in this study, where every northern bottlenose whale detection happened at areas that were more than 400 m deep. A hint of a pattern was also seen for harbour porpoises. Most porpoise detections happened at areas shallower than 300 m, which is in agreement with previous studies and with what we know about the species' ecology (Booth et al., 2013). However, the low number of data points makes impossible to conclude anything.

Due to the lack of detected individuals, it was not possible to establish any pattern on cetacean occurrence temporal variation. The towed hydrophone array detected much less porpoise detections (17 events) than CPODs (228 046 clicks). Every month had between one and four detections except September, which had none, and July which had 12. All detections in July were visual detections, and due to the hydrophone malfunctioning, none of those sightings were acoustically detected. Besides the lower number of hydrophone array recorded hours, it is believed that other factors may be behind the difference between the number of events and CPOD detections. For example, a recent study showed that porpoises seem to flee from approaching vessels, which could have affected towed hydrophone detections (Hao et al., 2024). The hydrophone array malfunctioning in July, or not being able to deploy the device close to the shore in Denmark may have had an impact too. Two possible explanations to the difference between months would be the number of observers and the weather. July and September were the only months with an additional observer, and the second transect in July had the lowest Beaufort values (0 or 1) out of all transects.

MOORED CPODS

Diel, seasonal and spatial variations were observed on harbour porpoise occurrence and vocal activity. They were both higher during the night and twilight than during the day. Diel migration of porpoise prey may be behind this pattern. Harbour porpoises generally feed on fish like Atlantic herring (*Cuplea harengus*) or European sprat (*Sprattus sprattus*) (Börjesson et al., 2003b; IMR & NAMMCO, 2018). Fish-prey (i.e. copepods, ichtyoplankton…) and thus, their common fish predators, like Atlantic herring and European sprat, feed close to the surface during the night and consequently, porpoises are attracted to the area to hunt (Donner & Lindström, 1980; Kotta & Kotta, 2001; Barz & Hirche, 2009; Hayden & Miner, 2009; Ogonowski et al., 2013; Schaffeld et al., 2016; Zein et al., 2019). During the day, some studies have reported that porpoises feed on benthic fish, at shallower sandy areas (Schaffeld et al., 2016; Williamson et al., 2017). Porpoises were more present during spring, and their vocal activity was also higher during that period of time. This coincides with the observations from other studies, such as Schaffeld et al. (2016) and Dracott et al. (2022). The spawning of harbour porpoise prey like Atlantic herring and European sprat and the porpoise parturition and mating seasons are believed to be the reason behind these peaks (Iles & Sinclair, 1982; Alheit, 1988; Sørensen & Kinze, 1994; Börjesson et al., 2003a; Börjesson et al., 2003b; Lockyer & Kinze, 2003; Eggers et al., 2014; Vitale et al., 2016; IMR & NAMMCO, 2018; Berg et al., 2022). It was also observed that porpoises seem to be more active when currents are stronger, probably due to prey aggregations that occur at these conditions as other studies pointed out (Johnson et al., 2005; Pierpoint, 2008; Gilles et al., 2011). However, I suspect that the design of this study and the low number of data points with high-speed currents are not adequate to establish this connection.

More porpoise clicks were detected in the north of the study area, especially in Trømoy and Møkkalasset. Homborsund, the southernmost station, registered the lowest number of total porpoise-clicks. This pattern was also portrayed by the presence and vocal activity models. Trømoy and Møkkalasset are located at the centre of Raet National Park, while Homborsund is the station furthest away from Raet. However, the proximity to the national park may not be the cause of the difference between stations, since neither the national park status nor the marine protected area status guarantees protection against fishing in Norway, and gillnet bycatch is one of the major hazards for harbour porpoises (Bjørge et al., 2013; Kindt-Larsen et al., 2023). In fact, fishing techniques such as trawling are allowed in the waters of Raet National Park (Eigaard et al., 2017).

Along the coast of the Norwegian Skagerrak a higher porpoise presence and vocal activity was detected during twilight and night than during the day. Previous studies using porpoise detectors have also reported this same behaviour in the German western Baltic Sea, German Wadden Sea (North Sea), Dogger Bank (North Sea), western Scotland and north-western British Columbia in Canada among others (Carlström, 2005; Todd et al., 2009; Schaffeld et al., 2016; Zein et al., 2019; Dracott et al., 2022). It is believed that this diel variation is a consequence of prey behaviour, like other studies have reported (Schaffeld et al., 2016; Zein et al., 2019; Dracott et al., 2022). Harbour porpoises are known to mainly prey on pelagic fishes like Atlantic herring and sprat (*Sprattus sprattus*) (Börjesson et al., 2003b; IMR & NAMMCO, 2018). However, porpoises that habit in the North Sea, Skagerrak and Kattegat prey on demersal and benthic fishes too, like saithe (*Pollachius virens*), Atlantic cod (*Gadus morhua*), gobies (family Gobiidae) or sand eels (family Ammodytidae), since the topography of those seas allow them to access benthic areas more easily (Fontaine et al., 2007). Fish prey like copepods, mysids and ichtyoplankton perform diel vertical migrations, moving to the surface at dusk and to the bottom at dawn in order to feed while avoiding predation (Donner & Lindström, 1980; Kotta & Kotta, 2001; Barz & Hirche, 2009; Hayden & Miner, 2009; Ogonowski et al., 2013). Pelagic predators like Atlantic herring and European sprat take advantage of these vertical migrations, and gather near the surface to feed during the night (Nilsson et al., 2003; Anderson et al., 2007; Espeland et al., 2010). Benthic fish like sand eels and goby, especially during autumn and part of winter in deep areas, are also known for preying in the water column during the night and hiding in the bottom during the day (Grabowska & Grabowski, 2005; Ehrenberg & Edjung, 2008). Furthermore, Cardinale et al. (2003) and Didrikas & Hansson (2009) reported that herring swim at a slower pace and tend to aggregate less in schools during the night than during the day, making them easier to catch. All these factors make hunting during the night easier for harbour porpoises. They probably focus on preying on pelagic fish during the night, close to the surface and at deep areas, which explains the higher porpoise presence and vocal activity detected in the study area at dark hours. This conclusion was reached and supported by several studies (Schaffeld et al., 2016; Zein et al., 2019; Dracott et al., 2022). The lower presence and vocal activity of harbour porpoises detected during the day is probably due to several reasons. First of all, as studies on inter click interval have reported, the porpoise foraging behaviour itself decreases during the day (Carlström, 2005; Ruffert et al., 2020). Secondly, as other studies performed in the Baltic Sea and northeastern Scotland observed, harbour porpoises may move to shallower areas during the day to prey on benthic fish (Schaffeld et al., 2016; Williamson et al., 2017). Lastly, harbour porpoises are known for using a foraging technique called bottom-grubbing to detect benthic prey hidden in the bottom (Lockyer, 2000). Bottom-grubbing consists on positioning vertically in the water column, and echolocating facing the bottom (Lockyer, 2000). Due to CPODs having the hydrophone pointed upwards, if they are deployed close to the surface and at a considerable distance from the bottom like in this study (10 m from the surface, 40 m from the bottom), detecting echolocation clicks produced when bottom-grubbing becomes challenging (Koschinski et al., 2008). These clicks can be recorded if CPODs are deployed close to the bottom. Summing up, the decrease on presence and vocal activity during the day is probably due to a decrease in foraging behaviour, movement to shallower areas, and CPODs struggling to detect certain clicks.

However, opposing this, some studies reported that prey availability may not be the reason behind the diel variations on vocal activity. Osiecka et al. (2020) observed this same variation in captive porpoises that were fed 3-5 times during the day. They argue that this proves that higher vocal activity during the night is not due to foraging behaviour. They suggest porpoises may have an unknown intrinsic circadian rhythm which makes them click more during the night. They, as well as Zein et al. (2019), also propose that porpoises may echolocate more during the night to compensate for the poor visibility due to lack of light. However, Kastelein et al. (2002) and Verfuß et al. (2005) demonstrated that porpoise vocal activity is the same in light and in darkness. While it could be true that an unknown circadian rhythm may have a more prominent effect on porpoise acoustic activity than prey presence, the fact that the presence of porpoises is higher at twilight and night shows that prey availability plays an important part in their behaviour. There is a possibility that a circadian rhythm makes porpoises click more during the night, which has turned out beneficial for navigation and hunting. However, it is worth noting that currently no evidence of mentioned circadian rhythm has been reported. Also, as Osiecka et al. (2020) stated in their article, comparisons between captive and wild individuals need to be done with caution. Nevertheless, it is clear that more research should be done to shed some light on this matter too.

The binomial and count GAMs reflected higher harbour porpoise presence and acoustic activity between April and June. After this, a prominent decrease on clicks and presence was observed at the end of July. While the increases and decreases in acoustic activity could be partially explained by the fluctuation in porpoise presence, it is believed that other factors have had an effect on these variations. Some studies reported that harbour porpoise ovulation and conception occur around the end of July and beginning of August in the North Sea, Skagerrak Sea and Kattegat Sea (Sørensen & Kinze, 1994; Börjesson et al., 2003a; Lockyer & Kinze, 2003). Since gestation approximately takes 10.5 months, parturition occurs generally in June (Sørensen & Kinze, 1994; Lockyer & Kinze, 2003), which is one of the most energy demanding periods in a female mammal's life (Sadleir, 1984). For example, according to Kastelein et al. (2002), captive dolphin females increase their daily intake by between 30% and 100% in this period. Therefore, in order to face this increase of energy demand, prey availability becomes a key factor that conditions porpoise presence and vocal activity (Sørensen & Kinze, 1994; Börjesson et al., 2003a; Lockyer & Kinze, 2003). The peaks in acoustic activity and presence detected in April and May match with the spawning peaks of herring and sprat (Iles & Sinclair, 1982; Alheit, 1988; Eggers et al., 2014; Vitale et al., 2016; Berg et al., 2022). The peak in herring spawning seems to happen between March and April in the western Baltic Sea (Berg et al., 2022), and while no herring spawning has been detected in the Skagerrak yet, Berg et al. (2022) reported an increase on herring abundance in the Skagerrak around the same period of time. This abundance increase seems to be dependent on the herring spawning in the western Baltic Sea (Berg et al., 2022). Sprat, on the other hand, has been reported to spawn between February and July, with peaks between May and July (Iles & Sinclair, 1982; Alheit, 1988; Eggers et al., 2014; Vitale et al., 2016; Berg et al., 2022). Sprat spawning does not seem to be dependent on other sprat populations in the area (Berg et al., 2022). Overall, this period of the year seems to be important for female porpoises to gain weight in order to face parturition and lactation later during the summer (Sørensen & Kinze, 1994; Börjesson et al., 2003a; Lockyer & Kinze, 2003). Another smaller vocal activity peak was observed in July, but no such peak was observed for presence. An explanation for this could be that female porpoises move to a different area to give birth after they feed on herring and sprat during the spring. This makes both presence and acoustic activity decrease during June. However, as other studies have reported, remaining female porpoises (those that have not given birth) and male porpoises may click more in July in order to find a mate (Sørensen & Kinze, 1994; Börjesson et al., 2003a; Lockyer & Kinze, 2003). After conception, porpoises may leave to a different area, and return to the study area in autumn and winter. This would mean that the Skagerrak region is an important feeding ground for porpoises during the first quarter of the year. They even may use this area to breed. Of course, only one year of data is not enough to establish if these patterns are recurrent for this porpoise population, and consequently, if the conclusions drawn are a possibility. Therefore, more research should be done in order to shed some light on the matter. Especially, after seeing that herring may be an important part in the harbour porpoise's life cycle, and that Skagerrak herring populations seem to be declining (ICES, 2023).

Finally, a relation between porpoise vocal activity and sea current speed was predicted by the models. Before anything, I should highlight that sea currents explained a small part of the variation. While the presence of the porpoises seemed unaltered by the strength of the currents, porpoises showed a higher vocal activity when surface currents approached speed around 1 m/s, and when deeper current speeds were around 0.8 m/s. Possibly, the reason why the models of this study predicted a porpoise vocal activity decrease for SC0 values higher than 1 m/s or for SC35 values higher than 0.8m/s, is because not many data points were collected when the sea currents were above those values, as the SE values show. Some studies have observed that harbour porpoises seem to prefer areas with strong currents, probably because prey often aggregates or gets aggregated there (Johnson et al., 2005; Pierpoint, 2008; Gilles et al., 2011). For example, Gilles et al. (2011) reported that they observed porpoises gather along steep gradients of chlorophyl concentration. These gradients are known for attracting predators like fish, which are then hunted by higher level predators such as harbour porpoises (Ballance et al., 2006). Maybe strong sea currents in the study area do not increase the presence of porpoises, as they are always around. However, strong currents may make porpoises more active since more prey has aggregated. While a possible explanation, it is believed that this study is not adequate enough to draw any conclusions on this topic and support this hypothesis. First of all, there is a lack of data for high current speeds. Second, the selected sampling stations are placed to a considerable distance from shore. This makes harder for the mentioned aggregations to happen, as there is nothing that would keep primary producers like phytoplankton still. This may happen inside the fjords or between the several islands that can be found along the Norwegian Skagerrak coast; however, the design of this study is not able to answer that.

CONCLUSION

In conclusion, this study has analysed the cetacean occurrence and its temporal variation throughout the year in the Skagerrak Sea, based on Passive Acoustic Monitoring (PAM). A study on harbour porpoise presence and click activity variation was also performed using CPODs. Harbour porpoises, northern bottlenose whales, a minke whale and a bottlenose dolphin were detected in the occurrence study, and while it was not possible to establish a temporal variation, it was possible to tie the location of some detections to the ecology and behaviour of the species. It is believed that more transects should be done, and it would be ideal if the number of monthly transects were to increase too. The harbour porpoise presence and vocal activity study revealed diel and seasonal variations for both variables. Overall, prey availability is suspected to be one of the main forces driving these variations, as well as breeding and parturition seasons. Overall, the Norwegian Skagerrak coast seems to be an important feeding ground for harbour porpoises. While some light was shed on porpoise population dynamics, it is believed more studies and monitoring should be done to get more robust conclusions. Possible main unknowns perceived in this study should also be addressed. For example, where do harbour porpoises move to during the day, whether harbour porpoises remain in the Skagerrak to give birth, the location where porpoises go after giving birth, or the dependency of porpoise populations on the decreasing herring populations. To answer some of these questions, and as a continuation to this study, CPODs could be distributed differently. Each device could be placed to a different distance from the coast to be able to track their movements, and some devices could be stationed at different depths to see if porpoise vocal activity varies inside the water column throughout the day or seasonally. Inter click interval could also be analysed for a more detailed study of click patterns. It is believed that these unknown factors are crucial for a proper harbour porpoise management program in the Skagerrak Sea.

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APPENDIX

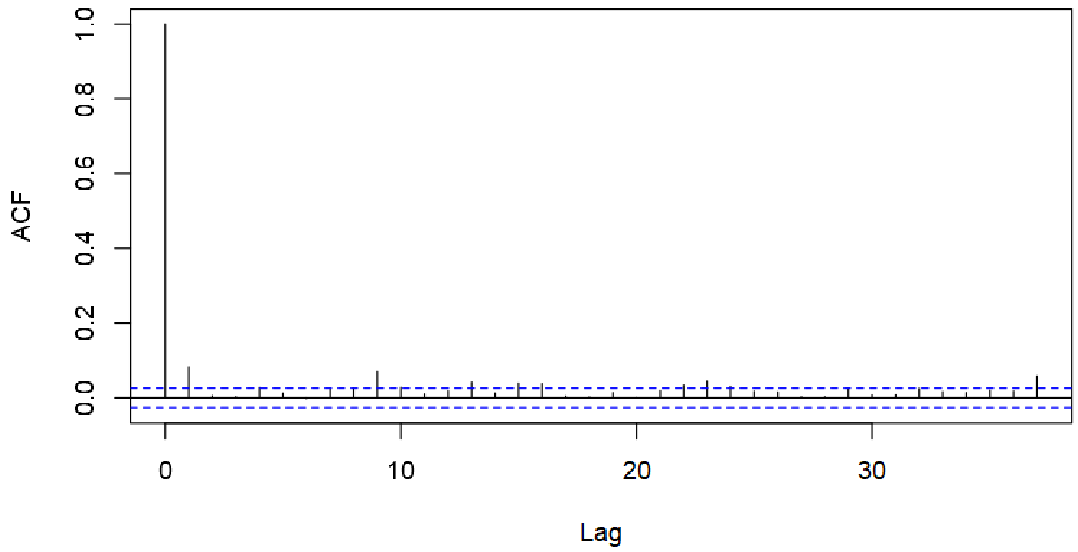

Figure S1. Autocorrelation Function Plot of the number of porpoise clicks detected per hour. Each lag corresponds to one hour. Blue dashed lines indicate the threshold levels of autocorrelation. This ACF Plot represents the data collected in Askerøy.

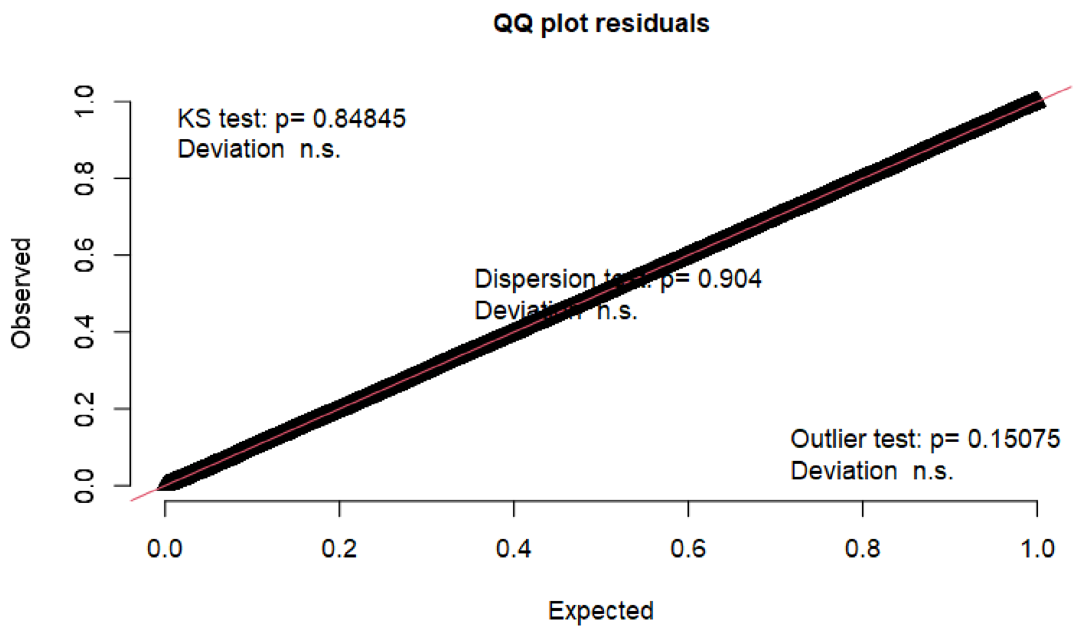

Figure S2. QQ plot between the observed and expected residuals of the binomial GAM. Red line indicates the correlation line if observed residuals = expected residuals. Black points indicate residuals of the model.

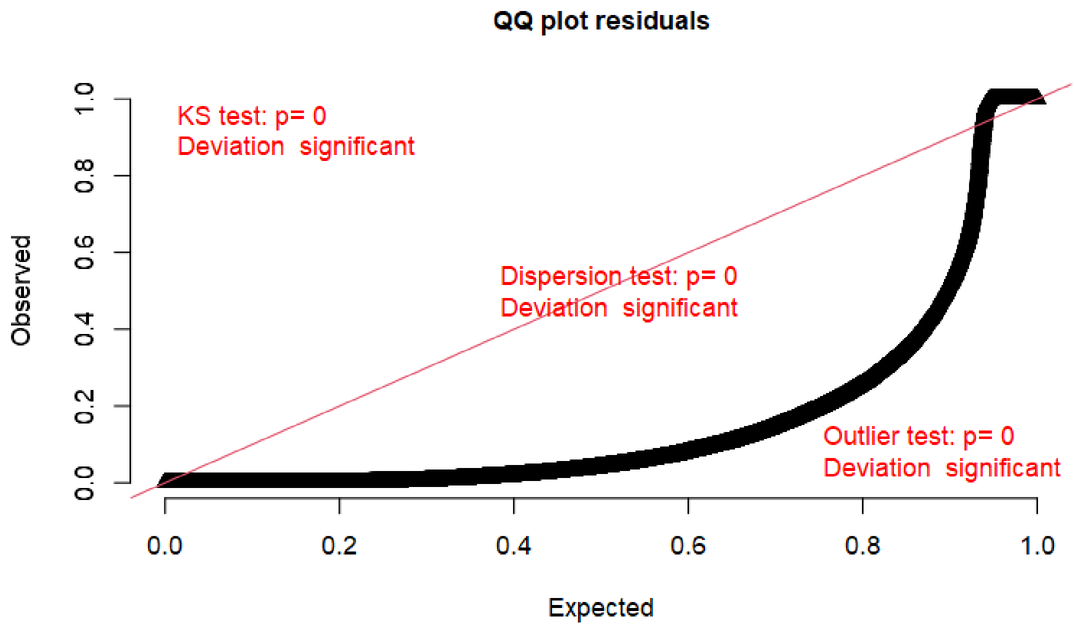

Figure S3. QQ plot between the observed and expected residuals of the count GAM. Red line indicates the correlation line if observed residuals = expected residuals. Black points indicate residuals of the model.

Table S1. AIC values of the binomial model variations and count model variations. The models marked in grey are the best fitted models.

Outcome var.	Response var.	df	AIC
Presence	*Month + SC0 + SC35 + Site + Period of the day*	19.14710	18091.47
	Month + SC35 + Site + Period of the day	18.15890	18090.10
	Month + Site + Period of the day	16.30839	18093.59
Number of clicks per hour	*Month + SC0 + SC35 + Site + Period of the day*	24.91816	1074872
	Month + SC35 + Site + Period of the day	20.89314	1077498
	Month + Site + Period of the day	16.92349	1081519

Table S2. Acoustic detections and sightings from the ship transects conducted between Norway and Denmark from April 2023 to February 2024. Number of observers refers to the number of observers in visual effort. The term inside parenthesis next to the species name indicates the confidence on the detection: Low = Low, Pos. = Possible, Def. = Definitive.

Detection time (UTC)	**Species (*Confidence*)**	**Number of individuals**	**Latitude**	**Longitude**	**Depth (m)**	**Method**	**Sea State**	**Number of observers**
2023-04-29 06:05	Harbour Porpoise (*Def.*)	1	58.26301	8.975422	398.91	PAM	-	0
2023-04-29 07:11	Harbour Porpoise (*Def.*)	1	58.13592	9.143514	641.64	PAM	-	0
2023-07-09 06:50	Harbour Porpoise (*Def.*)	1	57.71341	9.87826	72.63	Visual	0	2
2023-07-09 06:59	Minke Whale (*Def.*)	1	57.73816	9.85983	52.94	Visual	0	2
2023-07-09 08:50	Harbour Porpoise (*Def.*)	2	57.94651	9.69968	126.25	Visual	1	2
2023-07-09 09:14	Harbour Porpoise (*Def.*)	2	57.99943	9.6821	159.34	Visual	0	2
2023-07-09 09:25	Harbour Porpoise (*Def.*)	2	58.027	9.66921	201.56	Visual	0	2
2023-07-09 13:32	Harbour Porpoise (*Def.*)	1	58.57108	9.30848	274.90	Visual	0	2
2023-07-09 13:35	Harbour Porpoise (*Def.*)	2	58.57136	9.30885	274.90	Visual	0	2
2023-10-10 07:57	Harbour Porpoise (*Def.*)	1 - 2	57.82628	9.658410	35.12	PAM	5	1
2023-10-10 09:36	Northern Bottlenose Whale (*Pos.*)	1	58.03420	9.412172	481.85	PAM	3	1
2023-10-10 11:17	Northern Bottlenose Whale (*Pos.*)	1	58.22689	9.115647	457.71	PAM	1	1

Detection time (UTC)	**Species (*Confidence*)**	**Number of individuals**	**Latitude**	**Longitude**	**Depth (m)**	**Method**	**Sea State**	**Number of observers**
2023-10-10 11:18	Northern Bottlenose Whale (*Pos.*)	1	58.229653	9.110376	457.71	PAM	1	1
2023-10-10 11:29	Northern Bottlenose Whale (*Pos.*)	1	58.24601	9.065168	425.27	PAM	1	1
2023-11-10 09:05	Harbour Porpoise (*Def.*)	1	57.84425	9.828597	47.03	PAM	1	1
2023-11-10 13:06	Harbour Porpoise (*Def.*)	1 - 2	58.38300	9.464907	553.84	PAM	3	1
2023-11-10 13:18	Harbour Porpoise (*Def.*)	1	58.40965	9.458406	521.18	PAM	3	1
2023-11-10 14:17	Harbour Porpoise (*Def.*)	1	58.53072	9.36	459.47	PAM	3	1
2023-12-04 08:25	Bottlenose Dolphin (*Def.*)	1	57.6064	9.954066	11.73	Visual	1	1
2023-12-04 10:42	Harbour Porpoise (*Def.*)	1	57.91013	9.764763	77.55	PAM	2	1
2023-12-04 11:12	Harbour Porpoise (*Def.*)	1	57.98756	9.720569	138.15	PAM	2	1
2023-12-04 14:19	Northern Bottlenose Whale (*Low*)	1	58.414261	9.414104	479.47	PAM	5	1
2024-02-05 07:53	Harbour Porpoise (*Def.*)	1	58.33768	8.873069	238.89	PAM	4	1
2024-02-05 10:30	Harbour Porpoise (*Def.*)	1	58.02152	9.320766	451.80	PAM	4	1
2024-02-05 12:12	Harbour Porpoise (*Def.*)	1 - 2	57.82652	9.657968	35.12	PAM	4	1