ARTICLE
NAMMCO Scientific Publications

ASSESSING SHIPPING NOISE AS A POTENTIAL DRIVER OF HARBOUR SEAL (*PHOCA VITULINA*) HABITAT SELECTION

Skye Wynn-Simmonds[1,2], Gaëtan Richard[2] & Cecile Vincent[1]

[1] PELAGIS (UAR 3462) CNRS - La Rochelle Université, 5 allée de l'Océan, 17000 La Rochelle, France. Corresponding author: skye.wynn-simmonds100@orange.fr
[2] Société d'Observation Multi-Modale de l'Environnement, 300 Rue Pierre Rivoalon, 29200 Brest, France

ABSTRACT

Over the past decade, anthropogenic noise from activities such as shipping has significantly increased in the ocean, raising questions on their potential impact on coastal species such as harbour seals. In this study, we assessed the spatial overlap between ships (equipped with AIS transmitters) and harbour seals (tracked using telemetry) in the English Channel, one of the densest shipping areas in the world. We then studied how their habitat selection varied according to environmental parameters taking into account shipping noise as a potential driver. A total of 28 harbour seals were captured and equipped with GPS-GSM tags. AIS data (ships > 15 m length) was used to estimate shipping traffic density and model the associated shipping noise. We then used generalised additive mixed models to assess harbour seals' habitat selection using distance to haulout, distance to shore, bathymetry, tidal current, sediment type, and shipping noise as explanatory variables. The model selected had an explained deviance of 71.8%. Our findings indicate that distance to haulout sites was the primary driver of habitat selection (~91.5% deviance), while other environmental factors such as bathymetry (~4.4%), distance to shore (~3.1%), tidal current (~0.3%), sediment type (~0.6%), and shipping noise (~0.1%) had only minor influences on their selection. Despite a high spatial overlap between shipping activity and tracked seals (73% of overlap), the weak contribution of shipping noise suggests that either seals may be habituated to chronic noise exposure or that noise levels rarely exceed tolerance threshold levels. To the best of our knowledge, this is the first article integrating shipping noise into harbour seals' habitat selection models. These findings provide an understanding of harbour seal habitat selection in anthropogenic environments.

Keywords: anthropogenic impact, marine mammals, noise pollution, shipping noise, Phoca vitulina, co-occurrence, habitat selection, spatial modelling, acoustic modelling

INTRODUCTION

Assessing the impact of human activities on marine ecosystems is one of the main challenges in conservation and management of marine biodiversity. Over the past decade, anthropogenic activities in the ocean have increased (Frisk, 2012; Simmonds et al., 2014). This intensification raises questions about their cumulative effects on marine ecosystems. However, evaluating these impacts is very challenging because of the variety of stressors involved (Boehlert & Gill, 2010; Simmonds, 2018). Among these stressors, anthropogenic noise has recently been considered a threat to marine ecosystems and is often referred to as noise pollution, impacting many species (Erbe et al., 2018; Gomez et al., 2016; Simmonds, 2018). Anthropogenic noise alters the marine soundscape by contributing to the increase of ambient noise levels (Duarte et al., 2021). Shipping activity has become the primary contributor to rising ambient noise levels in the ocean (Erbe, McCauley & Gavrilov, 2016; Erbe et al., 2019; Frisk, 2012; Hildebrand, 2009). Indeed, 90% of global trade is transported by ships. In European waters, shipping has increased 33.6% between 2013 and 2017 and now this area stands out as one of the densest shipping areas in the world (Robbins et al., 2022; Wang et al., 2023).

Shipping activities are often concentrated in coastal waters, resulting in high-density traffic and increased noise levels in these areas. However, coastal waters represent important habitats for a wide range of marine species, including a great number of marine mammals (Avila et al., 2018; Learmonth et al., 2006). Many species use these areas as breeding and/or foraging grounds. Certain marine mammals may be particularly sensitive to the frequency bands dominated by shipping noise, such as pinnipeds, who have their main hearing frequency between 75 Hz and 75 kHz (Nowacek et al., 2007; Southall et al., 2007). Indeed, shipping noise generally consists of continuous noise over frequency bands ranging from 1 Hz to 100 kHz, with highest intensity levels between 10 Hz and 1 kHz (Bretschneider et al., 2014; Erbe et al., 2019). Hence, the combination of spatial and frequency overlap may lead to impacts on their communication (Erbe et al., 2018; Gabriele et al., 2018), behaviour (Blair et al., 2016; Mikkelsen et al., 2019; Prawirasasra et al., 2022), or even physiology (Lemos et al., 2022; Rolland et al., 2012).

Harbour seals (*Phoca vitulina*) are a coastal species and therefore may be particularly vulnerable to shipping activities in coastal waters. As central-place foragers, their behaviour is influenced by the need to return regularly to their haulout sites (Orians & Pearson, 1979). This constraint makes them more likely to encounter human activities and thus makes them more susceptible to elevated noise levels. Harbour seals are protected in France, and as top predators they contribute to the

Wynn-Simmonds, S., Richard, G. & Vincent, C. (2025). Assessing shipping noise as a potential driver of harbour seal (*Phoca vitulina*) habitat selection. *NAMMCO Scientific Publications 14*. https://doi.org/ 10.7557/3.8031

good health of marine ecosystems (Blanchet et al., 2021). Various studies have shown that shipping noise may have significant ecological effects on the behaviour of phocids (Mikkelsen et al., 2019; Prawirasasra et al., 2022; Trigg et al., 2020). Mikkelsen et al. (2019) have found that harbour seals can modify their foraging or resting patterns when impacted by shipping noise. Changes in behaviour can impact the energetic budget, health, and, therefore, fitness of a species (Erbe et al., 2018). Hence, with the increase of shipping activities, larger-scale studies are needed to understand how shipping noise affects harbour seal behaviour and to evaluate the potential consequences for their energy budgets and overall fitness.

In this paper, we assessed the spatial overlap between ships equipped with Automatic Identification System (AIS) transmitters and harbour seal density using telemetry tracking. We then evaluated harbour seals' habitat selection taking into account the potential effect of shipping noise. These results provide an understanding of the habitat selection of harbour seals in an environment impacted by anthropogenic activities, the English Channel. The English Channel is characterised by high vessel density (Robbins et al., 2022), resulting in chronic shipping noise. Offshore wind farm construction projects are currently underway in this region, and the noise generated during their construction and their operation will add to the existing anthropogenic noise, with potential cumulative impacts on species that live here. This study will therefore serve as a baseline for any studies looking at cumulative impacts of shipping noise and additional noise generated during the construction of wind farms.

MATERIALS AND METHODS

Study area

The study was carried out in the Baie des Veys, in the English Channel. The Baie des Veys, located in Normandy, France, is characterised by shallow waters (Figure 1). It covers an intertidal area of 37 square kilometres (Sylvand, 1995). This estuary is a hotspot for many species, attracting predators such harbour seals. In fact, the Baie des Veys holds the second largest harbour seal colony of mainland France (maximum haulout number of 254 individuals in 2023), with a yearly increase in abundance of ~11.0% per year (Poncet et al., 2024).

Seal capture and tagging

A total of 28 harbour seals (all males) were captured in the Baie des Veys in two deployment periods between October 2020 and January 2024 (Supplementary file 1). They were caught at their haulout site using hoop nets, weighed, and then anaesthetised with Zoletil (© Virbac, France). They were then fitted with GPS/GSM tags (Sea Mammal Research Unit, University of St Andrews, UK). Tags were glued to the fur, at the back of the neck, using quick setting epoxy glue. Four seals were captured twice during the study period. Seal V31 was captured and fitted with a tag a second time (V37) in the same deployment period (2023–2024). Data from both deployments were therefore merged. The other three seals were captured for the first time in 2020–2021 (V16; V17; V22) and recaptured in 2023–2024. We only used data from their first tagging in our analysis.

Telemetry data

The GPS/GSM tags included a GPS combined with a GSM modem to transmit the data. GPS coordinates were recorded every 10 minutes when the seal was at the surface, though this interval was extended when the individuals were underwater. Additionally, the tags had a wet/dry sensor indicating whether the individuals were at sea or resting on land. A haulout was defined as any period where the tag remained dry for more than 10 minutes, while an 'at sea' state was recorded when the tag was wet for a minimum of 40 seconds. They also had a pressure sensor that measures dive depth. In this study, a dive was defined when the seal went below 3 m in depth with a duration lasting more than 30 s. The dive locations were estimated by linearly interpolating positions from GPS data in order to have a GPS location for every dive recorded. If more than 20 min elapsed between consecutive GPS positions, we filtered out any dive data within that period. This 20 min threshold was determined through an analysis of the raw GPS data, showing that the highest frequency of delays in both deployment periods occurred within the first 20 minutes (Supplementary file 2). This method was necessary to ensure accuracy when modelling noise received by the seal. Indeed, underwater noise

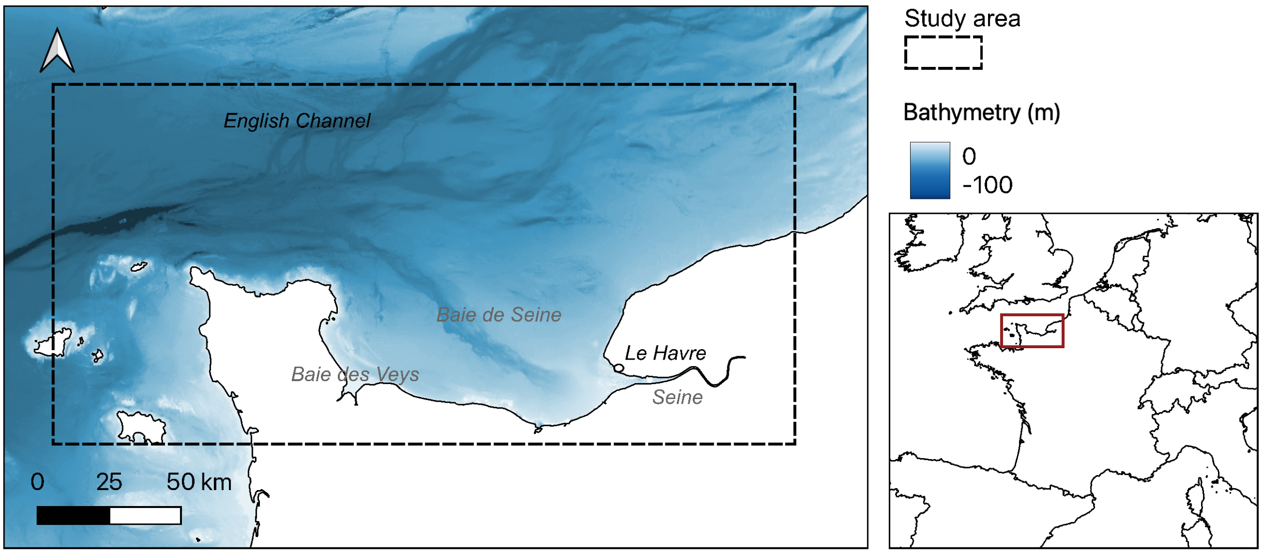

Figure 1: Map of the study area around the Baie des Veys and the bathymetry (m) of the continental shelf. The main bays are labelled in grey. The study area is indicated by the black dashed line.

modelling is sensitive to location precision, so even slight changes in a seal's estimated position can lead to significant differences in the modelled received levels. By limiting the interpolation window to 20 minutes, we minimise the accumulation of error in our estimated dive locations. After applying this filter, approximately 40% of the dive data was retained. Furthermore, all dives that extended within 20 km of the study area boundary or outside the study area are excluded from the analysis, to avoid potential underestimation of shipping noise.

AIS data

We used AIS (Automatic Identification System) data to identify the position of ships during the tracking period of the seals. AIS transmitters are mandatory for ships of over 300 gross tonnage engaged in international voyages, cargo ships of over 500 gross tonnage not engaged in international voyages, fishing vessels over 15 m long, and all passenger ships. While some vessels under 15 m voluntarily have AIS transmitters, we cannot assess how representative the available data are for this group. For this study, AIS data came from Orbcomm Premium and was purchased from CLS (https://www.cls.fr) for the periods of October 2020 to July 2021 and November 2023 to June 2024. The data contained information such as date and time, GPS coordinates, vessel characteristics, and speed. To ensure data accuracy, the dataset was filtered and speed values were corrected using the *AISanalyze* package in R (https://github.com/remip48/AISanalyze). Ships that were stationary (speed = 0 knots) were filtered out.

Spatio-temporal overlap

The first part of the study aimed to identify spatio-temporal overlap between harbour seals and ship traffic in order to estimate the risk of encounter. To achieve this, we used two datasets: seal dive locations and AIS ship data. We selected a temporal resolution of one hour to reflect the daily activity patterns of harbour seals. Seal usage maps and AIS ship traffic maps were produced at an hourly scale using a 5 km² grid cell resolution. For each hour, we counted the number of unique seals or vessels present in each cell. Hourly seal–ship encounters were then calculated, allowing us to estimate the risk of encounter, defined as the number of seal–ship overlaps per hour and per cell. Risk maps were produced using MATLAB R2023b (MathWorks Inc., 2023).

Habitat selection

The second part of this study focused on evaluating the habitat selection of harbour seals to explore the influence of various environmental factors and the potential impact of shipping noise on their selection.

Environmental variables

Five environmental variables were selected for the habitat analysis, based on previous studies demonstrating their influence on harbour seal habitat selection (Bailey et al., 2014; Huon et al., 2021; Wynn-Simmonds et al., 2024). Bathymetric data were obtained at a resolution of 0.1 minutes using the "getNOAA.bathy" function from the package *marmap* in R (Pante & Simon-Bouhet, 2013). The locations of harbours in Normandy were obtained from www.data.gouv.fr as a shapefile. Sediment data were obtained via the EMODnet Geology project with five seabed substrate classes at a resolution of 1:1,000,000 (European Commission 2019). Tidal current data were available hourly from the Previmer database (MARS2D model; Lecornu & De Roeck, 2009) with a resolution of 700 m.

Additionally, wind data were obtained at an hourly rate and a 0.125 degree spatial resolution from Copernicus (https://www.copernicus.eu) in order to estimate wind noise levels, which were used in the shipping noise estimation.

Shipping noise variable

To assess the effect of shipping noise in our habitat model, a proxy was constructed based on modelled ship noise for each harbour seal dive. The decidecade band centred at 1 kHz was chosen, as this frequency band is significantly impacted by ship noise (Duarte et al., 2021; MacGillivray & de Jong, 2021) and lies within the peak sensitivity range of harbour seal hearing (Kastelein et al., 2009). This frequency band has already been used in studies of noise effects on harbour seals (Mikkelsen et al., 2019). Acoustic modelling was conducted using the sonar equation, represented as:

$$RL = SL - PL \text{ (Eq 1)}$$

where RL denotes the received level, SL is the source level, and PL is the propagation loss. The source level (SL) was derived from the AIS data, using the JOMOPANS-ECHO model (MacGillivray & de Jong, 2021) to estimate SL based on vessel type, length, and speed. Propagation loss (PL) was calculated using a geometric spreading model, as follows:

$$PL = 15.log_{10}(distance) \text{ (Eq 2)}$$

This model was selected because it was shown to have a good trade-off between accuracy and computational efficiency and has been validated with field measurements in the study area (Wynn-Simmonds et al., 2025).

We estimated total received levels (RL_{total}) at each dive location by calculating the contribution from all ships present in the area, using:

$$RL_{total} = 10log_{10}(\sum_{i=1}^{n} 10^{\frac{RLi}{10}}) \text{ (Eq 3)}$$

To convert total received levels (RL_{total}) into perceived levels (RLw), we integrated the phocid audiogram, using the auditory weighting function for phocid carnivores in water (PCW) as described by Southall et al. (2019), which accounts for the hearing sensitivity of the targeted species across relevant frequency ranges.

The signal excess (SE_{1kHz}) were then calculated using:

$$SE_{1kHz} = RLw - NL \text{ (Eq 4)}$$

where NL represents the ambient noise level. During the validation measurements, ambient noise levels were recorded (Wynn-Simmonds et al., 2025) at Beaufort sea state level 3 conditions. However, since the ambient noise level varies with sea state, we corrected this value for each seal dive using the wind noise model described by Hildebrand et al. (2021).

Statistical analysis

Harbour seal habitat selection was assessed by using a pseudo-absence method (Keating & Cherry, 2004; Huon et al., 2021). Due to constraints related to AIS data availability, we filtered out tracks recorded outside the study area (Figure 1). One out of every ten dives for each individual were selected to avoid autocorrelation (Huon et al., 2015). For each dive location, two pseudo-absence points were created within the study area using the *sp* package in R (Pebesma & Bivand, 2005). The purpose of this approach was to evaluate habitat selection by comparing the environmental characteristics of dive locations with those of pseudo-absence points. We extracted environmental information (see above) for each dive location and pseudo absence point. Bathymetry data was linearly interpolated using the *marmap* package in R (Pante & Simon-Bouhet, 2013). In addition, we also calculated the Euclidean distance to shore, the Euclidean distance to haulout site (the distance to the closest previous/next haulout site of the seal), and the Euclidean distance to the nearest harbour using respectively the "gDistance", "gdist", and "st_distance" functions available in the *rgeos*, *Imap,* and *sf* packages in R (Bivand & Rundel., 2023; Pebesma, 2023; Wallace, 2012). Furthermore, we also used sediment type, tidal current, and signal excess, to assess the environmental factors influencing habitat selection of seals. Correlation between variables was calculated in order to identify strong collinearity that would affect model predictions.

A generalised additive mixed model (GAMM) with a binomial family argument was then fitted to the data by using the *mgcv* package in R (Wood, 2023). Dive locations and pseudo-absence points were used as the binary response variable with values of 1 and 0 respectively. Bathymetry, distance to the haulout site, distance to the shore, distance to the nearest harbour, signal excess, and tidal current were included as continuous fixed-effect predictors. Sediment type was included as a categorical fixed effect. To account for repeated measures within individuals, seal ID was included as a random effect. The most parsimonious model was then selected using the Akaike information criterion (AIC; Akaike, 1973). The model with the smallest AIC was selected. For each variable, partial deviance was estimated to assess its contribution to model performance (Brunbjerg et al., 2018). Model assumptions (e.g., residual independence, homoscedasticity, normality) were assessed using the "gam.check" function available in the *mgcv* package in R (Wood, 2023).

RESULTS

To assess whether shipping noise was a potential driver of harbour seal habitat selection, we first examined the spatial overlap between seal distribution and shipping activity. We then analysed the potential effects of shipping noise on their habitat preferences.

Usage maps

Of 28 harbour seals captured in the Baie des Veys between 2020 and 2024 (14 individuals in 2020–2021; 14 in 2023–2024), 25 tag datasets were used in this analysis. The tracking periods went from 13 October 2020 to 21 July 2021 and from 10 November 2023 to 3 June 2024. On average, the seals were tracked for 99 ± 35 days (Supplementary file 1). In total, 178,319 dives were recorded. During the tracking period, the seals remained mostly near the coast (Supplementary file 3) and most dive activity occurred near the main haulout site (Figure 2), where they were caught. Only two individuals left the study area during the tracking period (V35 and V39). Seal V35 performed 90% of its dives within 20 km from the study area boundary, while only 11% of V39's dives occurred within 20 km from the study area boundary (Supplementary file 3).

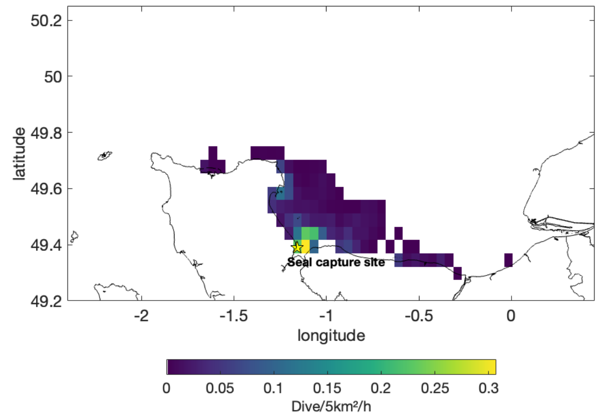

Figure 2: Usage map of 25 harbour seals captured and tagged in the Baie des Veys in 2020–2021 and 2023–2024. The seal capture site is represented by a red marker. The colour gradient represents the mean hourly count of dives from tagged seals per 5 km² cell.

A total of 19,867 ships were recorded in the study area during the study periods 2020–2021 and 2023–2024, 4,816 of which were recorded during both periods. Ship density in the two sub periods was relatively similar (2020–2021: 12,847 ships; 2023–2024: 11,836 ships). Bulker ships accounted for the largest proportion of unique vessels (26.2%), followed by the ship class "other" (21.5%), containership (19.3%), and tankers (16.2%). The highest density of ships was concentrated around the mouth of the Seine and Le Havre harbour (maximum 8 ships per hour; Figure 3). There was in general a high density of ships (~2 ships per hour) around harbours (represented by red markers in Figure 3). Additionally, the top left corner of the study area (Figure 3) stood out as a high-density shipping route (maximum 3 ships per hour; Figure 3). Finally, there was moderate ship density in the Baie de Seine aside from the ship traffic routes to and from the harbours (Figure 3). Large differences between ship classes were observed (Supplementary file 4). For example, bulker ships and tankers were primarily concentrated along specific shipping routes and near major harbours such as Le Havre harbour. Cruise vessels used specific routes to and from harbours. In contrast, ship classes such as fishing vessels exhibited different and less discernible patterns.

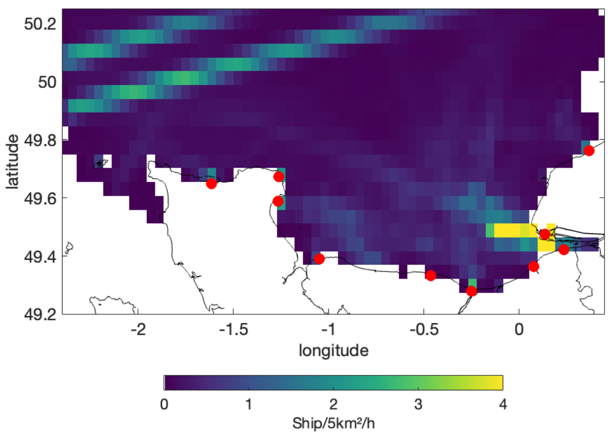

Figure 3. Density map of 19,867 ships with AIS transmitters recorded during 2020–2021 and 2023–2024 study periods. The main harbours are represented by red markers. The colour gradient represents the mean hourly count of AIS ships per 5km² cell.

Spatio-temporal overlap

The spatio-temporal overlap, estimated as the number of hourly co-occurrences of seals and ships transmitting AIS data per 5 km² cell, indicated that overlap was greatest in the Baie des Veys, particularly near the coast and the main haulout site of harbour seals (Figure 4). This overlap was present in 73% of cells within the seals' usage map, meaning that in 73% of the grid cells where harbour seals occur, there was at least one ship present at the same time. The highest overlap occurred around three main harbours: Saint-Vaast-la-Hougue (0.2 encounters per 5 km² per hour); Barfleur (0.1 encounters per 5 km² per hour) and Grandcamp-Maisy (0.1 encounters per 5 km² per hour).

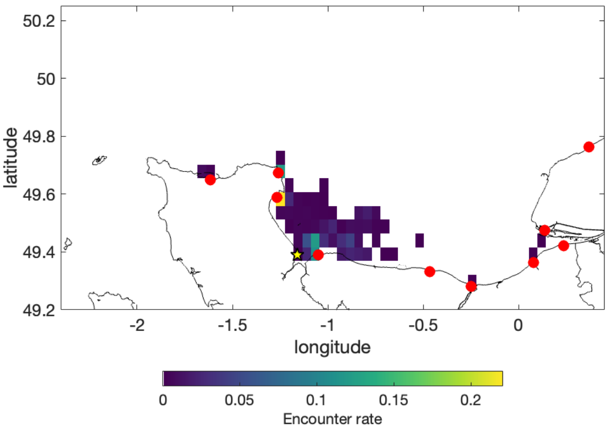

Figure 4. Map of encounter rate, estimated as the number of hourly co-occurrences of seals and ships per 5 km² cell in the Baie de Seine during 2020–2021 and 2023–2024 periods. Main harbours are represented by red markers and the seal capture site by a yellow star.

Habitat selection

The correlation between variables showed that the covariates had weak to moderate correlations with one another ($r < 0.75$), except for distance to the nearest harbour, which was strongly correlated with distance to the shore ($r = 0.97$). The model including distance to the shore had a smaller AIC than the model including distance to the nearest harbour, hence only distance to the shore was kept in the final model.

Among the models tested using the remaining variables, the model that retained all of them had the lowest AIC and was therefore selected as the most parsimonious (Supplementary file 5). The selected model explained a relatively high proportion of deviance (71.8%). The distance to haulout site accounted for the largest share of the deviance (91.2%). The other parameters, distance to the shore (3.7%), bathymetry (4.0%), sediment (<1%), tidal current (<1%), and signal excess (<1%), were retained in the final model but, collectively, explained less than 10% of the deviance (Figure 5, Table 1).

The probability of selection declined with increasing distance to the haulout site (Figure 6a, Table 1), with 77.0% of dives occurring within 20 km from the haulout site (median: 9.5 km, IQR: 5.7–19.1 km; Figure 5a). Similarly, distance to the shore had a negative influence on habitat selection (Figure 6b, Table 1), with 94.7% of dives occurring within 10 km of the shore (median: 2.6 km, IQR: 1.0–4.4 km; Figure 5b). Bathymetry also had a negative influence on habitat selection (Figure 6c, Table 1), with 82.6% of dives occurring at less than 20 m depth. In contrast, tidal current showed a positive relationship with habitat selection (median: 0.3 m/s, IQR: 0.1–0.4 m/s), with predicted values increasing as tidal current speed rose from approximately 0.5 m/s to 1.5 m/s (Figure 6d, Table 1). Signal excess in the 1 kHz decidecade band (median: 10.0 dB, IQR: 7.1–13.7 dB; Figure 5e) had a slight negative influence on habitat selection (Figure 6e, Table 1). Additionally, harbour seals selected areas with sand, coarse sediment or rock as opposed to mixed sediment (Table 1).

DISCUSSION AND CONCLUSIONS

Over the past decade, shipping activities have intensified, resulting in higher ambient noise levels in marine environments (Duarte et al., 2021), impacting many species (Erbe et al., 2018; Gomez et al., 2016, Simmonds 2018). Shipping noise may have significant ecological effects on phocids' behaviour (Maurer et al., 2025; Mikkelsen et al., 2019; Prawirasasra et al., 2022; Trigg et al., 2020), which can lead to potential consequences at the population level. This is the first study to evaluate shipping noise as a potential driver of harbour seal habitat selection. Noise only had a minor impact on our model results, which indicates that seals are not strongly impacted by noise in our study area, either due to relative low signal excess or that the seals have habituated to the current exposure levels.

Habitat selection of harbour seals

The habitat selection model indicated that harbour seals

Table 1: Effect of environmental variables on harbour seal habitat selection.

Variables	*edf*	*Chi.sq*	*p-value*	*Partial deviance (%)*
Distance to haulout	2.97	4598.84	≤ 0.001	91.2
Distance to coast	2.99	153.11	≤ 0.001	3.7
Bathymetry	2.90	390.25	≤ 0.001	4.0
Tidal current	2.81	27.86	≤ 0.001	0.3
Signal Excess	1.88	6.62	≤ 0.01	0.1
Sediment type				0.7
Sand			≤ 0.001	
Coarse sediment			≤ 0.001	
Rock			≤ 0.001	
Mixed sediment			1	

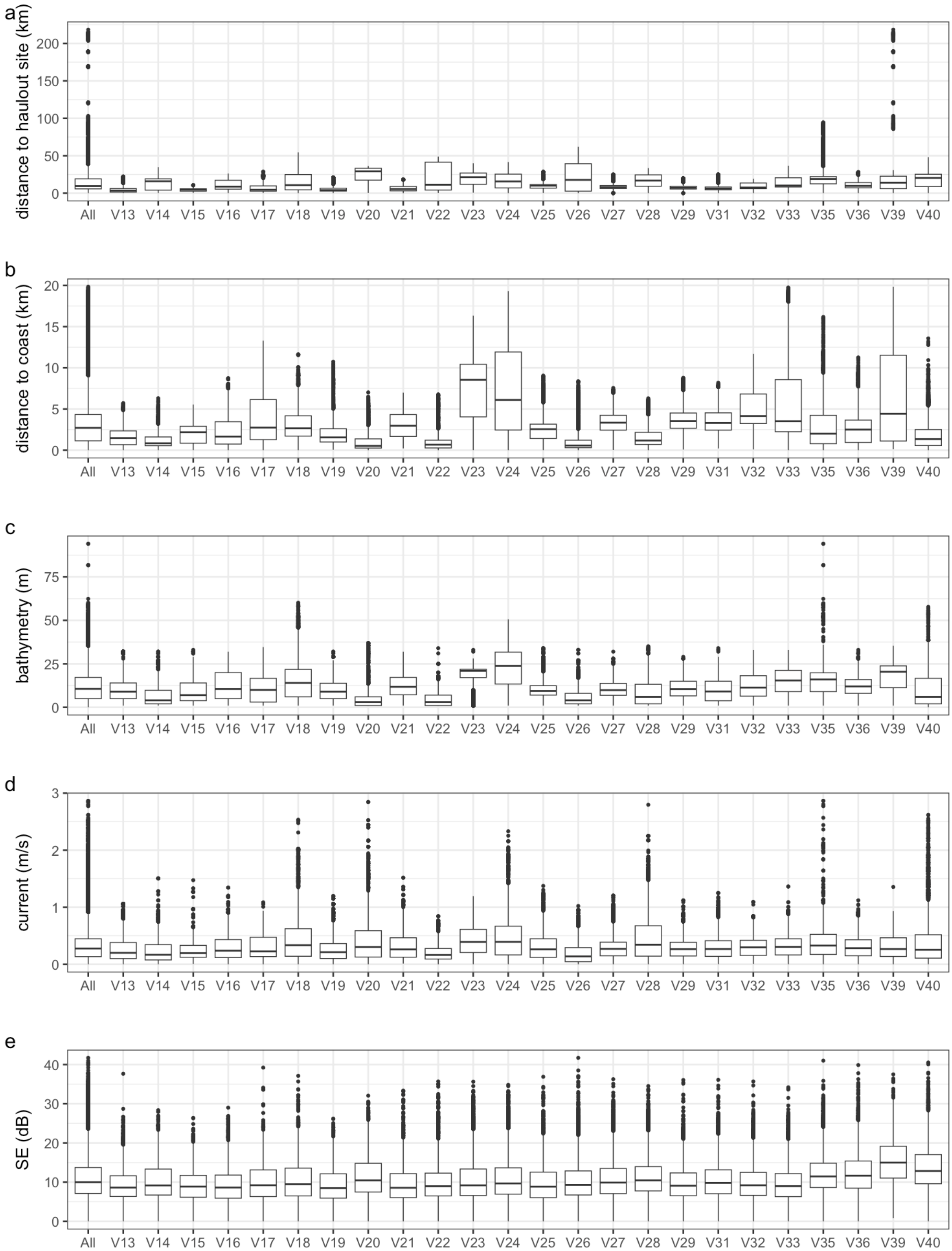

Figure 5. Environmental variables at dive locations used for evaluating harbour seal habitat selection, shown for each individual seal (V13–V40) and for all seals combined (All): a) distance to haulout site (km); b) distance to the shore (km); c) bathymetry (m); d) tidal current (m/s); e) signal excess (dB).

selected areas near their haulout sites, close to shore, in shallow waters and strong tidal currents. These preferred habitats were characterised by sand, coarse sediment, and rock. Although noise contributed to a slightly improved model, we found similar excess between dives and pseudo-absence points (dive locations: 10.0 dB, IQR: 7.1–13.7 dB vs pseudo-absence points: 11.7 dB, IQR: 8.3–15.6 dB).

The results of this study are consistent with findings from other regions, where haulout site proximity, distance to shore, and bathymetry have also been identified as primary drivers of habitat selection (Bailey et al., 2014; Huon et al., 2021; Wynn-Simmonds et al., 2024). Their foraging range is therefore constrained, leading them to select areas with high foraging success to maximise energy gain while minimising energy costs (Bailey et al., 2014). Additionally, they primarily target benthic prey (Spitz et al., 2010; Planque et al., 2021), even if they can occasionally forage on pelagic prey (Boyi et al., 2022; Sharples et al., 2009; Wilson & Hammond, 2019). As an estuary, our study area has a high level of productivity (Wolowicz et al., 2007). Harbour seals in the Baie des Veys do not need to travel far to forage, explaining the high influence of distance to haulout site in the habitat selection model (~91.5%). Previous studies also found that tidal current and sediment type played a minor role in habitat selection (Bailey et al., 2014; Huon et al., 2021). As generalist species, harbour seals target different prey species that likely use different types of sediment. Hence, the dependency of seals to a particular sediment type may be linked to the targeted prey (Huon et al., 2021). Additionally, strong tidal currents have been shown to influence harbour seal foraging behaviour (Hastie et al., 2016; Zamon, 2001), however in our study area, tidal currents were comparatively low (median: 0.3 m/s, IQR: 0.1-0.4 m/s), likely explaining the minor role of this environmental parameter on habitat selection.

The role of shipping noise

In this study, we aimed to examined whether harbour seals are affected by or have adapted to an anthropogenic environment, focusing on the potential role of noise as a driver of habitat selection. We analysed habitat selection at a broad spatio-temporal scale, as any impact at this level could have significant ecological consequences. We found that noise only had a minor impact on habitat selection although there was relatively large spatial overlap. Acute responses of harbour seals to noise have previously been documented (Maurer et al., 2025; Mikkelsen et al., 2019). Anthropogenic noise, especially the low-frequency bands where shipping noise dominates, can propagate over large distances (Possenti et al., 2024), making it important to assess its potential effects on coastal species such as harbour seals. Previous work has examined the influence of human activities on harbour seal habitat use without accounting for noise and found only weak effects of anthropogenic factors on distribution (Grigg et al., 2012). Anthropogenic noise, especially in low frequency bands, can travel over large distances (Possenti et al., 2024). Hence, it is important to examine whether noise affects habitat selection of coastal species like harbour seals, to understand to which degree they are influenced by noise exposure. Our study was conducted in the Baie des Veys, located in the English Channel, an area with high shipping activity (Dauvin, 2019; Robbins et al., 2022). Consequently, there was a spatial overlap between vessels and the tracked seals, with 73% of the cells in the seal usage maps showing ship occurrence. This overlap was especially pronounced near the coast and in proximity to the main haul-

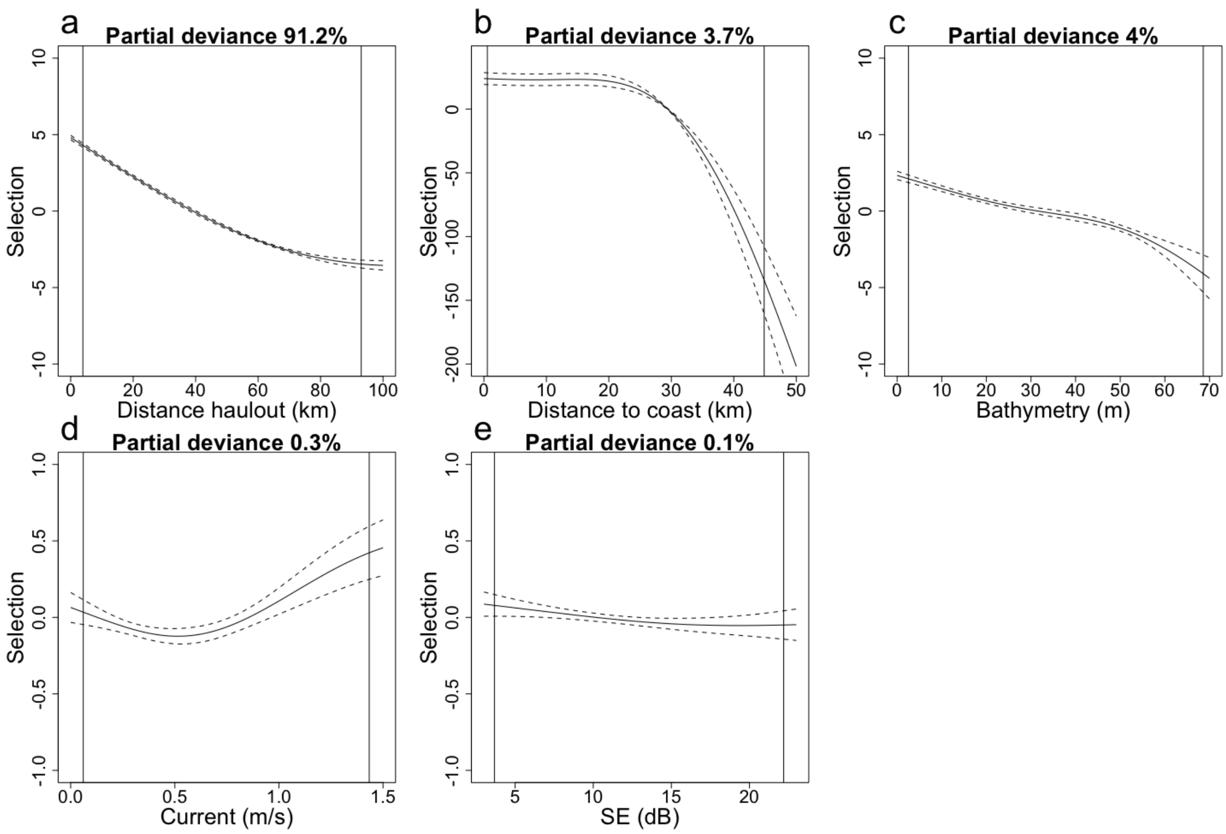

Figure 6. Effect of environmental variables on harbour seal habitat selection: a) distance to haulout site (km); b) distance to the shore (km); c) bathymetry (m); d) tidal current (m/s); e) signal excess in the 1 kHz decidecade band (dB). The dashed lines show the 95% confidence intervals and the vertical lines represent the 5th and 95th percentiles of the data.

out site, where seal activity was highest. These findings are consistent with Jones et al. (2017), who also reported high levels of spatial co-occurrence between vessels and both harbour and grey seals in UK waters, particularly within 50 km of haulout sites. This co-occurrence between vessels and the tracked seals raised questions about the potential impact of shipping noise on harbour seal population. In this study, seals were exposed to a median signal excess of 10 dB (Q1–Q3: 7.1–13.7 dB). In marine mammals, this level of excess is generally considered sufficient to be perceptible and potentially cause behavioural or auditory effects (Erbe, Reichmuth et al., 2016; Southall et al., 2007). There was only a minor effect of noise in our model, suggesting that shipping noise was not a primary driver of habitat selection of harbour seals in this area (partial deviance: < 1%). There are several reasons why this stressor may have played a minor role in harbour seal habitat selection.

In the English Channel, shipping activities have intensified by 20% between 2013 and 2017 (Robbins et al., 2022), and the area is now identified as one of the world's densest shipping areas (Robbins et al., 2022; Wang et al., 2023). Harbour seals have therefore been exposed to shipping noise for a long time, potentially causing habituation to this stressor. Additionally, previous studies have shown that marine mammals, such as phocids, may tolerate elevated noise levels in areas with high ecological importance (Bhagarathi et al., 2024; Grigg et al., 2012; Jacobs & Terhune, 2002; Van Neer et al., 2023). Hence, harbour seals may tolerate shipping noise in areas close to their haulout sites or areas with high prey availability. The benefits of abundant prey may outweigh the risks of chronic noise exposure, encouraging seals to remain in noisy environments that may have long-term consequences on their health. However, these consequences are not yet understood.

Secondly, even though there was a high percentage of overlap between seals and shipping activities, this does not necessarily mean that seals were consistently exposed to high noise levels. Seals might only respond to continuous noise when it exceeds tolerance threshold levels. The highest spatial overlap in this study occurred near three main harbours, where vessel traffic is typically high. However, speed restrictions are often implemented near harbours. For example, in France, vessels are required to reduce their speed within 300 m from the coast and near harbours, generally under 5 knots (N°2-68398-2013 PREMAR MANCHE/AEM/NP); it is important to note that the 300 m zone does not represent the majority of overlap cases in this study. Lower vessel speeds are associated with reduced noise levels (Findlay et al., 2023). Hence, if shipping noise levels rarely exceeded tolerance threshold levels, habitat selection of harbour seals might not be affected. This hypothesis could not be verified in this study because, to the best of our knowledge, no threshold for behavioural responses has been published for the frequency band of interest (Southall et al., 2019; Southall et al., 2021). Indeed, behavioural response to a noise is dependent on intra-individual parameters, environmental and behavioural context, and type of noise source (Kastelein et al., 2015). There are thresholds for temporary threshold shifts (TTS) and permanent threshold shift (PTS) that have been determined for groups of aquatic species (Southall et al., 2019); however, seals may exhibit behavioural responses before reaching these extreme noise levels (Gomez et al., 2016). In this study, harbour seals may continue using an area despite shipping noise levels if it provides essential ecological benefits. However, if those noise levels exceed individual tolerance threshold levels, they most likely will change their behaviour.

Lastly, in this study, we used AIS data, which track vessels generally over 15 m in length. However, harbour seals may encounter smaller vessels (without AIS transmitters). Indeed, Nachtsheim et al. (2023) found that only 31.8% of vessels recorded by long-term sound and movement tags (DTAGs) on tagged harbour seals were vessels with AIS transmitters. This suggests that an important portion of vessel activity may be underestimated.

Ecological implications and future research

In this study, shipping noise had a minor implication in harbour seal habitat selection. However, chronic exposure to shipping noise may still have effects on seals, such as stress, or changes in foraging/resting patterns (Erbe et al., 2019). Even minor behavioural changes, if persistent, can have cumulative population-level effects. Hence, it is important to monitor and mitigate anthropogenic noise in environments critical for harbour seals—ensuring that noise levels remain within acceptable thresholds for the seals will reduce potential impacts on them. The results of this study provide new insights into harbour seal habitat selection within an anthropogenic environment.

Conclusion

This study assessed the habitat selection of harbour seals in an environment influenced by anthropogenic activities, particularly shipping. Habitat selection was driven mainly by distance to haulout sites. As central place foragers, harbour seals are constrained to remain close to their main haulout sites, which may explain why they do not seem to be strongly affected by shipping noise on a large scale, despite overlap with intense shipping activity. While shipping noise did not stand out as a primary driver of habitat selection in our analysis, it is likely that seals still respond to acute noise events occurring at a finer spatial or temporal scale (i.e., responses during the moment of exposure). Future studies focusing on behavioural shifts at a finer scale could provide deeper insight into their responses to shipping noise.

ADHERENCE TO ANIMAL WELFARE PROTOCOLS

The research presented in this article has been done in accordance with the institutional and national laws and protocols for animal welfare that are applicable in the jurisdictions where the work was conducted. The permit for animal experimentation (number: #19256-2019020816355855 v4) was issued by the French Ministry of Research for the period 2019 to 2024. The permits for the capture of protected species in Baie des Veys were issued on 09/10/2020 and 14/12/2022 by the French Ministry in charge of Ecology.

ACKNOWLEDGEMENTS

This study was funded by both *Eoliennes Offshore du Calvados* and the Association Nationale de la Recherche et de la Technologie (ANRT), to whom we express our sincere gratitude for their financial support. We also extend our thanks to *CLS France* for providing the AIS data. We thank the curator and team of the *Réserve naturelle nationale du domaine de*

Beauguillot, as well as all participants involved in the fieldwork in the Baie des Veys.

REFERENCES

Akaike, H. (1973). Information Theory and an Extension of the Maximum Likelihood Principle. In B. N. Petrov, & F. Csaki (Eds.), *Proceedings of the 2nd International Symposium on Information Theory* (pp. 267–281). Budapest: Akademiai Kiado.

Avila, I. C., Kaschner, K., & Dormann, C. F. (2018). Current global risks to marine mammals: Taking stock of the threats. *Biological Conservation*, *221*, 44–58. https://doi.org/10.1016/j.biocon.2018.02.021

Bailey, H., Hammond, P. S., & Thompson, P. M. (2014). Modelling harbour seal habitat by combining data from multiple tracking systems. *Journal of Experimental Marine Biology and Ecology*, *450*, 30–39. https://doi.org/10.1016/j.jembe.2013.10.011

Bhagarathi, L. K., DaSilva, P. N. B., Maharaj, G., Balkarran, R., & Baksh, A. (2024). The impact of anthropogenic sound on marine mammals: A review. *International Journal of Life Science Research Archive, 7*(2), 009–033. https://doi.org/10.53771/ijlsra.2024.7.2.0070

Bivand, R., & Rundel, C. (2023). *rgeos: Interface to Geometry Engine - Open Source ('GEOS')*. R package version 0.5-9. https://CRAN.R-project.org/package=rgeos

Blair, H. B., Merchant, N. D., Friedlaender, A. S., Wiley, D. N., & Parks, S. E. (2016). Evidence for ship noise impacts on humpback whale foraging behaviour. *Biology Letters*, *12*(8), 20160005. https://doi.org/10.1098/rsbl.2016.0005

Blanchet, M.-A., Vincent, C., Womble, J. N., Steingass, S. M., & Desportes, G. (2021). Harbour Seals: Population Structure, Status, and Threats in a Rapidly Changing Environment. *Oceans*, *2*(1), 41–63. https://doi.org/10.3390/oceans2010003

Boehlert, G., & Gill, A. (2010). Environmental and Ecological Effects of Ocean Renewable Energy Development – A Current Synthesis. *Oceanography*, *23*(2), 68–81. https://doi.org/10.5670/oceanog.2010.46

Boyi, J. O., Heße, E., Rohner, S., Säurich, J., Siebert, U., Gilles, A., & Lehnert, K. (2022). Deciphering Eurasian otter (*Lutra lutra* L.) and seal (*Phoca vitulina* L.; *Halichoerus grypus* F.) diet: Metabarcoding tailored for fresh and saltwater fish species. *Molecular Ecology*, *31*(19), 5089–5106. https://doi.org/10.1111/mec.16635

Bretschneider, H., Bosschers, J., Choi, G. H., Ciappi, E., Farabee, T., Kawakita, C., & Tang, D. (2014, 31 August–5 September). Specialist Committee on hydrodynamic noise: Final report and recommendations to the 27th ITTC. *Proceedings of the 27th International Towing Tank Conference, Volume 2,* Copenhagen. https://www.ittc.info/media/6091/sc-noise.pdf

Brunbjerg, A. K., Hale, J. D., Bates, A. J., Fowler, R. E., Rosenfeld, E. J., & Sadler, J. P. (2018). Can patterns of urban biodiversity be predicted using simple measures of green infrastructure? *Urban Forestry & Urban Greening*, *32*, 143–153. https://doi.org/10.1016/j.ufug.2018.03.015

Dauvin, J.-C. (2019). The English Channel: La Manche. In *World Seas: An Environmental Evaluation* (pp. 153–188). Elsevier. https://doi.org/10.1016/B978-0-12-805068-2.00008-5

Duarte, C. M., Chapuis, L., Collin, S. P., Costa, D. P., Devassy, R. P., Eguiluz, V. M., Erbe, C., Gordon, T. A. C., Halpern, B. S., Harding, H. R., Havlik, M. N., Meekan, M., Merchant, N. D., Miksis-Olds, J. L., Parsons, M., Predragovic, M., Radford, A. N., Radford, C. A., Simpson, S. D., … Juanes, F. (2021). The soundscape of the Anthropocene ocean. *Science*, *371*(6529), eaba4658. https://doi.org/10.1126/science.aba4658

Erbe, C., Dunlop, R., & Dolman, S. (2018). Effects of Noise on Marine Mammals. In H. Slabbekoorn, R. J. Dooling, A. N. Popper, & R. R. Fay (Eds.), *Effects of Anthropogenic Noise on Animals* (Vol. 66, pp. 277–309). Springer New York. https://doi.org/10.1007/978-1-4939-8574-6_10

Erbe, C., Marley, S. A., Schoeman, R. P., Smith, J. N., Trigg, L. E., & Embling, C. B. (2019). The Effects of Ship Noise on Marine Mammals—A Review. *Frontiers in Marine Science*, *6*, 606. https://doi.org/10.3389/fmars.2019.00606

Erbe, C., McCauley, R., & Gavrilov, A. (2016). Characterizing marine soundscapes. In A. N. Popper & A. Hawkins (Eds.), *The Effects of Noise on Aquatic Life II* (Vol. 875, pp. 265–271). Springer New York. https://doi.org/10.1007/978-1-4939-2981-8_31

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., & Dooling, R. (2016). Communication masking in marine mammals: A review and research strategy. *Marine Pollution Bulletin*, *103*(1–2), 15–38. https://doi.org/10.1016/j.marpolbul.2015.12.007

European Commission (2019). *EMODnet Geology – Seabed Substrate Map of European marine areas (1:1,000,000 scale)*. European Marine Observation and Data Network (EMODnet). Available at: https://www.emodnet.eu/geology

Findlay, C. R., Rojano-Doñate, L., Tougaard, J., Johnson, M. P., & Madsen, P. T. (2023). Small reductions in cargo vessel speed substantially reduce noise impacts to marine mammals. *Science Advances*, *9*(25), eadf2987. https://doi.org/10.1126/sciadv.adf2987

Frisk, G. V. (2012). Noiseonomics: The relationship between ambient noise levels in the sea and global economic trends. *Scientific Reports*, *2*(1), 437. https://doi.org/10.1038/srep00437

Gabriele, C. M., Ponirakis, D. W., Clark, C. W., Womble, J. N., & Vanselow, P. B. S. (2018). Underwater Acoustic Ecology Metrics in an Alaska Marine Protected Area Reveal Marine Mammal Communication Masking and Management Alternatives. *Frontiers in Marine Science*, *5*, 270. https://doi.org/10.3389/fmars.2018.00270

Gomez, C., Lawson, J. W., Wright, A. J., Buren, A. D., Tollit, D., & Lesage, V. (2016). A systematic review on the behavioural responses of wild marine mammals to noise: The disparity between science and policy. *Canadian Journal of Zoology*, *94*(12), 801–819. https://doi.org/10.1139/cjz-2016-0098

Grigg, E. K., Allen, S. G., Craven-Green, D. E., Klimley, A. P., Markowitz, H., & Elliott-Fisk, D. L. (2012). Foraging distribution of Pacific harbor seals (*Phoca vitulina richardii*) in a highly impacted estuary. *Journal of Mammalogy*, *93*(1), Article 1. https://doi.org/10.1644/11-MAMM-A-128.1

Hastie, G. D., Russell, D. J. F., Benjamins, S., Moss, S., Wilson, B., & Thompson, D. (2016). Dynamic habitat corridors for marine predators; intensive use of a coastal channel by harbour seals is modulated by tidal currents. *Behavioral Ecology and Sociobiology*, *70*(12), Article 12. https://doi.org/10.1007/s00265-016-2219-7

Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Marine Ecology Progress Series*, *395*, 5–20. https://doi.org/10.3354/meps08353

Hildebrand, J. A., Frasier, K. E., Baumann-Pickering, S., & Wiggins, S. M. (2021). An empirical model for wind-generated ocean noise. *The Journal of the Acoustical Society of America*, *149*(6), 4516–4533. https://doi.org/10.1121/10.0005430

Huon, M., Jones, E. L., Matthiopoulos, J., McConnell, B., Caurant, F., & Vincent, C. (2015). Habitat selection of gray seals (*Halichoerus grypus*) in a marine protected area in France: Gray Seal Habitat Selection. *The Journal of Wildlife Management*, *79*(7), Article 7. https://doi.org/10.1002/jwmg.929

Huon, M., Planque, Y., Jessopp, M. J., Cronin, M., Caurant, F., & Vincent, C. (2021). Fine-scale foraging habitat selection by two diving central place foragers in the Northeast Atlantic. *Ecology and Evolution*, *11*(18), Article 18. https://doi.org/10.1002/ece3.7934

Jacobs, S. R., & Terhune, J. M. (2002). The effectiveness of acoustic harassment devices in the Bay of Fundy, Canada: Seal reactions and a noise exposure model. *Aquatic Mammals 28*(2), 131–146.

Jones, E. L., G. D. Hastie, S. Smout, J. Onoufriou, N. D. Merchant, K. L. Brookes and D. Thompson (2017). Seals and shipping: quantifying population risk and individual exposure to vessel noise. *Journal of Applied Ecology 54*(6): 1930-1940. https://doi.org/10.1111/1365-2664.12911

Kastelein, R. A., Wensveen, P. J., Hoek, L., Verboom, W. C., & Terhune, J. M. (2009). Underwater detection of tonal signals between 0.125 and 100kHz by harbor seals (*Phoca vitulina*). *The Journal of* *the Acoustical Society of America*, *125*(2), Article 2. https://doi.org/10.1121/1.3050283

Kastelein, R. A., Helder-Hoek, L., Gransier, R., Terhune, J. M., Jennings, N., & de Jong, C. A. F. (2015). Hearing thresholds of harbor seals (*Phoca vitulina*) for playbacks of seal scarer signals, and effects of the signals on behavior. *Hydrobiologia*, *756*(1), Article 1. https://doi.org/10.1007/s10750-014-2152-6

Keating, K. A., & Cherry, S. (2004). Use and interpretation of logistic regression in habitat-selection studies. *Journal of Wildlife Management*, *68*(4), 774–789. https://doi.org/10.2193/0022-541x(2004)068[0774:uaiolr]2.0.co;2

Learmonth, J. A., MacLeod, C. D., Santos Vazquez, M. B., Pierce, G. J., Crick, H. Q. P., & Robinson, R. A. (2006). Potential effects of climate change on marine mammals. *Oceanography and Marine Biology: An Annual Review*, *44*, 431-464. https://doi.org/10.1016/j.envint.2009.10.008

Lecornu, F., & De Roeck, Y.-H. (2009). PREVIMER-Observations & Prévisions Côtières. *La Houille Blanche, 95*(1), 60–63. https://doi.org/10.1051/lhb:2009006

Lemos, L. S., Haxel, J. H., Olsen, A., Burnett, J. D., Smith, A., Chandler, T. E., Nieukirk, S. L., Larson, S. E., Hunt, K. E., & Torres, L. G. (2022). Effects of vessel traffic and ocean noise on gray whale stress hormones. *Scientific Reports*, *12*(1), 18580. https://doi.org/10.1038/s41598-022-14510-5

MacGillivray, A., & de Jong, C. (2021). A Reference Spectrum Model for Estimating Source Levels of Marine Shipping Based on Automated Identification System Data. *Journal of Marine Science and Engineering*, *9*(4), 369. https://doi.org/10.3390/jmse9040369

MathWorks Inc. (2023). MATLAB version: 23.2.0 (R2023b), Natick, Massachusetts: The MathWorks Inc. https://www.mathworks.com

Maurer, N., Boyi, J. O., Schick, L. A., Nachtsheim, D. A., Schaffeld, T., Gross, S., Teilmann, J., Schnitzler, J., & Siebert, U. (2025). Unsealing behaviour: Variation in harbour seal (*Phoca vitulina*) responses to anthropogenic sound in relation to individual health. *Marine Pollution Bulletin 214*: 117777. https://doi.org/10.1016/j.marpolbul.2025.117777

Mikkelsen, L., Johnson, M., Wisniewska, D. M., van Neer, A., Siebert, U., Madsen, P. T., & Teilmann, J. (2019). Long-term sound and movement recording tags to study natural behavior and reaction to ship noise of seals. *Ecology and Evolution*, *9*(5), 2588–2601. https://doi.org/10.1002/ece3.4923

Nachtsheim, D. A., Johnson, M., Schaffeld, T., Van Neer, A., Madsen, P. T., Findlay, C. R., Rojano-Doñate, L., Teilmann, J., Mikkelsen, L., Baltzer, J., Ruser, A., Siebert, U., & Schnitzler, J. G. (2023). Vessel noise exposures of harbour seals from the Wadden Sea. *Scientific Reports*, *13*(1), 6187. https://doi.org/10.1038/s41598-023-33283-z

Nowacek, D. P., Thorne, L. H., Johnston, D. W., & Tyack, P. L. (2007). Responses of cetaceans to anthropogenic noise. *Mammal Review*, *37*(2), 81-115. https://doi.org/10.1111/j.1365-2907.2007.00104.x

Orians, G. H., & Pearson, N. E. (1979). On the theory of central place foraging. In D. J. Horn, R. D. Mitchell & G. R. Stairs (Eds.) *Analysis of Ecological Systems* (pp. 154–177). Columbus: Ohio State University Press.

Pante, E., & Simon-Bouhet, B. (2013). marmap: A package for importing, plotting and analyzing bathymetric and topographic data in R. *PLoS ONE*, 8(9), e73051. https://doi.org/10.1371/journal.pone.0073051

Pebesma, E. (2023). *sf: Simple Features for R*. R package version 1.0-14. https://CRAN.R-project.org/package=sf

Pebesma, E. J., & Bivand, R. S. (2005). Classes and methods for spatial data in R. *R News*, *5*(2), 9–13. https://CRAN.R-project.org/doc/Rnews/

Possenti, L., De Nooijer, L., De Jong, C., Lam, F.-P., Beelen, S., Bosschers, J., Van Terwisga, T., Stigter, R., & Reichart, G.-J. (2024). The present and future contribution of ships to the underwater soundscape. *Frontiers in Marine Science*, *11*, 1252901. https://doi.org/10.3389/fmars.2024.1252901

Planque, Y., Spitz, J., Authier, M., Guillou, G., Vincent, C., & Caurant, F. (2021). Trophic niche overlap between sympatric harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) at the southern limit of their European range (Eastern English Channel). *Ecology and Evolution*, *11*(15), Article 15. https://doi.org/10.1002/ece3.7739

Poncet, S., Parent, S., Sicard, M., Le Baron, M., Gaultier, M., Hemon, A., Fremau, M-H., Lecarpentier, T., Gabet, L., Gicquel, C., Monnet-Kassas, S., Rault, C., Mahieux, J., Karpouzopoulos, J., Lefebvre, J., Everard, A., Colomb, F., Diard Combot, M., Provost, P., … Vincent, C. (2024). Recensement des colonies et reposoirs de phoques en France en 2022 et 2023. *Rapport collectif du Réseau National Phoques*. 63 pp.

Prawirasasra, M., Jüssi, M., Mustonen, M., & Klauson, A. (2022). Underwater noise impact of a ferry route on dive patterns of transiting Baltic ringed seals. *Estonian Journal of Earth Sciences*, *71*(4), 201. https://doi.org/10.3176/earth.2022.14

Robbins, J. R., Bouchet, P. J., Miller, D. L., Evans, P. G. H., Waggitt, J., Ford, A. T., & Marley, S. A. (2022). Shipping in the north-east Atlantic: Identifying spatial and temporal patterns of change. *Marine Pollution Bulletin*, *179*, 113681. https://doi.org/10.1016/j.marpolbul.2022.113681

Rolland, R. M., Parks, S. E., Hunt, K. E., Castellote, M., Corkeron, P. J., Nowacek, D. P., Wasser, S. K., & Kraus, S. D. (2012). Evidence that ship noise increases stress in right whales. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1737), 2363–2368. https://doi.org/10.1098/rspb.2011.2429

Sharples, R., Arrizabalaga, B., & Hammond, P. (2009). Seals, sandeels and salmon: Diet of harbour seals in St. Andrews Bay and the Tay Estuary, southeast Scotland. *Marine Ecology Progress Series*, *390*, 265–276. https://doi.org/10.3354/meps08232

Simmonds, M. P. (2018). Marine mammals and multiple stressors: Implications for conservation and policy. In M. C. Fossi & C. Prati (Eds.) *Marine Mammal Ecotoxicology* (pp. 459–470). Academic Press. https://doi.org/10.1016/B978-0-12-812144-3.00017-6

Simmonds, M. P., Dolman, S. J., Jasny, M., Parsons, E. C. M., Weilgart, L., Wright, A. J., & Leaper, R. (2014). Marine noise pollution--increasing recognition but need for more practical action. *Journal of Ocean Technology, 9*(1), 71-90.

Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene, C. R., Jr., Kastak, D., Ketten, D. R., Miller, J. H., Nachtigall, P. E., Richardson, W. J., Thomas, J. A., & Tyack, P. L. (2007). Marine mammal noise exposure criteria: Initial scientific recommendations. *Aquatic Mammals, 33*(4), 411–521. https://doi.org/10.1578/AM.33.4.2007.411

Southall, B. L., Finneran, J. J., Reichmuth, C., Nachtigall, P. E., Ketten, D. R., Bowles, A. E., Ellison, W. T., Nowacek, D. P., & Tyack, P. L. (2019). Marine mammal noise exposure criteria: Updated scientific recommendations for residual hearing effects. *Aquatic Mammals*, *45*(2), 125–232. https://doi.org/10.1578/AM.45.2.2019.125

Southall, B. L., Nowacek, D. P., Bowles, A. E., Senigaglia, V., Bejder, L., & Tyack, P. L. (2021). Marine mammal noise exposure criteria: Assessing the severity of marine mammal behavioral responses to human noise. *Aquatic Mammals*, *47*(5), 421–464. https://doi.org/10.1578/AM.47.5.2021.421

Spitz, J., Mariotti, L., Ridoux, V., Caillot, E., & Elder, J. F. (2010). The diet of harbour seals (*Phoca vitulina*) at the southern limit of its European distribution (Normandy, France). *NAMMCO Scientific Publications*, *8*, 313. https://doi.org/10.7557/3.2696

Sylvand B., 1995. The baie des Veys (French coast of the English Channel, western bay of Seine), 1972-1993: structure and long-term evolution of a sedimentary tidal flat benthic ecosystem under estuarine influence. [Doctoral dissertation, University of Caen]. https://archimer.ifremer.fr/doc/00848/96031/

Trigg, L. E., Chen, F., Shapiro, G. I., Ingram, S. N., Vincent, C., Thompson, D., Russell, D. J. F., Carter, M. I. D., & Embling, C. B. (2020). Predicting the exposure of diving grey seals to shipping noise. *The Journal of the Acoustical Society of America*, *148*(2), Article 2. https://doi.org/10.1121/10.0001727

Van Neer, A., Nachtsheim, D., Siebert, U., & Taupp, T. (2023). Movements and spatial usage of harbour seals in the Elbe estuary in Germany. *Scientific Reports*, *13*(1), 6630. https://doi.org/10.1038/s41598-023-33594-1

Wallace, B. (2012). *Imap: Interactive Mapping*. R package version 1.32. https://CRAN.R-project.org/package=Imap

Wang, X., Du, D., & Peng, Y. (2023). Assessing the Importance of the Marine Chokepoint: Evidence from Tracking the Global Marine Traffic. *Sustainability*, *16*(1), 384. https://doi.org/10.3390/su16010384

Wołowicz, M., Sokołowski, A., & Lasota, R. (2007). Estuaries—A biological point of view. *Oceanological and Hydrobiological Studies*, *36*(3), 113–130. https://doi.org/10.2478/v10009-007-0025-2

Wilson, L. J., & Hammond, P. S. (2019). The diet of harbour and grey seals around Britain: Examining the role of prey as a potential cause of harbour seal declines. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*(S1), 71–85. https://doi.org/10.1002/aqc.3131

Wood, S.N. (2023). *mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation*. R package version 1.9-0. https://CRAN.R-project.org/package=mgcv

Wynn-Simmonds, S., Planque, Y., Huon, M., Lovell, P., & Vincent, C. (2024). Foraging behavior and habitat selection of harbor seals (*Phoca vitulina vitulina*) in the archipelago of Saint-Pierre-and-Miquelon, Northwest Atlantic. *Marine Mammal Science*, e13134. https://doi.org/10.1111/mms.13134

Wynn-Simmonds, S., Vincent, C., Mathias, D., & Richard, G. (2025). Comparative analysis of underwater acoustic propagation models: Evaluating the trade-off between accuracy and computational demands for coastal noise predictions. *Marine Pollution Bulletin*, *215*, 117905. https://doi.org/10.1016/j.marpolbul.2025.117905

Zamon, J. E. (2001). Seal predation on salmon and forage fish schools as a function of tidal currents in the San Juan Islands, Washington, USA. *Fisheries Oceanography, 10*: 353–366. https://doi.org/10.1046/j.1365-2419.2001.00180.x