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NOTE

Foraging behavior and habitat selection of harbor seals (*Phoca vitulina vitulina*) in the archipelago of Saint-Pierre-and-Miquelon, Northwest Atlantic

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Studying the foraging behavior of marine top predators is crucial for gaining a comprehensive understanding of their role within the ecosystem and improving management plans around their foraging habitat (Pianka, 1976; Stearns, 1992). Harbor seals (*Phoca vitulina vitulina*) are upper-trophic level predators belonging to the phocid family (Teilmann & Galatius, 2018). They are commonly seen as sedentary remaining in coastal waters, although they can occasionally forage offshore in some study sites (Lesage et al., 2004). Throughout their geographic distribution, they inhabit a wide range of habitats, relying heavily on the availability and distribution of their prey in that specific environment (Bowen & Harrison, 1996). As a result, the harbor seal is often regarded as a generalist species with potentially individualistic foraging behavior. Many studies showed that they are benthic feeders with a diet consisting of a wide variety of prey, including various species of benthic and demersal fish, cephalopods, and crustaceans, but can occasionally forage on pelagic prey (Lesage, 1999; Sharples et al., 2009; Thompson, 1993).

In the Northwest Atlantic, harbor seals are generally found in small, isolated groups (Blanchet et al., 2021). They have been documented in the archipelago of Saint-Pierre-and-Miquelon (France) as far back as the 1940s (Templeman, 1957). Despite the absence of prior studies on the foraging behavior of harbor seals in this area, conflicts with recreational fisheries have been noted, and managers have expressed the need to better understand the trophic ecology of these harbor seals. Therefore, this study aimed to characterize the behavior of harbor seals around Saint-Pierre-and-Miquelon by identifying their habitat selection and investigating their foraging behavior at sea (diving behavior and spatio-temporal trends at sea) around the archipelago.

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Telemetry data were used to study habitat selection, foraging activity rhythm, and foraging behavior of harbor seals located at Saint-Pierre-and-Miquelon. Ten harbor seals (five females and five males) were captured in September 2019 and September 2020, and fitted with Satellite Relay Data Loggers developed by the Sea Mammal Research Unit (University of St Andrews, UK). The location data and detailed information of individuals are accessible on SEANOE (<https://www.seanoe.org/data/00799/91059/>). The capture method used was detailed in Vincent et al. (2005). The Satellite Relay Data Logger (SRDL) includes a GPS that attempts to obtain a location when at the surface, subject to a minimum interval of 20 min. In addition, the tag features a pressure sensor that enables the recording of the maximum depth, duration, and shape of each dive (<-1.5 m) as well as the time and depth delimiting the descent, bottom, and ascent phases (Photopoulou et al., 2015), and the duration of interdive surface periods. It also includes a wet/dry sensor and a 3-axis accelerometer operating at 25 Hz. The tag preprocesses the accelerometer data to calculate three parameters related to the behavior of the animal at a rate of 1 Hz. Pitch refers to the angle between the anteroposterior axis of the tag/animal and the horizontal plane. To isolate the orientation signal, a 0.2 Hz low-pass filter is applied. Swimming effort is calculated by summing the output of a 0.5–2 Hz filter applied to the lateral axis only. Prey capture attempts (PCA) are identified as peaks in the root-mean-square of triaxial jerk (rmsJerk), measured over an averaging window of 250 ms, as described by Ydesen et al. (2014). Given that the criterion for scoring a dive as a foraging dive is based on the behavior of only one captive seal, there is uncertainty associated with the proportion of dives classified as foraging. Thus, some caution is needed in the interpretation of our results.

Potential foraging dives were defined by the detection of at least one PCA. A binary response (foraging/non-foraging) was used, and statistical analysis was performed in R (R Core Team, 2021).

We studied the influence of the tide and the diurnal period on the activity rhythm of harbor seals using generalized linear mixed models (GLMMs). The dives were used as the response variable with values of 1 for foraging dives and 0 for nonforaging dives. The tide was treated as a continuous variable; diurnal period was used as a categorical variable with values being “Day” and “Night” (based on local time of dusk and dawn). The “individual” variable was used as a random effect to account for intraindividual autocorrelation and the model was selected using the Akaike information criterion (AIC; Akaike, 1973). The selected model highlighted an influence of the diurnal period on the foraging behavior of harbor seals (Table 1). Most foraging dives were carried out during the night (average 79.8% \pm 12.6% of foraging dives; Figure 1a). This pattern is consistent with findings in previous studies, where a significant number of seals have been observed foraging nocturnally (Bjørge, 1995; Lesage et al., 1999; Thompson et al., 1991). On the other hand, the models that included a tidal effect on foraging behavior were less parsimonious (Table 1). The distribution of foraging dives according to the tide remained relatively constant, which is not surprising, since the tidal range is only 1.5–2.4 m (Figure 1b). This finding agrees with behavioral observations by Renouf et al. (1981), who also suggested that there was no tidal effect on the at sea activity of harbor seals in Miquelon (Figure 1b; Table 1).

On average, harbor seals spent 88% \pm 3% (minimum–maximum: 84%–92%) of their time at sea and 23% \pm 6% of dives were considered foraging dives. We studied habitat selection using a pseudo absence method explained in Huon et al. (2021), and then fitted the data using a generalized additive mixed model (GAMM). The spatial data were estimated by interpolating the GPS location data (filtered following McConnell et al., (1992)) for each dive. The

TABLE 1 The different models on the activity rhythm selection of harbor seals at Saint-Pierre-and-Miquelon between 2019 and 2020 with Akaike’s information criterion (AIC) values.

Models	AIC	Δ AIC
Activity_rhythm_selection ~ DayNight + (1 + DayNight Seal)	20,960.91	0
Activity_rhythm_selection ~ DayNight + Tide + (1 + DayNight Seal)	20,962.91	2
Activity_rhythm_selection ~ Tide + (1 + DayNight Seal)	20,971.18	10.27

Note: The model in bold was considered the most parsimonious (Δ AIC <2).

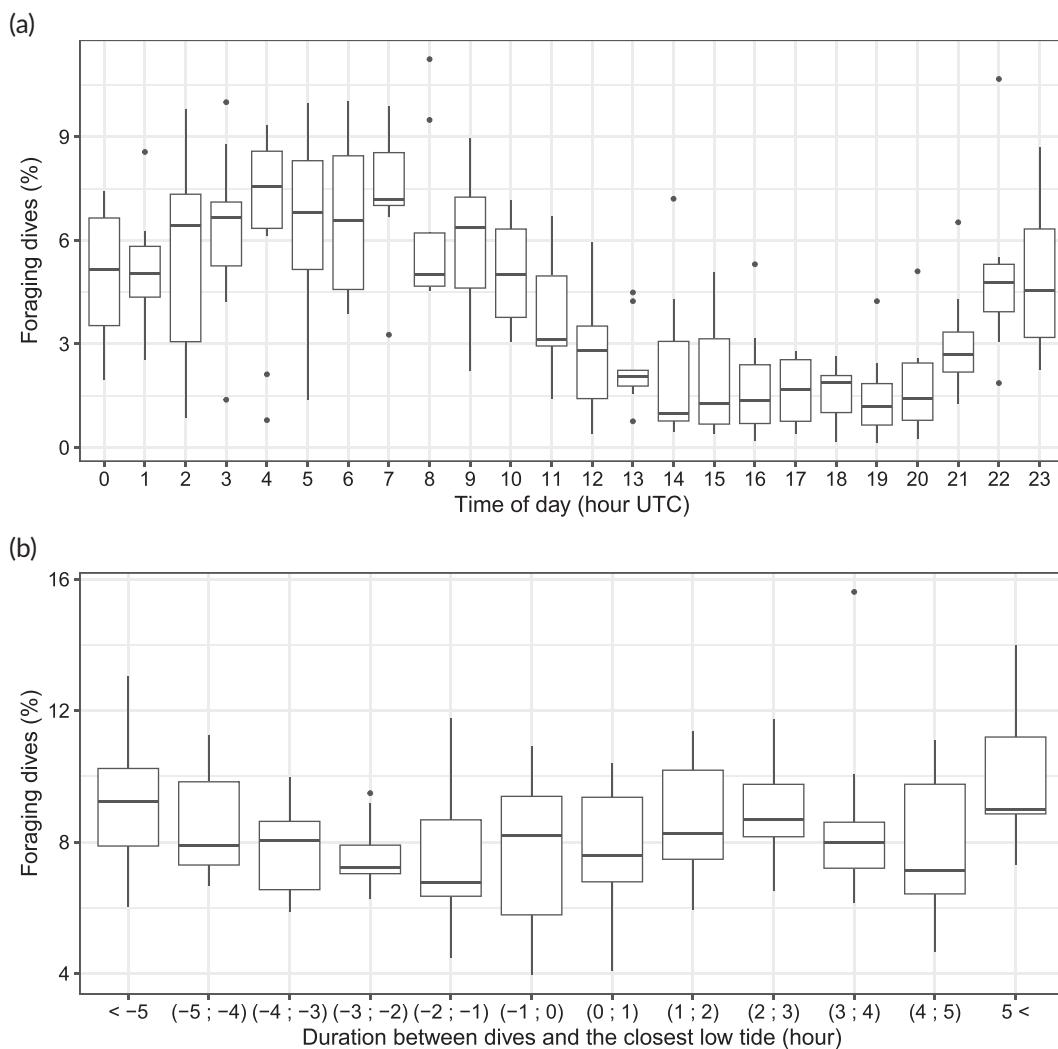


FIGURE 1 Distribution of foraging dives (sample size: $n = 10$) depending on temporal parameters. (a) The time of day in UTC time (local time in winter in Saint-Pierre-and-Miquelon is UTC-3). (b) The time between a foraging dive and the nearest low tide (negative if the dive occurs before low tide, positive if it occurs after low tide, and 0 at low tide).

TABLE 2 The different models on the habitat selection of harbor seals at Saint-Pierre-and-Miquelon between 2019 and 2020 with Akaike's Information Criterion (AIC) values.

Models	AIC	Δ AIC	Explained deviance
Habitat_selection ~ distance_haul-out + bathymetry + re (Seal)	3,835.87	0	78.9%
Habitat_selection ~ distance_haul-out + re (Seal)	4,192.64	356.77	76.9%
Habitat_selection ~ bathymetry + re (Seal)	10,543.54	6350.90,	41.9%

Note: The model in bold was selected (Δ AIC <2).

foraging dive locations, and the random points, generated using a pseudo absence method, were used as the response variable with values of 1 and 0 respectively. The bathymetry, the distance to the last haul-out and the distance to the shore were used as continuous variables. We calculated the correlation between each variable and found a strong correlation between distance to haul-out sites and distance to the coast ($r = 0.94$) but only a

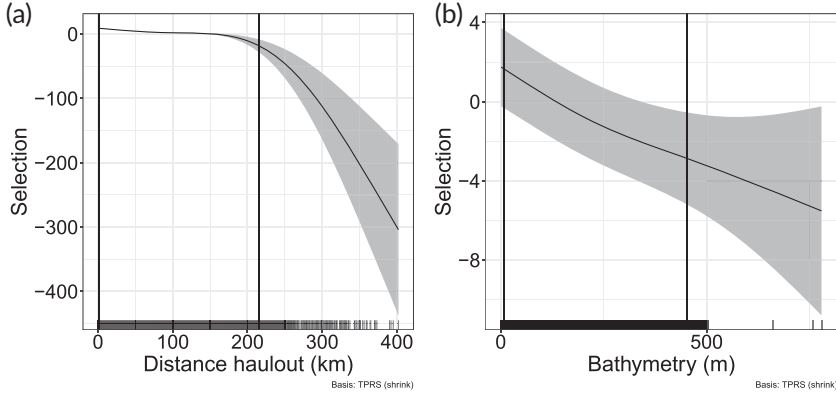


FIGURE 2 Effect of environmental variables on harbor seal spatial foraging selection around Saint-Pierre-and-Miquelon between 2019 and 2020. (a) Distance to haul-out, (b) Bathymetry. Vertical lines represent the 95% confidence intervals of the model.

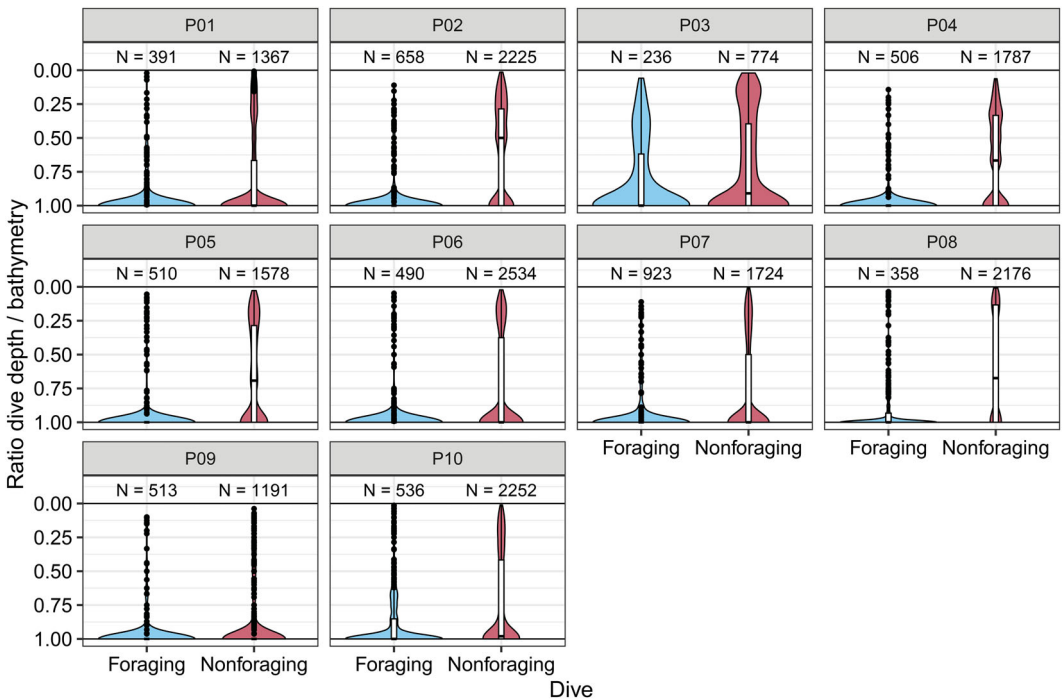


FIGURE 3 Distribution of foraging dives (blue) and nonforaging dives (red) according to the ratio between maximum dive depth and the bathymetry vertically aligned with the dive locations. Ratio of 0 corresponds to dives located at the surface and a ratio of 1 corresponds to dives located near the seabed. The number of dives specified for each category and individual.

moderate correlation between distance to haul-out sites and bathymetry ($r = 0.55$). Hence, we excluded distance to the coast from the models. The model with the smallest AIC value was selected (Table 2). Habitat selection was influenced by the distance to haul-out site and the bathymetry, with an explained deviance of 78.9%. The selected habitat of harbor seals was located between 0 and 100 km from their haul-out sites with 84% of foraging dives located within the first 20 km (Figure 2a). Lesage et al. (1999) also observed that harbor seals select areas close to their haul-out sites. Indeed, harbor seals are considered central place foragers, meaning that they tend to regularly return to their haul-out sites after each foraging trip (Orians & Pearson, 1979). As a result, they predominantly forage in the vicinity of their haul-out sites (Bajzak et al., 2013; Dietz et al., 2013; Huon et al., 2021; Lesage et al., 1999; Thompson et al., 1996). Bathymetry had a negative influence on habitat selection, in other words, habitat selection was highest in shallow waters (87% of foraging dives <100 m; Figure 2b). Previous studies on both sides of the Atlantic have consistently observed that harbor seals primarily forage at a maximum depth of 50 m (Bajzak et al., 2013; Huon et al., 2021; Lesage et al., 2004; Tollit et al., 1998). Around the archipelago, the bathymetry is highly variable, with depths exceeding 100 m at only 1 km from the coast. This may explain the difference of dive depth between this study and previous studies (Huon et al., 2021; Lesage et al., 2004; Tollit et al., 1998).

We then looked at the vertical distribution of foraging and nonforaging dives within the water column by using the ratio between maximum dive depth and the bathymetry (Figure 3). It varied between 0 and 1, 0 being close to the surface and 1 being at the seabed. The ratio averaged at 0.9 ± 0.2 for foraging dives versus 0.7 ± 0.4 for nonforaging dives, meaning that seals performed dives with a maximum depth closest to the seabed when foraging (U-shape dives), i.e., benthic foraging dives. Our findings are consistent with previous studies describing harbor seals as benthic feeders, preying on benthic and demersal prey (Lesage, 1999, Hammill et al., 2010) while occasionally feeding on pelagic prey (Sharples et al., 2009; Thompson, 1993).

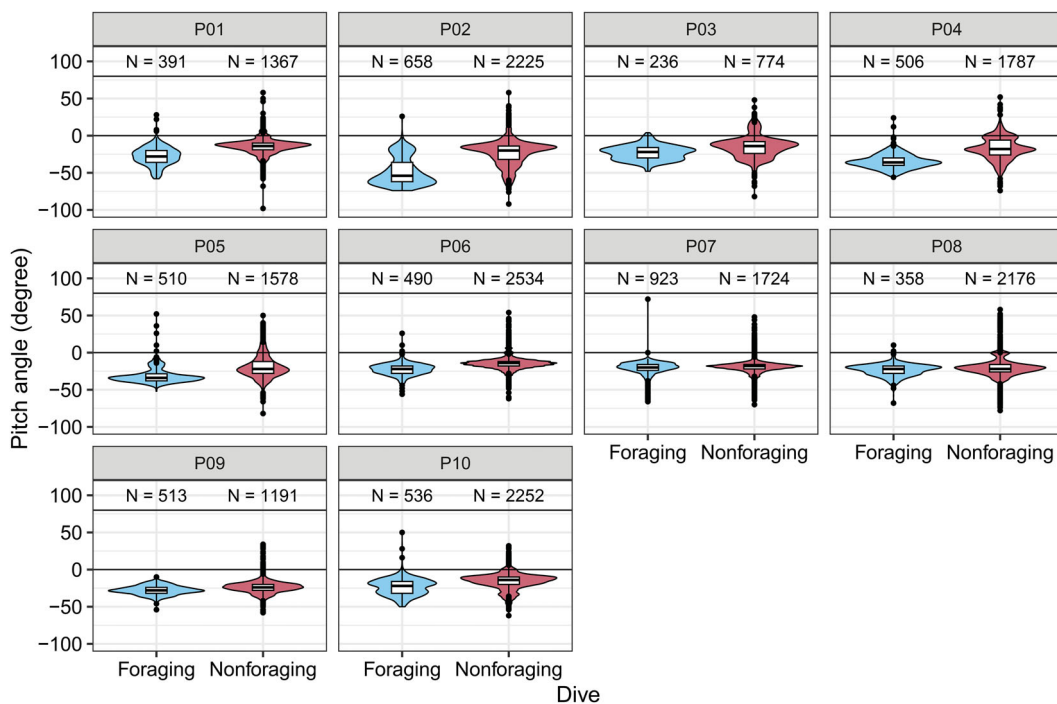


FIGURE 4 Distribution of foraging dives (blue) and nonforaging dives (red) according to the pitch angle (degree). The seal's head is oriented upwards when the pitch angle is positive and downwards when the pitch angle is negative. The number of dives specified for each category and individual.

The pitch angle (orientation of the head relative to the horizontal plan) was studied for foraging dives (blue) and nonforaging dives (red) of each seal (Figure 4). This parameter was negative for both categories, which means that the seal was facing downwards, as similarly detected on a previous study on harbor seals in the North Sea (Vance et al., 2021). Hence, seals have their head downwards while foraging, but also when searching for prey. These results are consistent with benthic behavior suggesting that the seals are searching for prey on the seabed (Lesage, 1999; Sharples et al., 2009; Thompson, 1993).

In conclusion, this study focused on the foraging behavior of harbor seals at Saint-Pierre-and-Miquelon. Like in the northeast Atlantic, harbor seals in this area are coastal, benthic feeders foraging mainly during nighttime (Björge, 1995; Huon et al., 2021; Thompson et al., 1991, 1996). This study represents the first study on the at-sea behavior of harbor seals at Saint-Pierre-and-Miquelon and the first study in 20 years surrounding Newfoundland. Furthermore, this research provides to wildlife managers information regarding the foraging areas and rhythms of harbor seals in this region.

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AUTHOR CONTRIBUTIONS

Skye Wynn-Simmonds: Conceptualization; data curation; formal analysis; methodology; writing – original draft. **Yann Planque:** Supervision; writing – review and editing. **Mathilde Huon:** Supervision; writing – review and editing. **Phil Lovell:** Methodology; software; writing – review and editing. **Cecile Vincent:** Conceptualization; funding acquisition; project administration; supervision; writing – review and editing.

DATA AVAILABILITY STATEMENT

The location data and detailed data on individuals presented in this study are publicly accessible. They can be found online on the SEANOE website (<https://doi.org/10.17882/91059>). Bathymetric data was obtained through Gebco (<https://www.gebco.net>) at a spatial resolution of 450 m. Tidal information was obtained for the whole study period on an hourly basis through the SHOM (<https://www.shom.fr>). The diurnal period was also determined using the sunrise and sunset times in Saint-Pierre-and-Miquelon during the monitoring period (<https://www.sunrise-and-sunset.com/fr/sun/saint-pierre-et-miquelon/saint-pierre>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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