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Seasonal foraging behavior of Weddell seals relation to oceanographic environmental conditions in the Ross Sea, Antarctica

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Abstract

Understanding the foraging behavior of marine animals is crucial for assessing their ecological significance and responses to environmental changes. In the context of Antarctica, marine animals face rapid and profound environmental changes related with global warming. However, our understanding of their responses remains limited owing to the formidable challenges inherent in conducting observations, particularly during the harsh austral winter months. In this study, we investigated the influence of changes in seawater properties and light conditions on the seasonal foraging behavior of Weddell seals (*Leptonychotes weddellii*) in the Ross Sea, Antarctica. We affixed 35 Weddell seals with CTD tags to record their locations and dive profiles, including depth, head acceleration, temperature, and salinity. We found that seals foraged more frequently in modified shelf water and ice shelf water compared to Antarctic surface water. This preference could be connected to greater food availability. Additionally, seals also dove to greater depths and displayed increased activity in capturing prey during daylight hours. This behavior may correspond to the diel vertical migration of pelagic prey in response to varying light conditions. Our findings suggest that Weddell seals have adjusted their foraging behaviors to adapt to spatial and temporal changes in oceanographic conditions. This highlights the importance of extrinsic factors in estimating their seasonal foraging behavior.

Keywords

Dive behavior, foraging habit, CTD, seal-tagging, bio-logging

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1. Introduction

In the Antarctic ecosystem, marine animals must adapt to environmental changes, such as changes in sea water conditions and light availability. Extrinsic factors play a vital role in their foraging success and food availability, particularly under the challenging conditions they face rapid changes such as oceanic warming, complex bathymetry and changing sea-ice covers (Speakman et al., 2020; Harcourt et al., 2021; Arce et al., 2022). Therefore, understanding how marine animals adapt to spatial and temporal shifts in oceanographic conditions is of utmost importance. Antarctic animals are currently experiencing rapid environmental change (Schofield et al., 2010; Doney et al., 2011). Glacier melting and the associated oceanic changes pose significant challenges for these animals (Huang et al., 2011; Ainley et al., 2015; Sahade et al., 2015; Hückstädt et al., 2020). As top and mesopredators, marine mammals serve as indicators of such changes. For example, calving on the Nansen Ice Shelf in the Ross Sea offers Adélie penguins (*Pygoscelis adeliae*) additional foraging habitats with potentially high prey availability (Park et al., 2021). Seal species, sea ice extent, and oceanographic conditions all influence seal movements and diving behaviors (Bailleul et al., 2007; Labrousse et al., 2021).

The Ross Sea is the world's largest (2.09 million km^2) Marine Protected Area (MPA) owing to its ecological significance (Brooks et al., 2021). It also stands as Antarctica's largest continental shelf region. Because of its limited human accessibility, the Ross Sea has been preserved as a primary habitat for predatory animals, maintaining a pristine ecosystem (Smith et al., 2012). Notably, 40% of the world's Weddell seals (*Leptonychotes weddellii*), 38% of Adélie penguins, and 26% of emperor penguins (*Aptenodytes forsteri*), along with a majority of South Polar skuas (*Stercorarius maccormicki*) in the Pacific sector, reside in the Ross Sea (La Rue et al., 2021; Smith et al., 2012). In the coastal polynyas of the Ross Sea, dense shelf water, a parent water mass of the Antarctic Bottom Water (AABW), is formed by strong polynyal activity (Rusciano et al., 2013; Yoon et al., 2020). This water mass contributes approximately a quarter to the total AABW production in Antarctica (Orsi et al., 1999; Orsi and Wiederwohl, 2009; Jendersie et al., 2018; Silvano et al., 2023). Hydrographic observations have been actively conducted in the Ross Sea since the 1950s, revealing changes in its marine environment resulting from recent climate shifts (Jacobs et al., 2002; Castagno et al., 2019; Yoon et al., 2020; Silvano et al., 2020; Thomas et al., 2020). According to these observations, hydrographic variations in the Ross Sea, including changes in the properties of shelf water, respond sensitively to air-sea interactions driven by katabatic winds and the advection of meltwater or sea ice from the Amundsen Sea (Rusciano et al., 2013; Castagno et al., 2019; Piñones et al., 2019; Yoon et al., 2020; Silvano et al., 2020). It is anticipated that climate-induced variations in the marine environment of the Ross Sea could significantly impact the behavior of marine mammals. However, our understanding of their responses remains limited due to logistical and technological challenges.

Recent advancements in technology, employing miniaturized CTDs, have enabled researchers to monitor sea water temperature and salinity (Kokubun et al., 2021; McMahon et al., 2021; Zheng et al., 2021). Deep-diving seals have mainly been used in oceanographic observation studies, with seal-tagging datasets being shared among researchers, particularly within the realm of polar ocean studies (Treasure et al., 2017). In addition to physical oceanographic data, behavioral data, such as diving patterns and acceleration serve as valuable indicators for estimating underwater foraging. Detailed feeding indices can be estimated from foraging diving depths and prey capture movements (Nachtsheim et al., 2019; Aubone et al., 2021; Viviant et al., 2010; Heerah et al., 2019; Volpov et al., 2015; Photopoulou et al., 2020).

Weddell seals are resident and primarily forage within the continental shelf of the Ross Sea (Goetz et al., 2023; Harcourt et al., 2021). Within this region, their primary diet consists of fish (notothenioids), supplemented by minor dietary components such as cephalopods and invertebrates (Burns et al., 1998; Dearborn, 1965; Goetz et al., 2017; Plötz et al., 1991). Ranked as the second deepest diving phocid species after the southern elephant seal (*Mirounga leonina*), Weddell seals have been used to collect oceanographic and behavioral data at depths exceeding 600 m (Heerah et al., 2013; Zheng et al., 2021). These seals endure energetically demanding periods during the austral spring and autumn (October–February) seasons, marked by colony formation for pup birthing, rearing pups, breeding, and molting, often leading to considerable weight loss (Wheatley et al., 2006; Wheatley et al., 2008; Harcourt et al., 2007). Although both male and female Weddell seals sporadically forage during the reproductive season, they are classified as capital breeders that rely on energy reserves accumulated before breeding (Goetz et al., 2017; Harcourt et al., 2007; Wheatley et al., 2008). Consequently, the overwintering period (February–September) may be critical for seals to replenish their body mass and condition.

In this study, we aimed to present the foraging behavior of Weddell seals according to the temporal changes in hydrographic factors using acceleration-combined CTD data obtained from seal-tagging observations during the Antarctic summer to winter (March to July) in the Ross Sea. By categorizing different water masses, we examined whether seals displayed preferences for specific water masses and if these preferences varied seasonally. In addition, we estimated foraging behavior in response to daylight conditions.

2. Materials and Methods

2.1 Study area and CTD deployment

We conducted seal-tagging in early February of 2021 and 2022 along the shores of Jang Bogo Station (74° 37′ 26″ S, 164°13′ 44″ E) and Gondwana Station (74° 38′ 7″ S, 164°13′ 18″ E) situated in Terra Nova Bay, Ross Sea, Antarctica. We approached Weddell seals on the shore to deploy 35 CTD-Satellite Relay Data Loggers (CTD-SRDLs) or 7 CTD-SRDLs with GPS (weight: 545 g, size:105 × 70 × 40 mm, SMRU, UK). Of the 35 CTD-SRDLs affixed to individuals (19 in 2021 and 16 in 2022), 33 were attached to their head, and two were secured to their backs. Additionally, seven CTD-SRDLs (five in 2021 and two in 2022) with GPS technology were attached to their backs. These devices are equipped with temperature, conductivity and pressure sensors, which collect hydrograhpic data. The sea water temperature was recorded with an accuracy of 0.005°C, pressure (depth) with an accuracy of 2 dBar, and conductivity with an accuracy of 0.01 mS/cm. Detailed information on the tagged individuals is provided in Supplementary Table 1.

Before deployment, we used an anesthetic (Zoletil 50; a combination of 125 mg tiletamine and 125 mg zolazepam in a 50 ml solution) administered through a blowpipe. Following the injection, we allowed for a sedative effect, maintaining a distances from the seals for over 10 min. Once the seals exhibited no response to the researcher’s approach, we proceeded to affix a CTD device to the seal’s head using Loctite glue (Loctite 401 in 2021 and Loctite 422 in 2022) or Araldite epoxy resin (Araldite 2012).

Prey capture attempts were estimated from the transmitted head acceleration data (referred to as “accelerometer processing,” as detailed in the SMRU Instrumentation manual 2023). The accelerometer mounted on this tag was initially configured to measure the three-axis acceleration at a frequency of 25 Hz. However, owing to limitations in network bandwidth, summarized information was transmitted in lieu of complete acceleration data. To summarize prey capture behavior, the total jerk (m s^{-3}), which is the time derivative of acceleration, was calculated using the method outlined by Ydesen et al. (2014). For each second, the tag compared the maximum value of the root-mean-square (RMS) jerk to a threshold of 250 m s^{-3} to ascertain the occurrence of a prey capture attempt (PrCA) within that specific second. If the RMS jerk exceeded the threshold for several consecutive seconds, it was considered a single PrCA event. The loggers divided each dive into three distinct segments. First, each dive was fitted to 12 broken-stick points (i.e., the depth at the first point below the dive threshold, 10 internal points, and the final point before the dive threshold). The descent segment commenced from the beginning of the dive and concluded at the first internal point, encompassing depths greater than 75% of the maximum depth. Similarly, the ascent segment was begun at the first internal point, where depths exceeded 75% of the maximum, and ending at the conclusion of the dive. The number of PrCA events for each segment was computed by the tags and subsequently transmitted through a satellite network system.

2.2 Hydrological data

2.2.1 Quality control for hydrographic data

Temperature and salinity profiles obtained from seal-tagging observations were quality controlled in accordance with procedures widely used in studies involving instrumented seals (Boehme et al., 2009; Roquet et al., 2011; Yoon and Lee, 2021). The procedure comprises three steps:1. tag-by-tag visualization; 2. pressure effect correction: 3. delayed mode calibration.

First, in Step 1, we checked reasonable ranges of temperature and salinity in Terra Nova Bay, Ross Sea, using historical (2014–2018) ship-based CTD data and ocean mooring (sourced from Yoon et al., 2020), and removed outliers from both the 2021 and 2022 seal-tagging data. We also determined the density inversion depths at this step; the data at the density inversion depths were removed and filled with linear interpolation. We found 500 (1630) irregular profiles out of the 3315 (7552) seal-tagging profiles recorded in 2021 (2022) through Step 1; therefore, we used 2815 (5922) profiles from Step 2.

Second, in Step 2, we corrected the pressure effect for the temperature and salinity profiles using at-sea experimental data (Roquet et al., 2011). The at-sea experiment constituted a ship-based calibration cast for CTD-SRDL sensors, involving the attachment of CTD-SRDL sensors to the ship’s CTD frame. Using at-sea experimental data, we derived linear relationships between temperature and salinity differences between for each CTD-SRDL sensor, and ship-based CTD data according to pressure (Roquet et al., 2011). Temperature and salinity biases were then removed from the entire profile of each tag according to the pressure calculated from each relationship (Roquet et al., 2011; Yoon and Lee, 2021). The calibration cast was conducted only before the 2022 deployment; therefore, Step 2 was conducted only for the 2022 seal-tagging data.

Finally, in Step 3, we implemented a delayed-mode calibration approach to correct the offsets in the temperature and salinity profiles. Here, we used the High Salinity Shelf Water (HSSW) method (Yoon and Lee, 2021), as an alternative to the LCDW method generally used for correcting seal data in the Southern Ocean (Roquet et al., 2011) because LCDW is rarely found in the continental shelf region of the Ross Sea (Budillon et al., 2011), and HSSW, characterized by a homogeneous layer (Yoon et al., 2020), offers a very stable absolute reference for estimating offsets of seal-tagging data in Terra Nova Bay (TNB). Approximately one month after the 2021 and 2022 deployments, we conducted full-depth CTD casts at 56 (43) stations within Terra Nova Bay, Ross Sea, from December 6 to 25, 2020 (March 15–19, 2022) aboard the ice-breaking research vessel ARAON (Fig. 2). We corrected the offsets of the seal-tagging data by comparing the salinity and temperature of HSSW within the TNB observed from ship-based CTD profiles with those from seal-tagging profiles. Potential density over 28 kg m^{-3} and potential temperature below −1.9 ℃ were used as criteria for HSSW (Yoon et al., 2020). As depicted in Figure 2, the temperature and salinity of the quality-controlled seal tagging-data demonstrated consistency with those derived from ship-based CTD data in Terra Nova Bay, Ross Sea.

Furthermore, to investigate the spatial and temporal variations in water masses within the continental shelf region of the Ross Sea, we classified these water masses based on potential temperature and potential density (Yoon et al., 2020). Potential temperature and potential density criteria for HSSW are defined as below −1.9 ℃, and over 28 kg m^{-3}, respectively. Potential temperature and potential density for ice shelf water (ISW) are defined as below −1.9 ℃, and below 28 kg m^{-3}, respectively. modified shelf water (MSW) is defined as colder (warmer) than −0.5 ℃ (−1.9 ℃), and denser than 27.74 kg m^{-3}. for modified circumpolar deep water (MCDW), potential temperature is defined as over −0.5 ℃ and potential density ranges between 27.74–27.88 kg m^{-3}. Antarctic surface water (AASW) is defined by temperatures colder than −0.5 ℃ and densities lighter than 27.74 kg m^{-3} (Fig. 2).

2.2.2 Kriging

A total of 8737 profiles were observed (2815 in 2021 and 5922 in 2022) and these were filtered through quality control procedures. To investigate the relationship between foraging behavior and the oceanographic environment, we calculated the physical characteristics of the water column at the maximum depth of each dive. Because the oceanographic and behavioral data obtained from the CTDs was not temporally matched, we employed the Kriging method, a commonly used technique for interpolating autocorrelated data, to calculate salinity and temperature (Oliver and Webster, 1990). Kriging was performed using the *gstat* package (Pebesma, 2004) in R, and the salinity and temperature at the maximum depth of each dive were obtained by calculating the 2-dimensional space of depth and time. Water masses were classified based on these values. To account for the spatiotemporal anisotropy, we scaled the values between 0 and 1 based on the maximum and minimum values, and multiplied the time values by 50. Separate Kriging processes were conducted for the 2021 and 2022 datasets, and the reliability of the results was confirmed via 5-fold cross-validation. The mean errors, root mean squared errors, and mean absolute errors were calculated (ME < 0.001 for salinity and temperature in 2021 and 2022; RMSE: 0.1119 and 0.1816 for salinity and temperature, respectively, in 2021 and 0.1305 and 0.1477 for salinity and temperature, respectively, in 2022; MAE: 0.0766 and 0.1090 for salinity and temperature, respectively, in 2021 and 0.0897 and 0.0827 for salinity and temperature, respectively, in 2022).

2.4 Dive data classification and filtration

We distinguished between benthic and pelagic seal dives. The bathymetric depth corresponding to each dive location was assigned using bathymetry data from IBCSO (IBCSO.org, Dorschel et al., 2022). Dives characterized by a submergence depth of 80% or more of the assigned depth were classified as benthic dives (Kokubun et al., 2021). The Python package *pvlib* (Holmgren et al., 2018) was used to determine the solar altitude at each dive location and time, with altitudes above 0 being categorized as daytime and altitudes below 0 as nighttime. Dives with bathymetric values greater than 0 were excluded to eliminate inaccurately recorded dives. Furthermore, dives with durations that were too short or long and depths that were too great (0 < dive duration < 5760 s, dive depth

< 906; Heerah et al., 2013), were also excluded. Dives characterized by speeds exceeding 5.1 m s^{-1} were also excluded (Davis et al., 2003).

2.5 Statistics

To investigate the factors influencing the feeding behavior of Weddell seals, we set the response variable as log-transformed prey capture attempts (log(PCA_BTM + 1)) and used dive type (benthic or pelagic), season (month), sex, water mass, and year as explanatory variables to determine the minimal model through backward elimination. First, we compared the full model containing all explanatory variables against the models with each variable systematically removed using a likelihood test; through this process, we eliminated variables deemed non-contributory. After repeating this process, we obtained a parsimonious model containing only the important variables. Additionally, we compared all possible models created using different combinations of explanatory variables by comparing their Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values and obtained the best model with the smallest AIC and BIC values (Supplementary Tables 2 and 3). The explanatory variables of the best model obtained using the three methods (backward elimination, AIC, and BIC) were consistent. After finding the minimal model, we conducted post-hoc tests using the *multcomp* R package (Hothorn et al., 2008) to investigate differences in the categorical variables included in the minimal model (season and water mass). We then tested whether dive depth, number of dives, and prey capture attempts were determined by day and night to examine diurnal patterns. Throughout this process, we created a linear mixed-effects model using the *nlme* R package, in which we set each individual identity as a random effect and included a temporal autocorrelation term.

3. Results

The telemetry data revealed that the Weddell seals in this study dispersed from the tagged region (near Jang Bogo Station; 62.2° S, 58.8° W) and traveled throughout continental shelf regions in the Ross Sea (Fig. 1). Among the 48,799 dives observed, 9,192 were categorized as benthic dives and 39,607 were pelagic.

Seal CTD sensors have been used to observe five water masses in the continental shelf region of the Ross Sea: AASW, MCDW, MSW, ISW, and HSSW (Fig. 2; Orsi and Wiederwohl, 2009). When compared to the ship-based CTD data collected in the TNB during the austral summer of the same year, the seal tagging data showed a wider range of temperature and salinity of AASW(Fig. 2). The wide range of temperature and salinity values of the AASW represents its seasonal variation, being icy cold and fresh during the sea ice melting period (mainly austral summer), and subsequently transitioning to being warm and saline due to latent heat release and brine rejection during the sea ice formation period (mainly austral winter). The lower boundary depth of the AASW exhibited a deepening trend from February onwards, eventually aligning with the lower boundary depth of the MSW by May (Fig. 3). These results support the notion that our seal-tagging data captured the increase in the density of AASW over the period between austral summer and winter.

Moreover, the presence of MCDW was more discernable in the seal-tagging profiles compared to the ship-based CTD data obtained from the TNB, despite its limited occurrence (only 107 depths of 8,737 profiles) (Fig. 2; Supplementary Fig. 1). This prominence arises because of seals diving into the northwestern part of the continental shelf region of the Ross Sea (Drygalski and Joides troughs), where MCDW is known to flow in (Jendersie et al., 2018; Supplementary Fig. 1). Furthermore, the ISW observed across the continental shelf region of the Ross Sea demonstrates a wider salinity range than the ISW observed in the TNB. This expansion can be attributed to the influence of ISW sourced from the McMurdo and Ross Ice Shelves (Fig. 2) (Budillon et al., 2011). In both 2021 and 2022, HSSW were mainly observed in the western part of the continental shelf region of the Ross Sea (Supplementary Fig. 1), proving that HSSW formed in the polynyas of the continental shelf region flows to the continental shelf break region along the Victoria Land (Silvano et al., 2020).

The Weddell seals tagged in this study exhibited distinct diving behaviors across months. Figure 4 and Figure 5 (a) illustrates the seasonal changes in dive depth. The dive depth seems to show a trend of increasing from March to July, whereas the number of PrCA events appears to decrease in June and July compared to March and April. When considering diving depth ($p < 0.001$; log likelihood ratio test between the best model and a model excluding the variable “season”), the shallowest dives were undertaken in April, whereas the deepest diving occurred in July (197 ± 134 m in April, 270 ± 158 m in July; mean ± standard deviation) (Fig. 3, Table 1, 3). In terms of PrCA ($p < 0.001$; log likelihood ratio test between the best model and a model excluding the variable “season”), the highest number was observed in April, whereas the lowest occurred in June (3.48 ± 5.24 in April, 2.43 ± 3.77 in June) (Fig. 4 (a), Table 2, 4). Additionally, PrCA values varied based on water mass and dive type (benthic or pelagic) ($p < 0.001$ for both; log likelihood ratio test between the best model and a model excluding the variables “water mass” and “dive type”) despite the relative proportion of benthic dives not being predominant (9192 out of a total of 48799 dives, Fig. 4(c)). Based on our water mass definition, Weddell Seals performed many dives in MSW, and dives with a high number of PrCAs were also frequently observed in MSW. The kernel density plots of distribution of dives on a TS-diagram are shown in Supplementary Figure 3. Notably, Weddell seals displayed a higher number of PrCA events in MSW and ISW compared to AASW (an additional 0.24 and 0.22 in PrCA per dive for MSW and ISW, respectively, compared to AASW). Conversely, there were no significant differences between HSSW and the other water masses (Tables 2 and 5). Our seals had 0.26 more PrCA ($p < 0.001$) during benthic dives than in pelagic dives (Fig. 4 (b), Table 2).

Weddell seals demonstrated different diving behaviors between daytime and nighttime, delineated by solar altitude. During daylight hours, seals dived an average of 79.8 m deeper and had a higher proportion of benthic dives compared to nighttime (Fig. 5 (a) and (d), Table 6). Additionally, seals demonstrated higher foraging activity during the daytime, with an average of 2.97 foraging attempts per dive, compared to 2.12 attempts during the nighttime (Fig. 5 (b), Table 6). Interestingly, there was no discernible difference in the number of dives between the day and night (Fig. 5(c), Table 6).

4. Discussion

In this study, we observed a distinct pattern in the diving behavior of Weddell seals: shallower dives were observed in April and deeper diving behavior was observed in July. Additionally, foraging frequencies were the highest in April and lowest in June. The detected water masses in the attached CTD were MCDW, MSW, ISW, AASW, and HSSW. Among these, Weddell seals exhibited a preference for MSW and ISW over AASW as their foraging habitats. In contrast, MCDW was rarely detected, and no significant preference differences were found between HSSW and the other water masses concerning foraging activity. Furthermore, a higher number of PrCA events was observed during benthic dives in contrast to pelagic dives. Finally, a diel diving pattern among the seals was observed, with variations in the proportion of benthic dives, foraging frequencies, and diving depths between day and night.

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Our results conclusively illustrate that a seasonal shift exists in diving depth and the number of PrCAs per dive. This phenomenon can be attributed to fluctuations in oceanographic and light conditions. Notably, Weddell seals exhibited a preference for MSW or ISW over AASW during their foraging dives. As the lower boundary of the AASW shifted downward during June and July, it is plausible that the seals engaged in progressively deeper dives during the winter months to follow the MSW or ISW. Secondly, a seasonal decrease in sunlight could limit prey accessibility, particularly pelagic fish species. The number of daylight hours in this region significantly decreased from March to July. Based on data from Jang Bogo Station, on 1 March, the duration of daylight was over 16 h with a meridian altitude of over 23°, but the onset of the Polar night in early May led to the sun remaining below the horizon. In the Ross Sea, the euphotic zone, where sufficient light for photosynthesis is available, is situated at a depth of 34 ± 13 m in spring, 26 ± 9 m in summer (mean ± standard deviation), and within a range of 14–66 m (range) in winter (Smith et al., 2013, Fabino et al., 1993). Below the euphotic zone lies the dysphotic zone, where light is present but not sufficient for the process of photosynthesis to occur. Based on the findings of Sipler and Connelly (2015), the dysphotic zone in the Ross Sea extends to a depth of 170 m. Notably, Antarctic silverfish and holopelagic prey in the Ross Sea are found at depths of 0–700 m (De Witt et al., 1990), and their prey abundance is high in the upper water layers (50–200 m, Mintenbeck, 2008). This implies that Antarctic silverfish may inhabit within the euphotic and dysphotic zones. Weddell seals have been reported to use light and other senses, including vibrissal sensations, for swimming, detecting, and catching prey (Wartzok and Davis, 1992, Davis et al., 2004). Therefore, when sunlight is available, Weddell seals employ a combination of visual and other sensory inputs to capture pelagic or cryopelagic prey. Conversely, when sunlight is not available, or benthic prey are target, they must solely rely on non-visual sensory inputs for effective foraging. The diminished light conditions experienced in June and July posed challenges for seals to locate prey, thereby leading to a decrease in PrCA events per dive and an increase in diving depths during these months compared to March.

The seasonal changes in diving behavior likely reflect corresponding seasonal changes in the distribution or composition of prey. Previous studies analyzing the diet of Weddell seals in the Ross Sea through scat or stomach contents have highlighted Antarctic silverfish as the primary pelagic prey consumed by Weddell seals across all seasons (Burns et al., 1998; Dearborn et al., 1965; Plötz et al., 1991; Goetz et al., 2017). Therefore, the increased dive depth of Weddell seals may suggest that the distribution of Antarctic silverfish, their main prey, and only holopelagic fish in the Ross Sea shifts deeper as winter approaches. Although, the seasonal variations in the vertical distribution of Antarctic silverfish remain unknown, Antarctic krill (*Euphausia superba*), one of their primary food sources, may migrate to deeper waters during winter when the sea surface is covered with ice and food in the upper waters becomes scarce (Smidt et al., 2011; Meyer et al., 2017). This could imply that Antarctic silverfish may migrate to deeper waters as winter approaches. It is recognized that as Antarctic silverfish mature, they tend to inhabit deeper waters (La Mesa and Eastman, 2012), suggesting a shift in the prey composition towards larger and deeper-dwelling adult Antarctic silverfish as winter approaches. Another plausible factor behind this seasonal shift in diving behavior could be a corresponding shift in dietary preferences, involving greater consumption of benthic fish compared to pelagic or cryopelagic fish. Additionally, seasonal variations in interspecific competition, particularly involving emperor penguins, another apex predator species in the Ross Sea year-round (Smith et al., 2012; Burns and Kooyman, 2015), could affect the foraging behavior of Weddell seals. In winter, emperor penguins must actively seek sustenance to nurture their offspring, a necessity that potentially intensifies interspecific competition with Weddell seals (Burns and Kooyman, 2001). Given that the diving capacity of emperor penguins is lower than that of adult Weddell seals (Kooyman and Kooyman, 1995; Kooyman et al., 1980; Burns, 1999), Weddell seals may forage at greater depths to minimize interspecific competition.

Our seal CTD data revealed a dynamic alteration in the vertical distribution of water masses in accordance with the seasons. During early austral fall, the water columns within the Ross Sea are clearly structured, with HSSW, MSW, and AASW from the bottom up; however, this stratification weakens as winter advances; strong mixing owing the influence of winds coupled with active sea ice formation at the surface serve to diminish the density difference between AASW and shelf water, effectively erasing their distinct boundaries (Fig. 3). Additionally, ISW exists near the ice shelves instead of spreading out to the central part of the continental shelf region. This behavior might be associated with the relatively lower rates of basal melt and meltwater flux of ice shelves in the Ross Sea (Supplemetnary Fig. 1; Rignot et al., 2013; Rignot et al., 2019).

Weddell seals exhibited more frequent feeding behavior in MSW and ISW compared to AASW and they rarely ventured into MCDW. These findings might reflect the inherent nutrient composition of each water mass. MSW is formed through the mixing of shelf water with surrounding water masses, including MCDW, within the continental shelf region. MCDW plays a crucial role in heat and nutrient cycling in the Southern Ocean because it is warm and nutrient-rich (Smith et al., 2012; Kutska et al., 2015; Gerringa et al., 2020). MCDW contain significantly higher concentration of macro-nutrients and also contributes to the basal melt of ice shelves, which may in turn increase primary production. However, the dissolved oxygen (DO) levels in MCDW are notably low, falling below 5 ml/L (Jenkins et al., 2018; Yoon et al., 2020). This is lower than the critical threshold of oxygen concentration for krill, implying that the prey availability for seals in MCDW would be limited (Brierley et al., 2010; Kils, 1979). However, MSW may contain a high amount of nutrients from MCDW and sufficient oxygen contents (Orsi and Wiederwohl, 2009; Smith et al., 2021). According to ship-based CTD observations with SBE43 DO sensor values in TNB during the austral summer 2021 and 2022, it was found that the DO of MSW was over 6.5 ml/L. ISW is a water mass formed by the melting of ice shelves and is characterized by a potential temperature below the freezing point. This water mass can harbor essential nutrients, such as iron, which may be present on ice shelves; thus, potentially making ISW a nutrient source (Sedwick and DiTullio, 1997; Smith et al., 2014). Nutrient-rich hydrographic conditions may be related to the high prey availability. In other regions, Weddell seals exhibit increased foraging behavior under nutrient-rich conditions (Heerah et al., 2013; Nachtsheim et al., 2019; Kokubun et al., 2021). Moreover, ISW also has relatively higher oxygen, for example, DO sensor values of ISW in TNB during the austral summer 2021 and 2022 are higher than 6.4 mL L^{-1}. AASW is generally deficient in nutrients by vigorous biological processes despite the high DO. Therefore, Weddell seals could have a higher number of PrCA events in MSW and ISW than AASW and MCDW because they satisfy both rich-nutrients and high-DO characteristics.

Although only 18.8% of all dives were categorized as benthic dives, a greater number of foraging attempts were observed during these dives. From an energy-efficiency perspective, the costs associated with the diving behavior of Weddell seals increase as the duration of their dives increases. In particular, dives lasting longer than 23 min entail additional anaerobic costs. Despite the substantial energetic costs associated with prolonged dives, the benthic zone serves as a habitat for numerous sizeable prey species weighing over 1 kg, including the Antarctic toothfish and icefish (La Mesa, 2004; Goetz et al., 2017). Hence, Weddell seals can reap substantial benefits in the benthic zone. This dynamic could result in a higher frequency of foraging attempts per dive during

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benthic dives compared to than pelagic dives for larger prey. However, only 18.8% of all dives were categorized as benthic dives. Furthermore, PrCA instances were estimated by tallying the occurrences of jerks (the temporal derivatives of acceleration) surpassing the predefined threshold (250 m s^{-3}), as recorded on the bio-logger attached to the head of the Weddell seal. Benthic prey in the Ross Sea predominantly comprises hefty fish, such as Icefish or Antarctic toothfish, and other fish that are heavier than the Antarctic silverfish, the only holopelagic fish in the Ross Sea whose adult form exceeds 50g. Diving predators require increased mobility to effectively handle larger prey, resulting in higher variance in behavioral data, including acceleration (Volpov et al., 2015, Watanabe and Takahashi, 2013). Weddell seals also handle large prey such as Antarctic toothfish, the flesh part of which are exclusively consumed by them (Ainley and Sniff, 2009; Davis et al., 2004; Goetz et al., 2017). Therefore, this study acknowledges the likelihood that foraging frequency may have been overestimated during the instances when Weddell seals handling larger prey.

Differences in diving behavior between the day and night were also observed. Although the total number of dives did not differ between the day and night, Weddell seals performed deeper dives during the day, marked by a higher incidence of benthic dives and PrCA events. The variation in diel patterns of diving depth could potentially be attributed to the vertical migration behavior of pelagic prey. This migration phenomenon is well-documented among pelagic fish species, including Antarctic pelagic fish, which exhibit a diel vertical migration pattern. Such fish dive to greater depths as the amount of light at the surface increases, effectively reducing their vulnerability to visual predators that rely on light to locate and pursue prey (Childress, 1995; Fuiman et al., 2002; Hays, 2003; Robison, 2003; Sutton, 2013). Weddell seals also rely on their visual senses to detect prey (Davis et al., 1999). Thus, these seals can dive to greater depths during the day, corresponding to the migratory behavior of pelagic prey in the Ross Sea. Additionally, the energy expenditure associated with hunting pelagic prey may increase with deeper dives during the day, whereas the cost of hunting benthic prey may decrease as the amount of light increases. Therefore, the proportion of benthic dives is inclined to rise during the day. As visual predators, Weddell seals are better equipped to seek and pursue prey in the daytime compared to nighttime, when their senses other than sight are predominantly employed. Consequently, the number of PrCA events increased during the daylight hours.

5. Conclusion

Concurrently analyzing hydrographic and behavioral data from the Ross Sea revealed seasonal variations in the foraging behavior of Weddell seals, closely linked to shifts in oceanographic environmental conditions (Fig. 6). The seals demonstrated a preference for water masses, which could potentially be both nutrient-rich and high-DO, and exhibited distinct foraging strategies depending on the light conditions during the day and night. This study demonstrates that Weddell seals adjust their foraging behavior, adapting both spatially and temporally in response to environmental factors. Over the last several decades, the hydrography of the Ross Sea has undergone considerable changes with an increasingly warming world (Castagno et al., 2019; Yoon et al., 2020; Silvano et al., 2020; Thomas et al., 2020). This suggests a continuous process of adaptation in the foraging behaviors of marine mammals, including Weddell seals, as they navigate changing marine environments. Therefore, it is necessary to continuously monitor the foraging behavior of marine mammals in the Ross Sea. Our findings serve as a baseline and establish a foundational understanding for future research, particularly concerning the impact of marine environmental changes on the ecosystem of the Ross Sea MPA.

Data Availability

The behavioral and oceanographic data related to this study can be accessed at the Korea Polar Data Center (KPDC) website, kpdc.kopri.re.kr. The datasets are available under the following DOIs:

- https://dx.doi.org/doi:10.22663/KOPRI-KPDC-00002402.1
- https://dx.doi.org/doi:10.22663/KOPRI-KPDC-00002401.1
- https://dx.doi.org/doi:10.22663/KOPRI-KPDC-00002077.1
- https://dx.doi.org/doi:10.22663/KOPRI-KPDC-00001658.4

Author Contributions

This part will be filled out before submission.

Competing Interests

The authors declare no competing interests.

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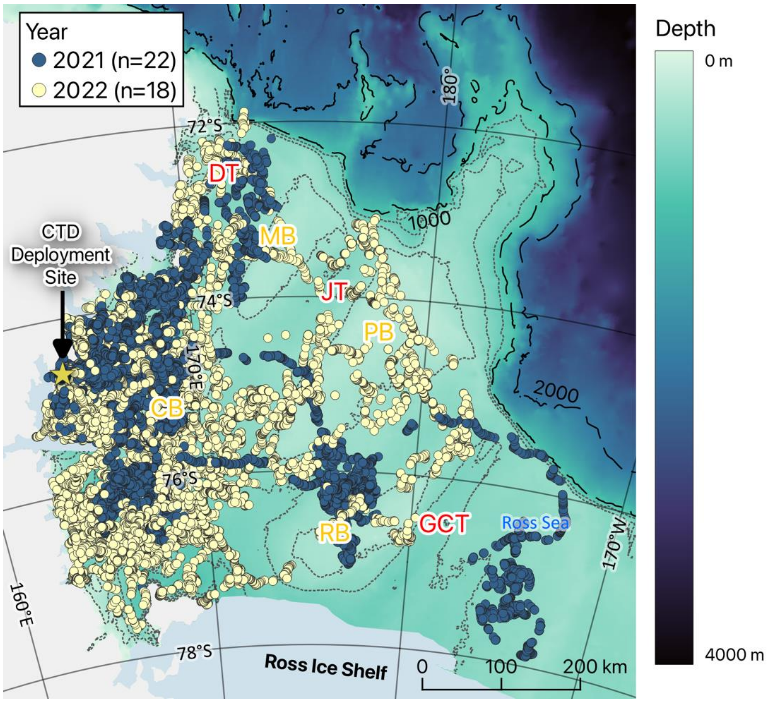


Figure 1. **Dive locations of seals tagged at Terra Nova Bay in the Ross Sea (blue dots indicated seal ARGOS locations in 2021 and yellow dots indicate the locations in 2022).** The abbreviations CB, MB, PB, RB, DB, DT, JT, GCT mean Crary Bank, Mawson Bank, Pannell Bank, Ross Bank, Drygalski Trough, Joides Trough, Glomar Challenger Trough, respectively. The dashed line represents the shelf break (at depths of 1000 and 2000 m), while the dotted line represents bathymetry at 200 m intervals (200-800 m).

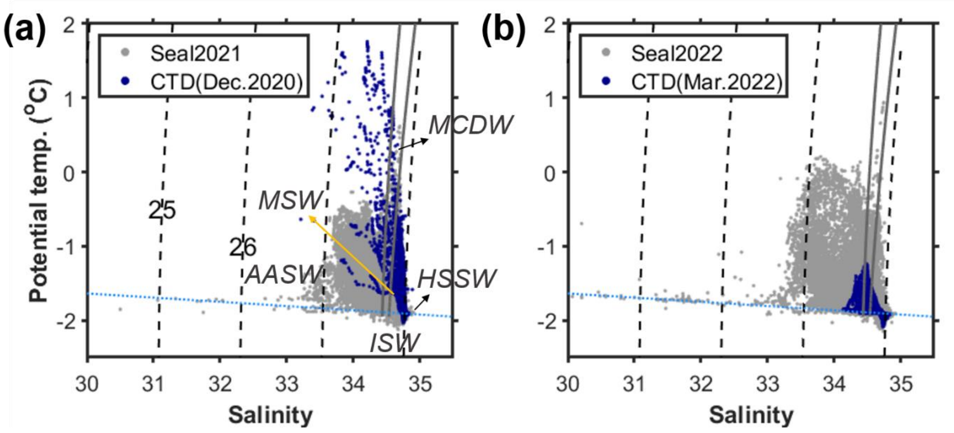


Figure 2. *θ*–*S* diagram from seal tagging data and ship-based data (a) *θ*–*S* diagram for seal tagging data obtained during 2021 (gray) and ship-based CTD data recorded from 6 to 25 December, 2020 (blue). The dashed black lines indicate isopycnals (kg m^{-3}), and solid gray lines represent 28 and 28.27 kg m^{-3} neutral density surfaces. The dotted blue line indicates the surface freezing point depending on the salinity. The abbreviations AASW, MCDW, MSW, ISW, and HSSW correspond to Antarctic surface water, modified circumpolar deep water, ice shelf water, and high salinity shelf water, respectively; (b) Depicts the same information as. panel (a), but for seal tagging data obtained during 2022 and ship-based CTD data recorded from 15 to 19 March, 2022.

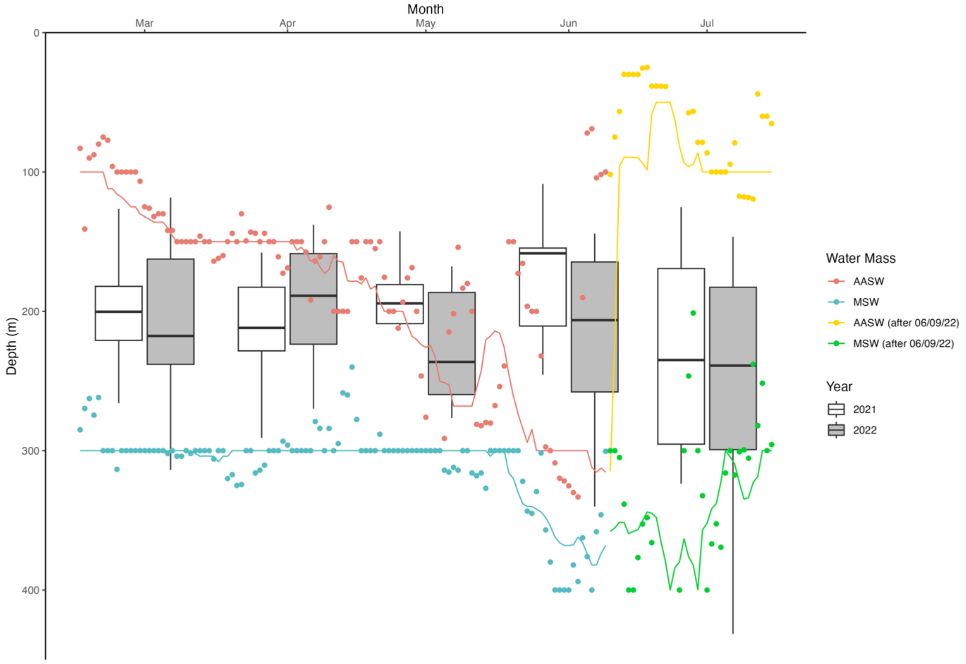


Figure 3. Temporal variation in Weddell seal dive depths for 2021 and 2022, with lower boundaries of Antarctic Surface Water (AASW) and Modified Shelf Water (MSW) based on calibrated data from 2022 only. White and grey boxes indicate diving behaviors in 2021 and 2022, respectively, showing a tendency for deeper dives as austral winter approaches. Curves represent the 95th percentile of profiles within a 10-day window, while dots indicate single-day data. Green and blue represent the lower boundaries of MSW and red and yellow represent the lower boundaries of AASW, respectively. Data after June 9 are color-coded differently (in green and yellow) due to low reliability from limited observations (3,446 out of 65,013 total).

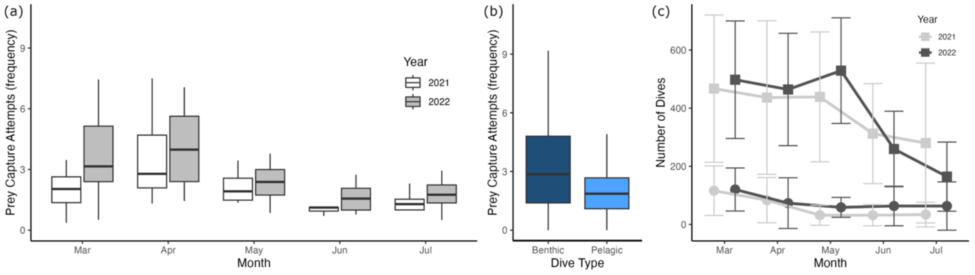
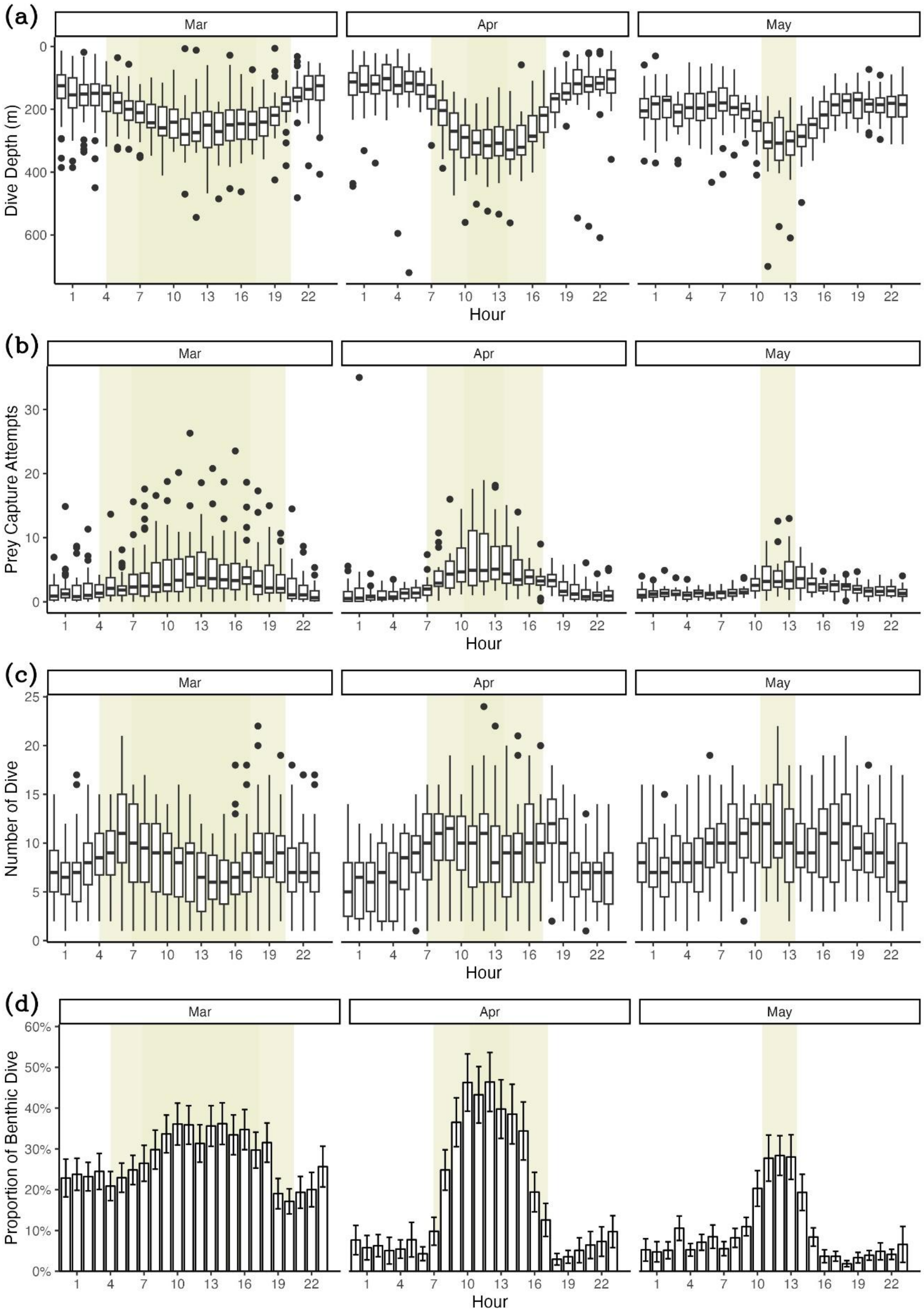
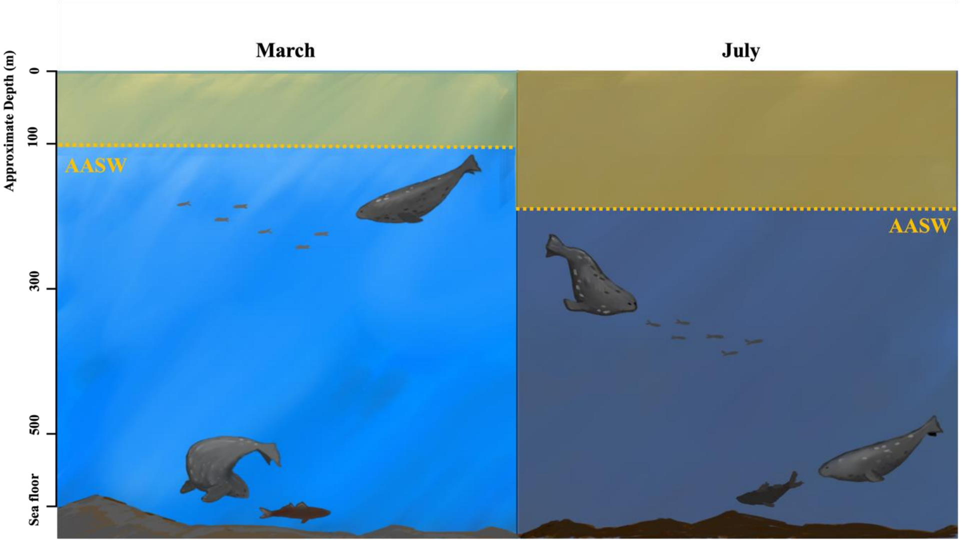


Figure 4. Prey capture attempts (PrCA) among (a) seasons (month) and (b) dive types (benthic or pelagic) and seasonal change of the dive frequency. Prey capture attempts were highest in April and lowest in June. Prey capture attempts were higher in benthic dives compared to pelagic dives. The dark blue box indicates the number of PrCA events per dive during benthic dives, whereas the lighter blue box represents the same statistic during pelagic dives. In (c), curves with square marker represents number of total dives and curves with circle marker represents the number of benthic dives of each month. The error bars represent the mean ± standard deviation.



715 **Figure 5. Diel variation in diving behaviors.** (a) dive depth, (b) prey capture attempts, (c) number of dives, (d) proportion of benthic dives. The yellow-shaded area denotes the duration of sunlight exposure during the day. The lighter yellow shaded area indicates the period of daylight at the beginning of the month, while the darker yellow shaded area represents the period of daylight at the end of the month.



720 **Figure 6. Schematic summary of seasonal variation in oceanographic conditions and foraging behaviors.** The area shaded in yellow represents the AASW, and the dashed line indicates the lower boundaries. In March, AASW is positioned at shallower depths, whereas in July, the AASW shifts to deeper locations. AASW is a water mass less preferred by Weddell seals, possibly due to reduced prey availability, which in turn appears to result in deeper dive depths during pelagic dives for Weddell seals.

725

Table 1. Best model for dive depth AIC, BIC, and backward elimination approaches revealed that sex, season (month), and year are important variables for predicting prey capture attempts.

Dive Depth ~ Sex + Season + Year + (1|IID) + corAR1(1|IID)			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	198.21536	185.47 – 210.96	**<0.001**
Sex [Male]	18.09773	3.32 – 32.88	0.2303
Season [Apr]	-10.04762	-13.37 – -6.73	**0.0025**
Season [May]	7.68411	4.17 – 11.2	**0.0287**
Season [Jun]	7.36096	2.95 – 11.77	0.0952
Season [Jul]	40.2231	34.81 – 45.64	**<0.001**
Year [2022]	1.98895	-12.7 – 16.67	0.8932
N $_{\text{IID}}$	33		
Observations	48799		

730 **Table 2. Best model for prey capture attempts** AIC, BIC, and backward elimination approaches revealed that water mass type, season (month), and dive type (benthic or pelagic) are important variables for predicting prey capture attempts.

log(PCA_BTM + 1) ~ Water Mass + Dive Type + Season + (1|IID) + corAR1(1|IID)			
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.8	0.54 – 1.05	**<0.001**
Water Mass [ISW]	0.04	-0.20 – 0.29	0.735

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Water Mass [MSW]	0.07	-0.18 – 0.31	0.6
Water Mass [AASW]	-0.18	-0.42 – 0.07	0.156
Dive Type [Benthic]	0.26	0.24 – 0.28	**<0.001**
Season [Apr]	0.1	0.06 – 0.14	**<0.001**
Season [May]	-0.05	-0.10 – -0.01	**0.014**
Season [Jun]	-0.25	-0.31 – -0.20	**<0.001**
Season [Jul]	-0.1	-0.17 – -0.03	**0.004**
N_{IID}	33		
(Intercept)	0.8	0.54 – 1.05	**<0.001**
Observations	48799		

Table 3. Post hoc (Tukey HSD) test for "Season" variable included in the best model for dive depth

Group 1	*Group 2*	*Mean Difference (Group 2 - Group 1)*	*Standard Error*	*Z value*	*Pr(>|z|)*
Mar	Apr	-10.0476	3.3225	-3.024	**0.0199**
	May	7.6841	3.5134	2.187	0.1773
	Jun	7.361	4.4112	1.669	0.443
	Jul	40.2231	5.4133	7.43	**<0.001**
Apr	May	17.7317	3.5504	4.994	**<0.001**
	Jun	17.4086	4.4684	3.896	**<0.001**
	Jul	50.2707	5.4782	9.177	**<0.001**
May	Jun	-0.3232	4.4502	-0.073	1
	Jul	32.539	5.4637	5.956	**<0.001**
Jun	Jul	32.8621	5.919	5.552	**<0.001**

Table 4. Post hoc (Tukey HSD) test for "Season" variable included in the best model for prey capture attempts

Group 1	*Group 2*	*Mean Difference (Group 2 - Group 1)*	*Standard Error*	*Z value*	*Pr(>|z|)*
Mar	Apr	0.09689	0.02044	4.74	**< 0.001**
	May	-0.07335	0.02193	-3.344	**0.00692**
	Jun	-0.27982	0.02752	-10.169	**< 0.001**
	Jul	-0.13716	0.03341	-4.105	**< 0.001**
Apr	May	-0.17024	0.02186	-7.787	**< 0.001**
	Jun	-0.37671	0.02767	-13.614	**< 0.001**
	Jul	-0.23405	0.03362	-6.961	**< 0.001**
May	Jun	-0.20647	0.02754	-7.497	**< 0.001**
	Jul	-0.06381	0.03349	-1.905	0.30481

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Jun	Jul	0.14266	0.0366	3.897	**< 0.001**

Table 5. Post hoc (Tukey HSD) test for "Water Mass" variable included in the best model for prey capture attempts

Group 1	*Group 2*	*Mean Difference (Group 2 - Group 1)*	*Standard Error*	*Z value*	*Pr(>|z|)*
HSSW	ISW	0.04	0.12	0.34	0.98
	MSW	0.07	0.12	0.53	0.94
	AASW	-0.18	0.12	-1.42	0.44
ISW	MSW	0.02	0.02	1.47	0.40
	AASW	-0.22	0.02	-10.72	**<0.001**
MSW	AASW	-0.24	0.01	-17.25	**<0.001**

Table 6. Regression analyses of dive parameters (dive depths, prey capture attempts per dive, number of dives per day) with respect to the presence of sunlight (day or night).

Dive Depth ~ Day/Night

Predictors	*Estimates*	*CI*	*P*
(Intercept)	172.47	155.94 – 189.00	**<0.001**
Day_boolTRUE	79.78	76.16 – 83.40	**<0.001**
N_{IID}	33		
Observations	30823		

log(Prey Capture Attempts + 1) ~ Day/Night

Predictors	*Estimates*	*CI*	*P*
(Intercept)	0.75	0.65 – 0.85	**<0.001**
Day_boolTRUE	0.34	0.31 – 0.37	**<0.001**
N_{IID}	33		
Observations	30823		

Number of Dives ~ Day/Night

Predictors	*Estimates*	*CI*	*P*
(Intercept)	19.00	18.06–19.94	**<0.001**
is_daytimeTRUE	-1.43	-2.17—-0.7	0.051
N_{IID}	33		
Observations	3188		