Factors Influencing Haul-out Behaviour of Non-reproductive Weddell Seals (*Leptonychotes weddellii*) at Cape Royds, Antarctica

A dissertation submitted in partial fulfilment of the requirements for the Degree of Master of Antarctic Studies
at the

University of Canterbury

by Arkady Michael Tadeusz Aspinwall

Gateway Antarctica

July 2021

Abstract

The Weddell seals (*Leptonychotes weddellii*) are a fast-ice obligate phocid that plays a pivotal role as both predator and prey within the wider Antarctic marine ecosystem. Weddell seals face an uncertain future with the threat of habitat loss and pressures of marine resource extraction from the Southern Ocean. Monitoring of Weddell seal population dynamics provides us with an understanding of wider ecosystem health. Remote sensing technologies such as satellite imagery are increasingly being used to monitor remote populations in the Antarctic. However, satellite imagery needs to be validated by ground-truthing data, and an understanding of Weddell seal behaviour is critical for accurately interpreting Weddell seal counts from space. While the presence of a diurnal haul-out cycle in Weddell seals has been well documented, it is often not corrected for the variation of environmental conditions over a 24-hour period. I review 5,054 images from Cuddeback trail cameras between the 30th of October and 28th December 2017 from Cape Royds, Antarctica for a colony of non-reproductive Weddell seals. I use Generalised Additive Models to correct haul-out behaviour for the environmental variables of temperature, pressure, and wind-speed to determine a more accurate diurnal haul-out pattern. I find that more Weddell seals haul-out when air temperatures are higher, or wind speeds lower. Secondly, the haul-out cycle persists, with most seals hauled-out in the afternoon, and the fewest seals hauled out in the morning. Haul-out patterns can be used to calibrate satellite census counts of Weddell seals, integrating environmental parameters to correct time-of-day patterns may be the next step in generating better population estimates for the Ross Sea region and the wider Antarctic continent.

Acknowledgements

I'd like to acknowledge the mana whenua, Ngāi Tūāhuriri, on whose lands I have spent the past two years working towards this degree.

I would like to extend my deepest gratitude to my supervisors, Michelle LaRue and Jonathan Tonkin without whose tireless advise and edits, this thesis would not have been possible. Furthermore, as this project is an extension of my Post Graduate Certificate of Antarctic Studies (PCAS), I'd like to thank Adrian McDonald, Daniela Liggett, Rob Lindeman, our field trainer Steve Greaves, and PCAS team of Alex Aves, Hannah Dawson, Chrissy Emeny, Lucy Howell, Emily McGeorge, Shannon Williams, and Bella Zeldis.

I thank Carey Treleaven and Mary Botting for their administrative support, as well as Jean Pennycook and David Ainley for their technical assistance.

I thank the Southern Ocean Coalition and Potter Head Running Club for providing the initial funding for this research, as well as Gateway Antarctica, Antarctica New Zealand, and the United States Antarctic Program for their logistical support.

Finally, thank-you to Kelly Herrmann, for all her love and support. As well as to my family: Mike, Olenka, Chris, & Jean Aspinwall, who made it possible for me to study in Aotearoa New Zealand in the first place.

Table of Contents

List of tables

List of figures

List of abbreviations:

WESE: Weddell seal
AWS: Automated Weather Station
GAM: Generalised Additive Model

Introduction

Seal ecology

Weddell seals (*Leptonychotes weddellii*; WESE) are the southern-most of all seal species, and are endemic to the Antarctic (Garrott et al., 2012; Goetz, 2015; Rotella et al., 2012). Due to their key role as one of Antarctica's mesopredators, their population dynamics are of great importance to the current ecology of the Ross-Sea region. With a lifespan in the region of 30 years, and adult weights reaching 500kg, WESEs are a long-living heavyweight of the Antarctic ecosystem. Large vertebrates have often been used as an indicator of ecosystem health due to their relatively high position within the trophic chain (Landres et al., 1988). The same is true for WESEs, serving a unique role as a predator of various pelagic fish, Mollusca and Crustacea, a competitor to Adélie (*Pygoscelis adeliae*) and Emperor (*Aptenodytes forsteri*) penguins (Larue et al., 2019), and prey to Leopard seals (*Hydrurga leptonyx*) and Antarctic killer whales (*Orcinus orca*) (Fenwick, 1973). The complexity of WESEs trophic interactions with the local ecology of the Ross Sea is clearly demonstrated by their relationship with another key mesopredator, the Antarctic toothfish (*Dissostichus mawsoni*). Both WESEs and Antarctic toothfish compete to exploit the pelagic Antarctic silverfish (*Pleuragramma antarcticum*) (Ainley et al., 2020). Secondly, Antarctic toothfish are preyed upon by Weddell seals (Ainley et al., 2015; Ainley & Siniff, 2009). Simultaneously, WESEs are competing with Type-C killer whales who also eat Antarctic toothfish (Ainley & Ballard, 2012). Such intraguild predation between WESEs and toothfish contributes to creating a highly interconnected system where a small change to just one species can cause a large shift in the overall ecological equilibrium.

As a fast-ice obligate species, WESEs are found along the entire coastline of Antarctica, congregating around ice-cracks and dive-holes that allow them to rest and pup on the ice surface and forage in the ocean below (Madden et al., 2014). WESEs have been observed and their ecology described, since the beginning of European Antarctic exploration in the early 1900s. The close relationship between WESE colonies and perennial sea-ice cracks has been known for a long time (Wilson, 1907). These cracks are formed by the tidal motion of fast ice against an immovable landmass such as Ross Island. WESEs use these cracks as an interface between the sea-ice surface and the ocean below. Whilst generally kept open by a consistent diurnal tide pattern, individuals have been observed maintaining such cracks and holes by abrading sea-ice around the edges with their canine teeth (Stirling, 1969b). Paired with the WESEs strong homing abilities in locating and returning to various tidal cracks and ice-holes (Fuiman et al., 2020), these access points are of critical importance in the Ross Sea as they allow individuals to haul-out deep into the south of McMurdo Sound, near Ross Island, Out of reach of larger predators that may not be able to venture as far under the fast-ice without the ability to find the same access points, or ones large enough to accommodate them. This has led to a large concentration of breeding populations of WESEs deep in the McMurdo Sound, where the low predation rate may be one reason for high pup survivability (Hastings & Testa, 1998).

Early estimates placed around 50,000 individuals in the Western Ross Sea (Stirling, 1969a). Over the last 50 years, a wide selection of techniques have been employed to supplement ground monitoring of seal populations in the Antarctic. These techniques range from aerial flyovers by helicopters and light-aircraft photographing and to count populations (Gurarie et al., 2017), or utilizing imaging satellites to provide population snapshots and identify habitat preferences (LaRue et al., 2020). Modern advances in genetics have allowed for the estimation of population sizes through an understanding of genetic marker diversity, providing an estimate of 50,000 female WESEs in the Ross Sea (Zappes et al., 2017). Estimates driven by genetic analysis are particularly useful when dealing with rare and elusive species such as the Ross seal (*Ommatophoca rossii*) as only a relatively small fraction of the overall population needs to be sampled to gain an effective estimate of total population size (Curtis et al., 2011).

Unfortunately, emerging research suggests that there is a worrying declining trend in the size of WESE populations (Ainley et al., 2015). There remains an urgent need for further and more wide-scale monitoring of WESE behaviour and breeding patterns in the uncertain times ahead, governed by a warmer Antarctic and dominated by a loss of Antarctic sea-ice (Forcada et al., 2012). WESEs reliance on fast-ice for haul-out and breeding leaves them at risk of habitat loss driven by a warming climate (Donald B. Siniff et al., 2008). This can be further compounded by uncertainties surrounding the effect of the Ross Sea Antarctic toothfish fishery (Ainley & Siniff, 2009; Albrecht, 2014; Salas et al., 2017). Where the current ecological balance of the Ross Sea may be disrupted by further removal of toothfish from the ecosystem (Ainley et al., 2020; Tin et al., 2009). This vulnerability to environmental change and uncertainty around food-web interactions, provide the basis for arguments for increased and widespread monitoring of WESE populations in Antarctica.

Haul-out behaviour in Weddell seals

WESEs birth pups in the Austral spring**,** generally between September and October as the ambient temperature begins increasing. The exact timing of pupping corresponds with the latitude of the colony, with higher latitude mothers giving birth at a slightly later point in time (Stirling, 1969b). Despite weaning occurring at around 6 weeks, pups have been observed swimming and diving within two weeks of birth (Burns et al., 1999). For the early period of pup development, the mothers invest a large amount of energy into weaning large pups, (Mannas, 2011). WESEs however, cannot be classified as pure capital breeders, as they do not gain enough mass foraging during gestation to fully support lactation (Shero et al., 2015). This energy deficit requires supplementary foraging during lactation, leading to a delicate juggling act of time spent feeding young, resting on sea-ice, or searching for food in the ocean.

The haul-out cycle in WESEs is a phenomenon affecting both males and females, that represents a balance between foraging in the ocean and resting on the fast ice (Boehme et al., 2016; Davis et al., 1999). In the early afternoon, a larger percentage of WESE populations tend to be hauled-out on the ice surface than in the early morning (Siniff et al., 1971; Smith, 1965). This haul-out cycle exists in conjunction with other factors that may determine whether an individual seal chooses to haul-out or forage in the ocean. Haul-out behaviour can be affected by environmental factors such as wind speed and temperature, or the more elusive singular effects such as “bad weather” (Siniff et al., 1971).

Remote sensing

Antarctic research is conducted in one of the most hostile environments on the planet. Katabatic winds can reach speeds of upward of 130km/h (Nylen et al., 2004), and even in the summer months temperatures can get well below -20°C. Consequently, data collection tends to be limited to certain locations and certain times of the year. This poses a challenge to researchers seeking to understand the ecology of WESE populations too remote to easily access, or at times of year too difficult to study (although arguably the austral spring-summer is of more interest due to WESE reproduction) (Kennicutt et al., 2019; Testa & Siniff, 1987). With this in mind, the vast majority of best-studied colonies tend to be near established research stations as this drastically limits the logistic challenge of accessing them for research. Secondly, WESE population research tends to be biased toward observations in the Austral summer, as it is hard to directly observe the abundance and distribution of seals in the dark and often dangerous weather conditions of mid-winter (Siniff et al., 1977).

Researchers have attempted to leverage various emerging remote sensing technologies to solve this challenge of difficult or unsafe in-situ observations (Andrews et al., 2008; LaRue et al., 2011). A useful technique is that of using satellite imaging to monitor populations that are inaccessible either by their distance from logistical support, or their proximity to hazardous terrains, such as the crevasses that tend to be associated with glaciers and ice tongues. With the increasing resolution and abundance of satellite imagery, this technique is becoming increasingly useful as a tool for population monitoring (Marvin et al., 2016; Moxley et al., 2017). Satellite imaging can be a cheaper solution for accessing remote locations when compared to in-situ observations or aerial flyovers, both of which require the logistics and infrastructure to send researchers to the continent (Fretwell et al., 2017). Furthermore, WESEs have proven an excellent study species for satellite sensing technologies due to their propensity to haul-out for long periods of time on the sea-ice and the stark contrast of their dark coat and the white ice (LaRue et al., 2020).

Trail cameras form another part of the suite of remote sensing technologies available, this time operating within much closer proximity of the study species (Cutler & Swann, 1999). Unlike satellite imagery, trail cameras still require physical access to the study population as researchers need to place cameras within the visual range of their intended targets. The advantage of trail cameras is that they only need to be placed once, before collecting information over a prolonged period of time. This limits the disturbance to the study species caused by the presence of human observers (Cutler & Swann, 1999; Griffiths & Van Schaik, 1993; Lynch et al., 2020; Marvin et al., 2016). Within an Antarctic context, trail cameras have been used to great success as part of the Penguin Watch program, allowing for high-frequency monitoring of Gentoo penguins (*Pygoscelis papua*) (Jones, 2019).

A principal problem in using satellite imagery to generate census data on WESEs is photograph timing is limited by weather (think cloud-cover) and satellite orbits (Banner, 2012). A satellite image will contain all the individuals hauled-out on the sea ice across a wide region, but only at that exact moment the photograph was taken. Any individuals that happened to be under the sea-ice at the time of the photograph would not be included within a satellite-based population estimate. This contrasts with in-situ census counts which take place over an entire, or series of days so that all individuals hauled-out over the length of the study can be counted, capturing a more accurate representation of the population size. Or, with trail-camera counts, where the camera can take photographs at a consistent rate over an extended period of time.

This problem is compounded further by the aforementioned haul-out cycle in WESEs (Stirling, 1969a; Testa & Siniff, 1987), a cyclical variation of sea haul-out over a 24-hour period leading to a systematic under-sampling by satellite imagery at specific times of day (LaRue et al., 2011). This cycle means that at different times of day a different proportion of the seal population is hauled-out onto the ice surface and there can be significant daily variation within satellite count data, with photographs in the early afternoon local time containing a larger proportion of the population on the fast-ice (Siniff et al., 1971; Smith, 1965). This difference in haul-out by time of day needs to be corrected between satellite images in order to correctly estimate a population size and not confound any further inferences on population dynamics.

My research objectives

With such a pivotal position within the trophic chain in mind, a fuller understanding of WESE ecology provides us with a great opportunity to understand wider ecosystem functions (LaRue et al., 2020). To elucidate the impact of a warming climate (Vaughan et al., 2003), fisheries management (Ainley & Siniff, 2009), and loss of seasonal sea-ice (Donald B. Siniff et al., 2008), the current dynamics and future trends of WESE populations need to be monitored carefully. This is especially important as the harsh environment and remote nature of Antarctic research might make other species that are influenced by WESE population dynamics much more difficult to observe directly. Due to these difficulties of research in such extreme and remote conditions, we need to leverage remote sensing technologies to monitor inaccessible populations toward these aims. WESEs tendency to spend large lengths of time hauled-out on sea-ice make them a species particularly well suited to ground census observations and remote satellite imaging (LaRue et al., 2020). However, remote sensing technologies such as satellite imagery carry associated assumptions that need to be accounted for before fully relying on the information they produce, such as a variation in WESE haul-out depending on the time of day, season, and local environmental conditions.

I attempt to use a different remote sensing technique, trail cameras, to build a model that describes WESE haul-out behaviour. By combining camera count data with weather data, I aim to develop an understanding of the proportion of WESEs hauled-out at a specific point in time given a specific set of environmental conditions. Such a model can be used as an adjustment factor to allow for the comparison of WESE counts between different satellite images taken at different points in time during different weather regimes, or provide a guideline to determine at what time, or under what conditions, census data should be collected. Both strategies aim to improve the monitoring quality of such a keystone species as the Weddell seal.

Methods

Study area

The study was conducted at the edge of Ross Island, near Shackleton's Hut at Cape Royds (77°33'33.8"S 166°09'46.1"E), about 35km due north of Scott Base. Cape Royds lies on the western shoreline of Ross Island, facing McMurdo Sound. This region experiences a large seasonal variability in sea-ice cover, with high ice coverage over the austral winter, sea-ice breakout between November to January, and open water throughout the summer period (Kim et al., 2018). The ocean floor along the coast initially slopes gently to around 100 m deep, before dropping off rapidly to over 800 m (Robinson, 1963). The presence of a large anti-cyclonic eddy to the west of Cape Royds generates a consistent northward current of cold low-salinity water from the Ross ice-shelf (Lewis & Perkin, 1985). Temperatures at Cape Royds tend to vary between a monthly mean of -30°C in the austral winter and 0°C in the summer (Stearns, 1988). In general Cape Royds experiences relatively warmer and calmer weather as the cold southerly winds coming off the Ross Ice Shelf are diverted eastward by the topography of Ross Island itself (Monaghan et al., 2005).

WESEs at Cape Royds co-exist with several other Antarctic species. There is a relatively small Adélie penguin colony consisting of 3,000-4,000 breeding pairs, however, this colony appears too small to attract many Leopard seals to the region (Ainley et al., 2005). The coast off Cape Royds is known to be frequented by Antarctic killer whales, including type-B killer whales that predate on large mammals; with pod sightings and predation events observed in late December through January (Ainley & Ballard, 2012), coinciding with the break-out of winter sea-ice. Finally, vagrant Emperor penguins are known to frequent the study area, most likely from the colony at Cape Crozier (M. LaRue, 2021, personal communications).

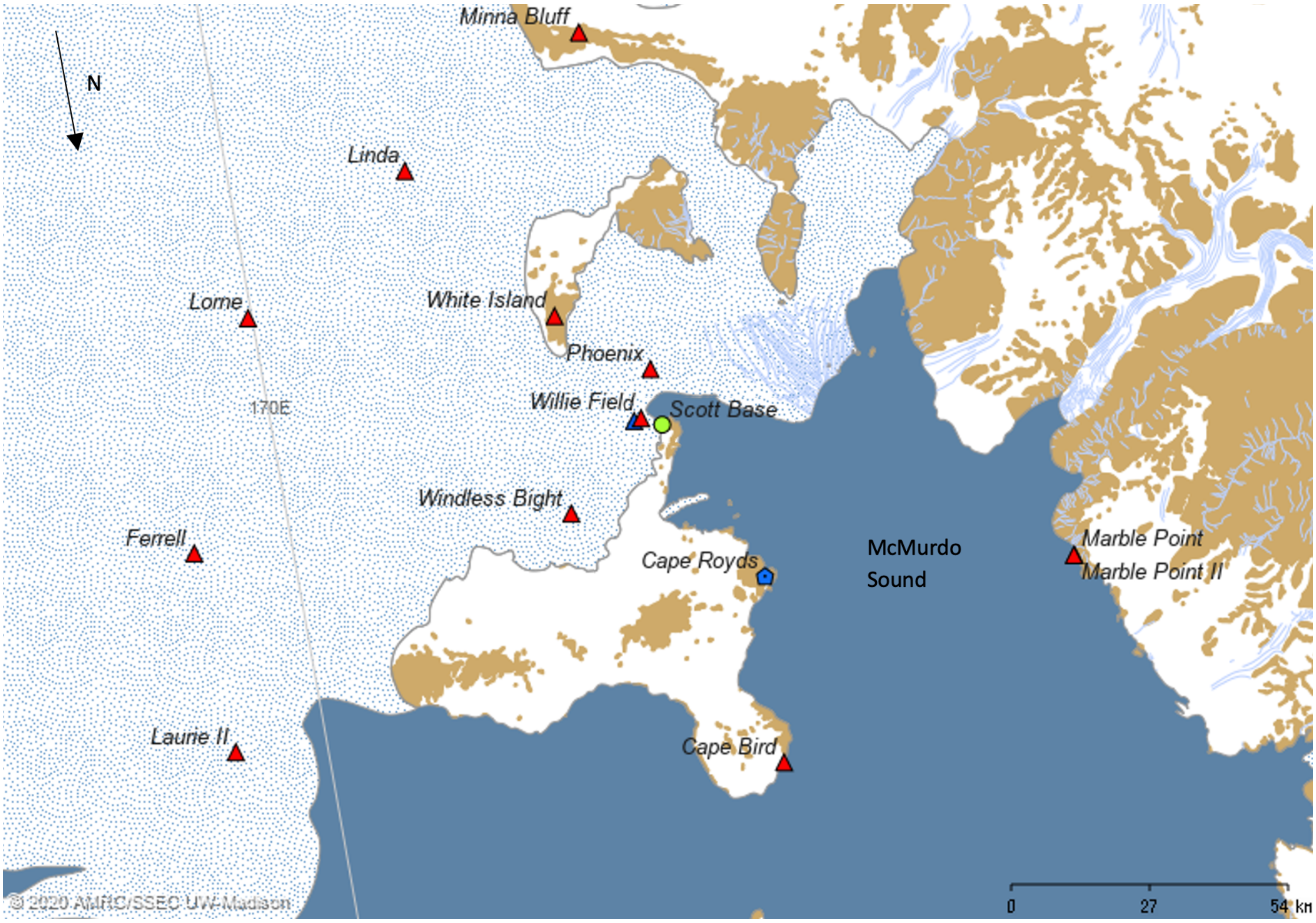

Fig.1: Map of Ross Island identifying the location of automated weather stations made available by the University of Wisconsin. Weather data are collected from Marble Point II, tidal data from Scott Base, and sea count data from Cape Royds. Map courtesy of publicly available data provided by https://amrc.ssec.wisc.edu/aws/

Environmental data

I used publicly available data from Automated Weather Stations (AWS, Appendix A) (https://amrc.ssec.wisc.edu/aws/). For this study, I used weather data from one of the closest available AWS at Marble point II, 60 km to the west across McMurdo Sound. Data at 10-minute time intervals were available across the length of the study period. The environmental variables collected were as follows: temperature (°C), pressure (hPa), wind-speed (ms^{-1}), wind-direction (°), humidity (%), and delta-T (°C). In the context of this AWS, delta-T represents the difference in temperature between two thermometers contained within the AWS and is used to identify whether or not the weather station is buried under snow (A. McDonald, 2021, personal communications). There is still some distance between the AWS at Marble point and the study site at Cape Royds, meaning that there will not be a perfect match between the weather at both locations. However, visual inspection of the weather data at Cape Bird, Marble Point, and Willie Field identified broadly similar trends in temperature, pressure, and wind speed, providing us with confidence that weather data from Marble Point would hold at least some explanatory power for WESE haul-out at Cape Royds.

I used tidal information publicly available for Scott Base approximately 35km south (https://www.linz.govt.nz/sea/tides/sea-level-data). Tidal data is at 5-minute intervals between the 30th of October and 28th of December 2017 and displays tidal elevation in meters above chart datum.

Seal data

Three Cuddeback trail cameras (20MP, model-E), were set up along the rocky shore of Cape Royds facing westward over McMurdo Sound at neighbouring patches of sea-ice. These cameras took one photograph every 30 minutes between the 30th of October - 31st December 2017. The cameras were pointed at a small population of WESEs that used the sea-ice near a series of tidal pressure ridges as a haul-out spot in between forages in the ocean. All three cameras were set up at varying heights along the island slope and consequently, the scope of the area captured in their photographs varied dramatically from camera to camera. Camera #2 was placed at the highest vantage point, capturing images of the largest sea-ice area; camera #3, being at the lowest vantage point, captured images of the smallest area. The three cameras were set up opportunistically by researchers working at the nearby Adélie penguin colony, who identified this location as a reliable haul-out of WESEs and decided to collect data for future study of WESE behaviour.

In order to investigate the presence of a haul-out cycle in non-reproductive Weddell seals at Cape Royds, I counted the number of observable individuals in every photograph taken by the three aforementioned trail cameras. Initially, I was interested in the questions pertaining to the orientation of hauled-out seals on the sea-ice, I recorded the angle of each WESE in all photographs, as well as the date and time of the photograph, the camera the photograph set belonged to, and the following associated metadata that I thought would be of ecological interest to this research: photograph quality, sea-ice cover, seal size, and whether or not the seal was in shadow (this was recorded to answer an auxiliary question on habitat preference). Initially, I attempted to estimate the angle of shadows in each photograph to get an indication of sun location. However, due to the unreliability of trying to obtain this estimate from the photographs, as well as the large number of overcast days across the study period, this effort was quickly abandoned. This is important as it leads to the main difference in definitions between medium and high-quality photographs I discuss later in the methods (Table. 1).

Dataset formatting

The format of data recording was as follows: each row contained the angle of individual seals recorded. This angle was measured with a on_screen_protractor.jar program (https://sourceforge.net/projects/osprotractor/) that measured the angle of a seal from tail to head, where possible, in radians. This angle was with respect to the upward direction of the photograph which, due to the fact the cameras were stationary throughout the dataset, was consistent. If there was no seal present in a photograph, the angle would be recorded as "none".

For each seal angle recorded, I recorded the photo_ID, the date of the photograph, and the time of the photograph. Time was recorded as the number of hours since midnight of that day (eg. 10:30 am would be 10.5) as well as in military time. For each seal record, I recorded a measure of photograph quality. This metric was included to account for the varying quality of the image and therefore my varying confidence of being able to accurately count the true number of seals present in a photograph. In some cases, due to either a white-out event or overexposure of the camera from sunlight reflected into the lens, the quality of the photograph was so low that it was recorded as "none". These photographs were later excluded from the dataset as it is impossible to tell whether seals were present at that time. In general, photographs were rated as anywhere between low (low confidence in recording all seals) through medium, to high (high confidence in observing all seals in a photograph). The definitions of photo quality are outlined in Table 1.

Table 1: Definitions of photograph quality recorded in order to identify possible under-sampling of Weddell seal counts. The quality of each individual photograph was assessed according to these requirements and placed in one of four categories representing my confidence that the number of seals I counted in a photograph was the true number of seals on the sea-ice captured in that image. If there is a temporal structure in photo quality distribution, this could indicate a systemic under-sampling of seal numbers at certain times of day thus suppressing or exaggerating the presence of a haul-out cycle.

Photograph Quality	**Category Requirements**
None	No discernible features in the photograph. These images tend to be fully or partially obscured due to blizzards obscuring the camera or direct reflection of sunlight off the sea-ice surface into the lens
Low	There is enough contrast within the photograph to identify the presence of seals. However, these photographs could have up to 25% of the image overexposed, or part of the lens is obscured by snow. Any seal hauled-out in an obscured part of the image would not be counted and therefore photos of low quality may under-sample the number of seals.
Medium	These photographs contain good contrast across the image. I have high confidence that all seals in medium and above quality images were correctly counted. Medium quality photographs are differentiated from high-quality photographs by lack of discernible shadow.
High	High-quality photographs contain excellent contrast leading to a low probability of under-sampling seal counts. Secondly, in high-quality photographs, shadows are clearly discernible and have sharp edges. Allowing for identification of whether a seal is resting in shadow and initially, estimation of sun angle.

I estimated the percentage of ice-cover in each photograph. This is important as data collection took place over a period of time where sea-ice break-out would be expected. As the proportion of ice-cover may affect the number of seals present (i.e., less ice, fewer seals), this information was included for potential use in future modelling. The ice-cover was calculated by dividing each photograph into four quadrants and estimating whether each quadrant is majority sea-ice or not. A quadrant would be 0 if it contained no sea-ice, 0.5 if it was approximately 50% sea ice, and 1 if it was majority sea ice. The scores for all 4 quadrants were summed to get an estimate of sea-ice cover ranging from 0-4.

Data processing

All data processing was conducted in R v4.0.3 (R Core Team, 2021) with the tidyverse package (Wickham et al., 2019). Weather, tide, and seal dates were adjusted to match time-zone (NZDT), before being merged by DateTime, so that for each DateTime there would be the number of WESEs observed at a single point in time, as well as all the associated environmental variables. In the rare case that a gap in weather station data coverage would prevent merging, the nearest DateTime was used instead. To elucidate the potential haul-out patterns, I calculated the number of seals by summing the total recorded angles per DateTime. After the removal of photographs with quality = none, where no information can be gained from a photograph due to events such as whiteouts or glare into the camera lens, the remaining dataset contained the photo_ID, date, time, number of seals present, and all the associated environmental variables. At the beginning of the dataset, camera #1 only took a photograph once an hour, before being recalibrated by the original researchers to take half-hourly images. Consequently, a subset of 159 photographs at the beginning of the dataset contained only hourly data as opposed to half-hourly data. I, therefore, interpolated half-hourly seal numbers for this subset by averaging the seal counts between each hourly interval and then matching the newly generated values with weather and tidal information available for that time (Fig. 1). I felt confident generating such averages as the gap between data points was never more than one hour. This was considerably shorter than most seals seemed to haul-out for, implying it was unlikely that between two-hourly points there would be a drastic, unobserved spike in seal numbers. Interpolated photographs also had an ice-cover value generated by averaging the two adjacent ice-cover values and rounding to the nearest 0.5. However, photograph quality was not simulated as this was not necessarily a parameter associated with the environment, but often due to the mechanics of the image taking process -specifically overexposure.

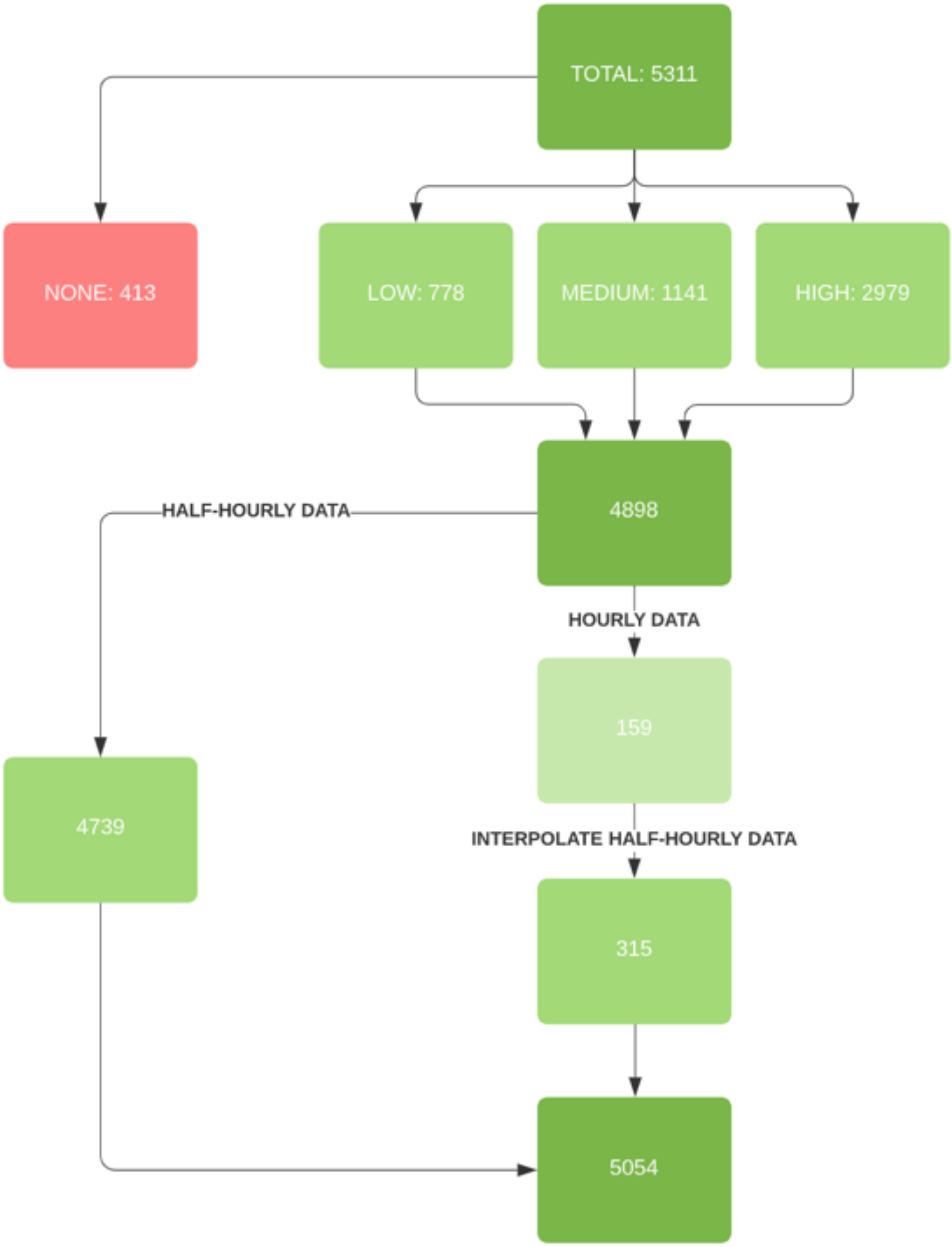

Fig. 2: Workflow diagram displaying photograph parameters and process to reach format imputable into the final statistical model. 413 photographs were of photo quality "none" and therefore rejected from further analysis. 159 photographs were taken at hourly intervals and consequently combined with interpolated half-hourly Weddell seal values.

Statistical modelling

Before I construct a model to determine what factors affect WESE haul-out, I need to interrogate my data for any unusual structures that may mislead my analyses. Within my dataset, there are several correlations that I need to keep an eye on (Fig. 2). For this analysis, the most important correlation structures are between date and temperature, as well as date and pressure, with a Pearson's correlation value of 0.67 and 0.47 respectively (both p-values <0.0001). Delta T has the second-highest correlation of -0.52 with date and some of the highest correlations with numerous other variables. This is a variable that has little importance for WESE ecology and is primarily used to check the condition of the AWS itself, as such it was excluded from further analysis.

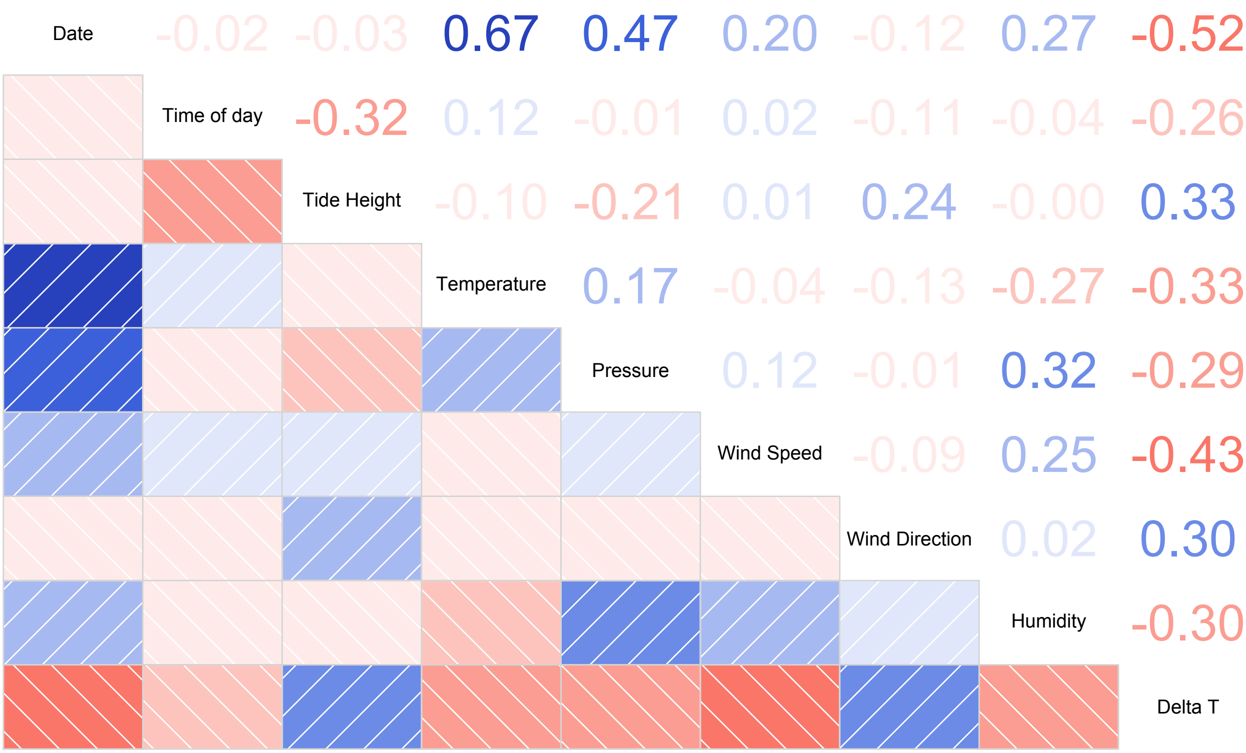

Fig. 3: Pearson's corrgram of collected environmental variables, date, and time of day generated by corrgram function (Wright, 2018). Blue colours represent a positive correlation, whilst red, a negative correlation. The intensity of the colour reflects the strength of the correlation. The relationship is visualized both through colour plots and numerically with Pearson's correlation coefficient. This corrgram allows for the comparison of relationships between many different variables simultaneously.

The strongest relationship is the positive correlation between date and temperature of 0.67. The second highest correlation is between delta T and date. The non-negligible correlations between delta T and most other variables, combined with its unconvincing ecological importance encouraged me to exclude this variable from further analysis.

To deal with the complexities of the dataset (such as the nonlinear relationship between environmental covariates and WESE haul-out behaviour, or temporal autocorrelation), I chose to use Generalised Additive Models (GAMs) provided by the R package 'mgcv' (Wood, 2017). One of the biggest strengths of GAMs is their ability to decompose complex temporal structures into their constituent components. Secondly, GAMs provide the tools necessary to account for the correlation and autocorrelation in my data (Ciannelli et al., 2008). The structure of GAMs is very similar to regular Generalised Linear Models (GLMs), however, they allow for the defining of much more complex non-linear relationships between explanatory and response variables through fitting an individual smoothing component to each parameter of the model.

I set date as a cubic smooth function ("cs") as cubic functions can handle temporal autocorrelation structures well (Ciannelli et al., 2008; Wood, 2006). Time of day is set as a cyclic cubic "cc" smooth. The end of one day is the beginning of another and a cyclic smooth with endpoints set as 0 and 24 hours allows the model to understand that these points in time are linked and the end of one cycle influences the start of the next.

All environmental covariates in my models were fitted as penalized thin-plate smooths ("ts") to account for their correlation structures and optimized by restricted maximum likelihood (REML) method as per (Blanchet et al., 2015; McIntosh et al., 2015). The penalization of these smooths automatically accounts for collinearity present variables (Marra & Radice, 2010; Wood, 2008), reducing the effective size of the smooth and accounting for overfitting.

I set the camera number as a simple random effect smooth ("re"). This is necessary as different cameras have different mean numbers of seals observed, most likely due to the difference in the sea-ice area that each camera covers. The random effect smooth allows for the movement of the intercept (accounting for the difference in mean in seal counts) between the three cameras, without generating unique smooths for each other variable per camera. Whilst the number of seals observed by each camera is different, all three capture different parts of the same population, so I would expect the impact of all my other variables to be the same across all three cameras (essentially, my model needs to account for a random intercept by camera). Therefore, by modelling camera number as a simple random effect smooth, I can remove variance due to camera number whilst still generating a single function for each other variable.

I generated a series of models, starting with a workhorse model containing all the environmental variables collected at Marble Point. I then progressively removed variables based on my hypothesis that weather can explain the haul-out behaviour of WESEs. I selected the best model by balancing simplicity with the explanatory power of the model. I did this by removing variables that did not have a strong foundation in the literature supporting their ecological importance (such as dT), and by comparing AIC and deviance explained scores to check this did not largely decrease the performance of my model (Table 2).

In my view, removing humidity and tide height from the final model is justified due to their limited contributions to model deviance explained, and their minimal improvement to AIC. Within my dataset, tidal height varied by approximately 0.5 m around the mean. With such a small tidal variation, I assume that its effect on haul-out in this region will be limited, a similar assumption as per (Boehme et al., 2016).

Table 2: Model selection procedure showing the effect of removing various parameters. Removing tide height and humidity reduces the deviance explained by 1.2% Whilst just removing pressure would reduce deviance explained by 1.9% whilst also generating the largest increase in AIC

Model parameters (excluded variables in bold)	**Deviance Explained**	**AIC value**
Date, time of day, temperature, pressure, tide height, wind-speed, humidity	58.1%	14037.64
Date, time of day, temperature, pressure, tide height, wind-speed, **humidity**	57.7%	14099.03
Date, time of day, temperature, pressure, **tide height**, wind-speed, **humidity**	56.9%	14196.88
Date, time of day, temperature, **pressure**, tide height, wind-speed, humidity	56.2%	14298.05

Results

Environmental data

Across the study period of 31st October to 28th December 2017, the temperature at Marble Point varied from -21.9°C to -0.9°C, with a mean temperature of -7.75°C. Marble Point was a generally low-pressure system with pressure readings varying from 954.7-985 hPa and a mean of 970.2 hPa, whilst relative humidity ranged from 25.1-91.2% with a mean of 65.0%. The predominant winds were north westerlies coming down the Victoria Land coast (150-160°). A mean wind speed of 3.9 m s^{-1} and the largest recorded wind speed of 13.79 m s^{-1} strongly suggested no wind events such as katabatic flow down from the Transantarctic mountains occurred over the study period. Tidal information from Scott Base indicated a consistent diurnal tide pattern consistent with the Ross Sea region with one low tide between 14:30-15:30 local time, and one high tide between 05:00-06:00 in the morning. The tidal range was in the region of 1.5 m with a low tide and high tide of 1.38 m and 2.95 m respectively.

Table 3: Descriptive statistics for selected environmental variables used as covariates to determine haul-out behaviour in Weddell seals at Cape Royds between the 31st of October -28th December 2017, collected by the Marble Point II Automated Weather Station, Antarctica. Variables included Temperature (in degrees Celsius), Pressure (in hectopascals), Windspeed (in meters per second), and Relative Humidity (as a percentage). All values are given to 1 decimal place.

Variable	**Minimum**	**Maximum**	**Mean**	**Standard Deviation**
Temperature/°C	-21.9	-0.9	-7.01	3.9
Pressure/hPa	954.7	985.0	971.4	6.9
Wind speed/ms^{-1}	0.2	12.8	4.0	2.3
Humidity/%	25.1	91.2	65.0	15.2

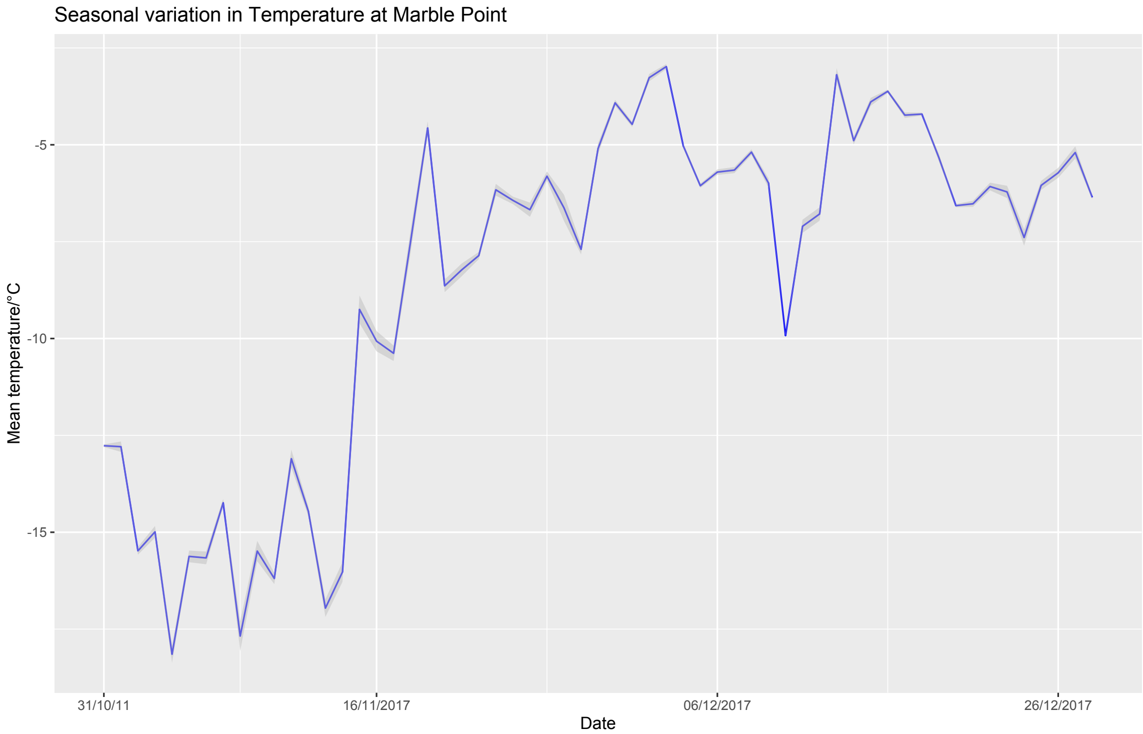

Fig. 4: Mean daily variation in temperature Marble Point II, used to build models explaining the temporal variation of non-reproductive Weddell seal haul-out at Cape Royds between the 30th of October and 28th of December 2017. Standard error represented by Grey ribbon.

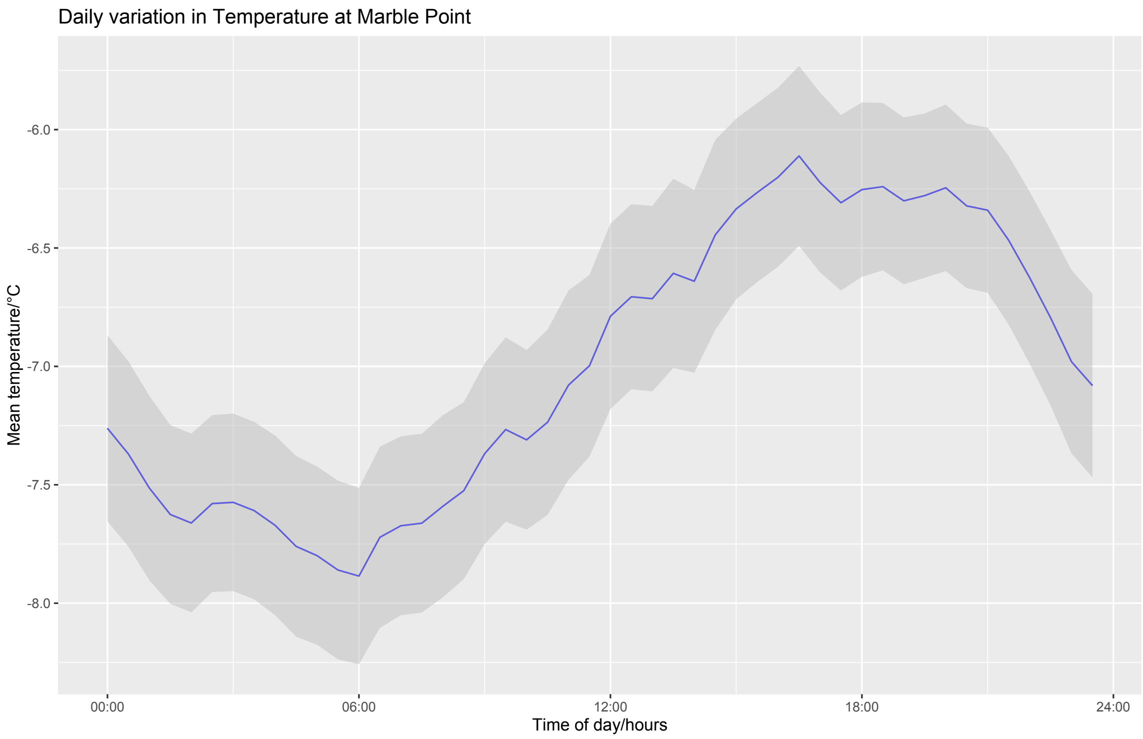

Fig. 5: Mean hourly variation in temperature Marble Point II, used to build models explaining the temporal variation of non-reproductive Weddell seal haul-out at Cape Royds between the 30th of October and 28th of December 2017. Standard error represented by Grey ribbon.

Photo analysis

In total 5,311 photographs across three separate cameras were captured and analysed as part of this study. Of these photographs, I categorised 2,979 as high quality, which means there was a high confidence of identifying every WESE present within the photograph; 1,141 were listed as medium quality, implying medium confidence, 778 were listed as low quality, and 413 were listed as no-quality (as described in table 1). These photographs were so poor in quality (primarily due to periods of white-out, or overexposure of the camera due to direct reflection of sunlight into the lens) that they were excluded from further analysis as it was impossible to determine whether a WESE was present at that time. Across the 2,507 half-hourly time points between the 31st of October and 28th December 2017, 895 DateTimes were captured across all three cameras; 601 DateTimes were captured by two cameras, and 1,011 by only one camera. Of the 4,898 photographs of low, medium, or high-quality remaining; 2,236 contained no WESEs, whilst in 2,662 at least one WESE was present. Of the 156 interpolated time points near the beginning of the study period, 6 contained no WESEs, and 150 contained at least one WESE. Interpolated time points are not included in further descriptive statistics, they do however inform the final model used to explain WESE haul-out behaviour reported at the end of this section.

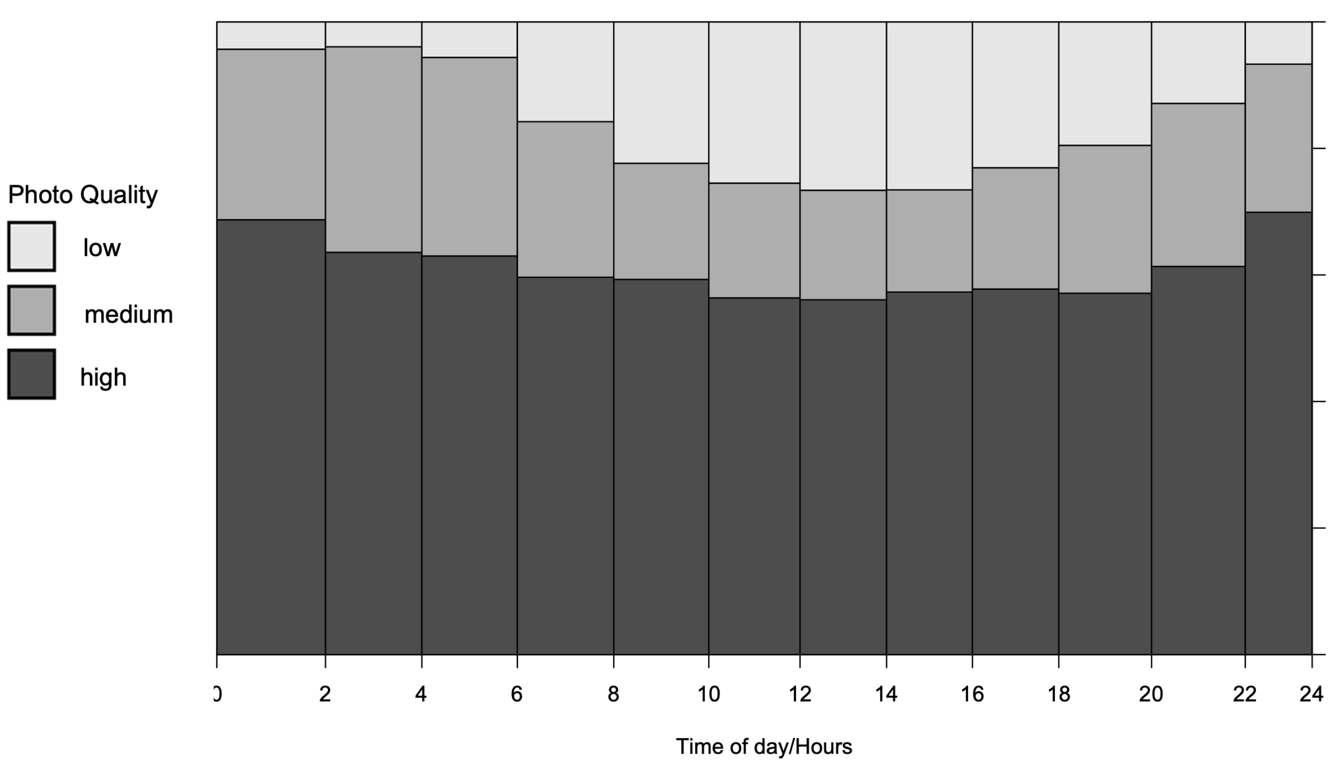

Fig. 6: Proportion of photographs listed as low, medium, or high quality by time of day. Photographs were taken at half-hourly intervals by three separate Cuddeback cameras at Cape Royds, Antarctica between the 30th of October and 28th December 2017.

The vast majority of photographs (75-90%) are of medium or high quality indicating high confidence of complete WESE count capture. The highest proportion of low-quality photographs occurs between 1200-1600 NZST.

Table 4: Percentage of photographs per camera that have a given level of ice cover ranging from an ice cover value of 50-100%. A value lower than 50% is not included in this table as no photograph had less than 50% sea ice cover. Photographs were taken at half-hourly intervals by three separate trail cameras at Cape Royds, Antarctica between the 30th of October and 28th December 2017. All percentages are given to the nearest whole number.

Camera number	**Percent of photographs with a given level of ice cover (%)**				
	50%	**62.5%**	**75%**	**87.5%**	**100%**
1	19	1	40	6	34
2	0	0	0	0	100
3	0	0	90	0	10

Variation in sea ice cover was mostly seen on camera #1, with values ranging from half to full sea-ice cover. Photographs from Camera #2 contained full sea-ice coverage across the entire dataset, while photographs from camera #3 had one quadrant of open water across most of the dataset. The majority of break-out of sea-ice was visibly observable in photographs from mid to late November (20th onward) on camera #1, reaching approximately half the image area being open water by the conclusion of data collection on 31st of December.

In total 8,153 individual WESE observations were recorded within the study. The mean number of WESEs observed per photograph was 1.72, the largest number of WESEs counted within one photograph was 14 individuals. The time with the fewest WESEs was 0330 NZT with a mean of 1.07 seals, whilst the time with most WESEs was 1330 NZST with a mean of 2.45 WESEs. The highest daily mean was 5.32 on the 30th of November. The most WESEs observed simultaneously across three cameras at the same point in time was 20 individuals.

Table 5: Descriptive statistics for the number of Weddell seals counted in photographs at Cape Royds, Antarctica between the 30th of October and 28th December 2017. Photographs were taken at half-hourly intervals by three separate Cuddeback cameras at Cape Royds, Antarctica between the 30th of October and 28th December 2017. There is a slight variation in the three calculated means as some days have fewer associated photographs due to events such as white-outs or sun-glare. All statistics are given to 1 decimal place.

Seal statistic	**Minimum**	**Maximum**	**Mean**
All photographs	0.0	14.0	1.7
Mean count per photograph per half-hourly interval	1.1	2.5	1.7
Mean count per photograph per day	0.0	5.3	1.9

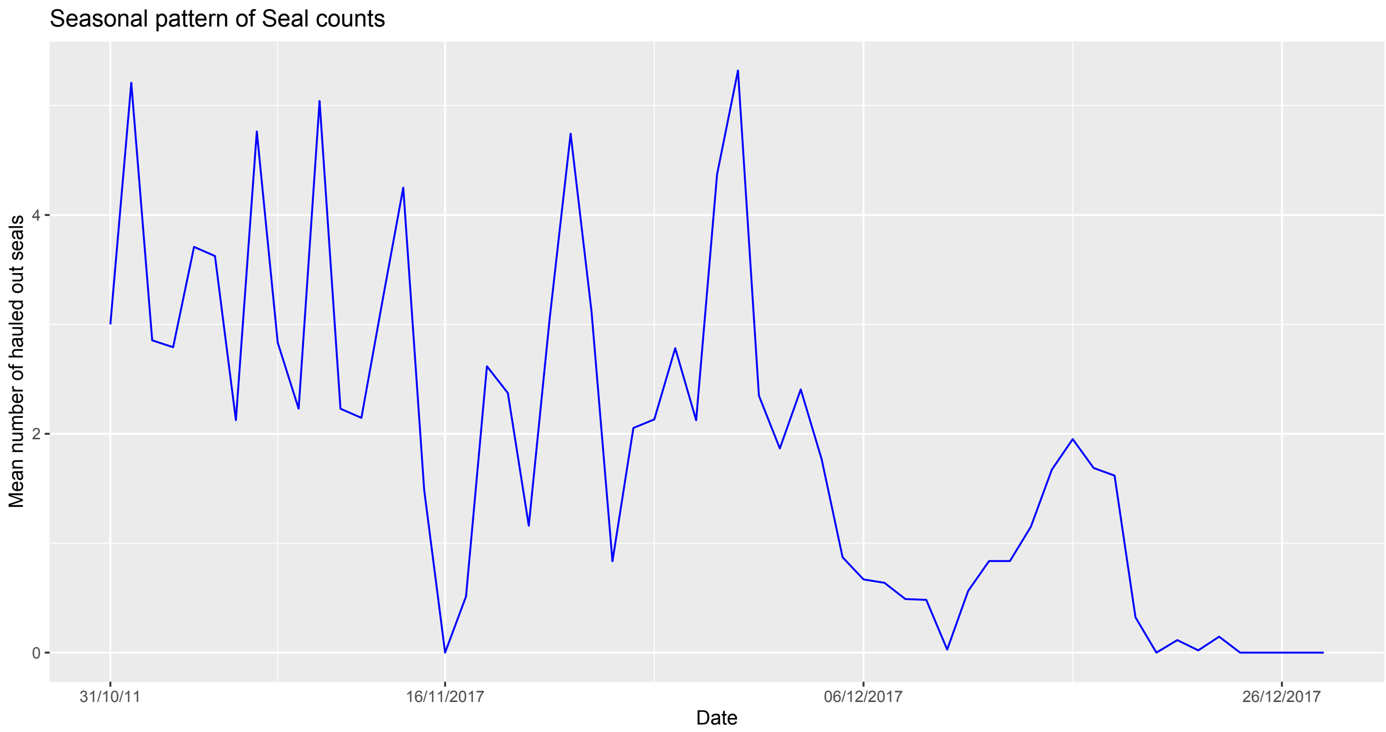

Fig. 7: Mean number of Weddell seals per photograph per day hauled-out on the sea-ice at Cape Royds, Antarctica between the 31st of October to 28th December 2017. Photographs were taken by three separate Cuddeback trail cameras at 30-minute time intervals.

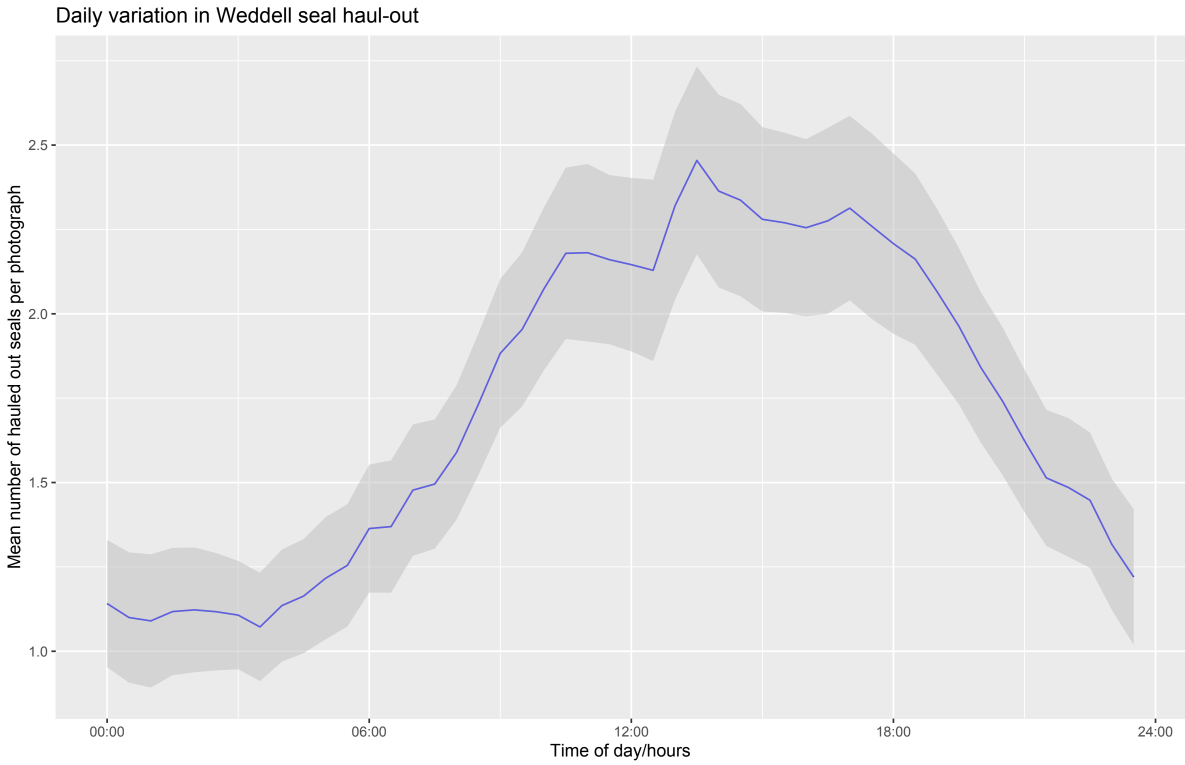

Fig. 8: Mean number of Weddell seals per photograph per 30 minute-time period hauled-out on the sea-ice at Cape Royds, Antarctica between the 31st of October and 28th December 2017 as recorded by three separate Cuddeback trail cameras.

Model results

I endeavoured to determine the presence of a haul-out cycle and further elucidate haul-out behaviour with respect to environmental variables in non-reproductive WESEs at Cape Royds, Antarctica. In order to answer this question, I constructed a Generalised Additive Model (GAM) identifying the relationship between the number of WESEs counted on the fast-ice across three trail cameras and: the Julian date and time of day of the photograph, and the temperature, pressure, and wind-speed from an AWS at Marble Point.

The final GAM took the following form:

$$gam(seal\ number \sim s_1(date) + s_1(time\ of\ day) + s_2(temperature) + s_3(pressure) + s_4(wind\ speed) + s_5(camera\ number)$$

Where **s** is the associated smoothing term as listed in table 6.

The largest effect on WESE count is date. Holding all environmental covariates constant, the mean number of WESEs hauled-out per image is 2.5 individuals lower at the end of December compared to the beginning of November (Fig. 9). This variation is larger than the mean number of WESEs hauled-out per photograph of 1.72. The raw data show that haul-out behaviour is diurnally cyclical, with an average of only ~1.1 WESEs hauled-out between 00:00 and 03:00 NZST and around 2.25 WESEs between 12:00 and 18:00

NZST (Fig. 8). However, once controlled for other variables such as temperature; the effect of time of day on haul-out persists but is reduced in magnitude, only explaining a variation of around 0.8 WESEs between early morning and early afternoon (Fig. 9). With increasing temperature there is an increased number of WESEs hauled-out on the sea-ice, this relationship appears to be bimodal. There were significantly more WESEs hauled-out when pressure was above 980 hPa, however, below this value pressure seemed to have little effect. There appears to be a linear relationship between wind speed and haul-out with the number of individuals on ice decreasing slightly as wind speeds increase up to 13 m s^{-1}. The final model explains almost 60% of the variation in WESE haul-out observed in photograph counts at Cape Royds (Table 6).

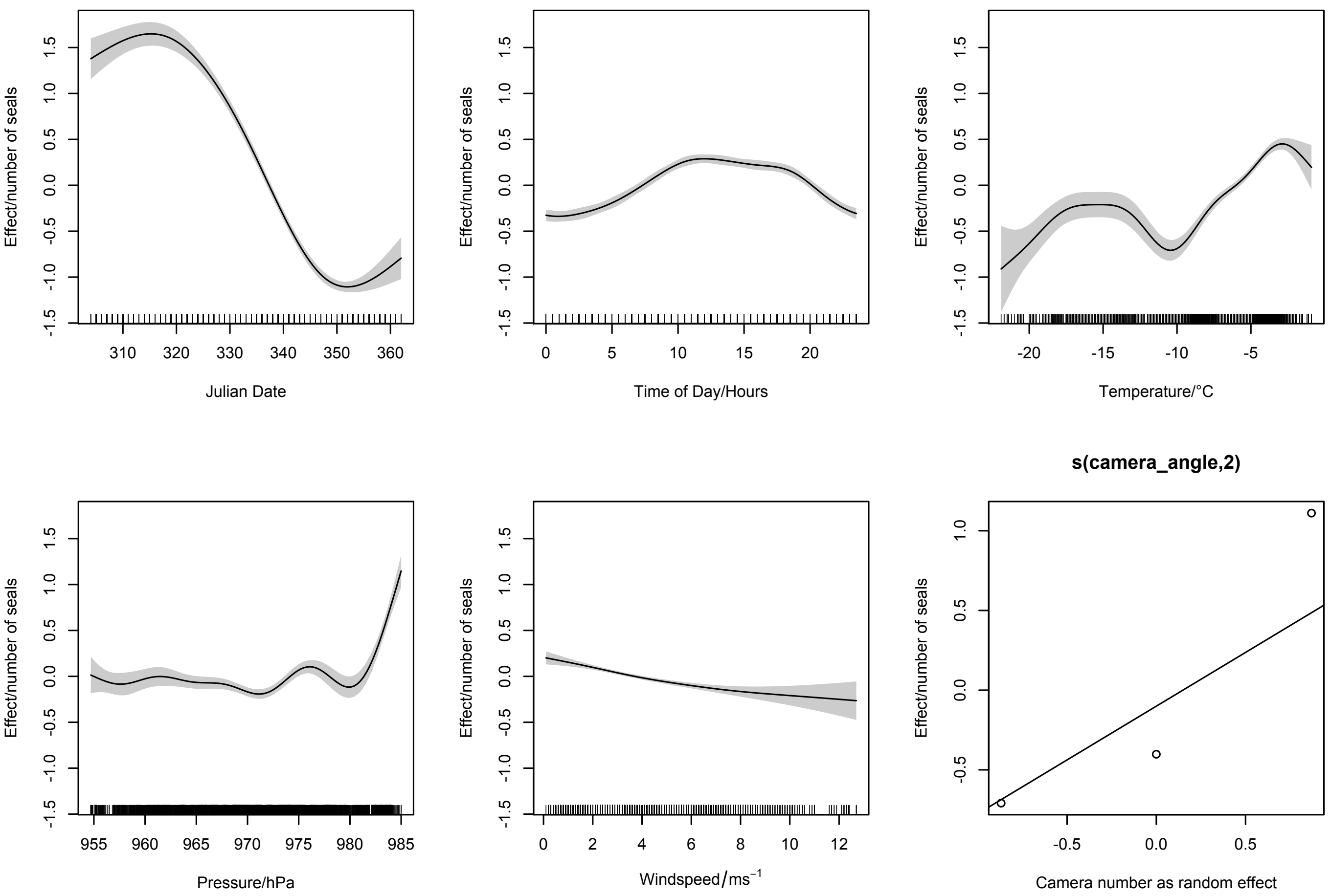

Fig. 9: Estimated smoothing plots for covariates of the Generalised Additive Model (GAM) used to explain non-reproductive Weddell seal haul-out behaviour at Cape Royds, Antarctica between the 31st of October and 28th of December 2017. Grey ribbons represent two standard errors around the respective smoothing function, while lugs on the x-axis show distribution of data points informing the smoothing function. The units of the Y-axis are in number of seals, identifying what effect each covariate has on the mean number of seals, all else being equal. Julian date and time of day refer to the date and time that photographs at Cape Royds were taken with Cuddeback trail cameras, from which the number of Weddell seals hauled-out was counted. Temperature (°C), pressure (hPa), and wind speed (ms^{-1}) are collected for those exact dates and times from an automated weather station at Marble Point, Antarctica.

Table 6: Results of the GAM used to explain non-reproductive Weddell seal haul-out behaviour at Cape Royds, Antarctica between the 31st of October and 28th of December 2017. The model explains 56.9% of deviance observed. Estimated degrees of freedom are a representation of the 'wiggliness' of a relationship between covariate and response variable, an estimated degree of freedom of 1 implies a linear relationship, larger numbers imply progressively more wiggliness.

Variable	**Smoothing terms**	**Estimated Degrees of Freedom**	**Chi-squared**	**P-value**
Date	cubic regression (cr)	3.962	1888.41	<0.0001
Time of Day	cyclic cubic (cc)	5.714	370.01	<0.0001
Temperature	thin-plate shrinkage (ts)	7.853	410.27	<0.0001
Pressure	thin-plate shrinkage (ts)	8.255	294.12	<0.0001
Wind Speed	thin-plate shrinkage (ts)	1.858	61.44	<0.0001
Camera	random effect (re)	1.998	2827.56	<0.0001

Discussion

Cape Royds population

My analysis of trail camera images clearly indicated that the WESE population at Cape Royds comprised of non-reproductive individuals, with a clear lack of pups or associated pupping behaviour in any of the images. There was little deviation in the size of WESEs observed in the images, which would be required to indicate the presence of pups. Furthermore, there was no pattern of paired individuals, with one consistently hauled-out on the fast-ice surface and the other displaying varied haul-out behaviour, repeatedly disappearing and returning to the same location. WESEs in the Ross Sea region tend to pup between September and October, weaning their young by mid-December (Stirling, 1969b). The lack of pups at any point in my data strongly suggests that the Cape Royds WESE subpopulation consists of non-reproductive individuals, either juvenile or skip-breeding adults. This is in concordance with previous observations that found significant stratifications by age in WESE subpopulations throughout McMurdo Sound, with a concentration of non-breeding, younger individuals near the vicinity of Cape Royds (Siniff et al., 1977), as well as observations by (Testa, 1986), who found that juvenile WESEs do not return into the far south of McMurdo Sound, past the Erebus Ice tongue, until fully reproductive. This distribution is likely tied to natal site fidelity in WESEs, which increases with age; a strategy that typically leads to a higher reproductive success for females (Cameron et al., 2007a).

The maximum number of WESEs observed was at 1430 NZST on the 29th of November 2017 where, between the three cameras, 20 individuals were counted. A mean haul-out of 1.7 seals per photograph is lower than other comparative studies of WESE haul-out behaviour, such as by (Banner, 2012) who recorded daily counts between 100-200 individuals at Big Razorback Island just south of the study area here, or (Lake et al., 1997) who recorded maximum daily counts in the Vestfold Hills of 68-84 individuals between October and December. However, the 30-minute resolution across the entire two-month study period provides a more granular analysis than both these studies, which used a 45-minute and 150-minute interval respectively.

Seasonal variation

My GAM indicates that the single largest variable affecting non-reproductive WESE haul-out was date (Table 6). The number of individual WESEs hauled-out per photograph declined across the length of the dataset, between the 30th of October and 28th of December (Fig. 9). This seasonal effect is responsible for a decrease of the mean number of WESEs observed per photograph by over 2.5 individuals, representing a

73% variation around the mean of 1.72 WESEs per photograph in my dataset. This decrease in apparent seal haul-out behaviour is unlikely to be caused solely by individuals spending less time hauled-out on the land-fast sea-ice in December compared to November. The more likely explanation for the size of the seasonal effect my model suggests is that between the 30th of October and 28th of December WESEs increasingly haul-out at a different location not captured by the three trail cameras. In other words, seals that were once hauled out and captured on these three trail cameras may have moved elsewhere in McMurdo Sound. First, non-reproductive WESEs still need to spend significant lengths of time resting on the fast-ice, but the lack of a pup allows individuals more flexibility in haul-out location based on environmental conditions. Second, the maximum length of time WESEs have been observed holding their breaths is in the region of 70-80 minutes (Zapol, 1987), making it highly unlikely they would be able to forage under the fast-ice for the entire length of time as some of the WESE-free gaps in my data, the longest of which reached five days. In the Vestfold Hills, East Antarctica, female reproductive WESEs were observed to spend less time hauled-out on fast-ice in December compared to October, but this decrease was around 10% –an order of magnitude less than my model suggests is occurring (Lake et al., 1997). This difference would be expected if female reproductive WESEs needed to continue hauling out to the same location to feed their pups.

Fewer WESEs hauled-out on the fast-ice at Cape Royds as the season progressed may reflect a geographic relocation of individuals in response to changes in land-fast sea-ice conditions or predator numbers. It is long known that WESEs exhibit regional movement within McMurdo Sound that is linked to fast-ice movement and the associated tidal cracks and pressure ridges that form at the interface between fast-ice and Ross Island (Stirling, 1969b). Reproductive individuals show high site fidelity, often breeding at the same site they were born (Cameron et al., 2007b). However, non-reproductive individuals such as those observed at Cape Royds tend to exhibit stronger regional movements associated with seasonal fast-ice availability (Croxall & Hiby, 1983). Furthermore, we know the distance to fast-ice edge is a significant predictor of WESE distribution, where there exists a certain 'ideal' distance away that WESEs are more likely to be located (Larue et al., 2019). The fact that a specific 'preferred' distance may exist implies that not only is there a benefit for WESEs to be located near the fast-ice edge (such as availability of access points to the ocean), but there must also be a cost associated with being too close to the ice-edge. In the case of the Cape Royds population, the likely cost is that of predation by mammal-eating, type-B killer whales. At Cape Royds, type-B killer whales arrive from mid-November onwards (Ainley et al., 2017). It is well known that the sequential breakup of fast-ice in the Ross Sea provides optimal foraging conditions for type-B killer whales, as the open water provides access to new pockets of prey on the fast-ice (Ainley & Ballard, 2012; Andrews et al., 2008). With this in mind, I find it plausible that the break-out of fast-ice at Cape Royds, from around the 20th of November (Table 4) and the associated increase in predation risk from killer whales are contributing to the decreasing trend of WESEs hauling-out as described by my model (Fig. 9).

The suggestion, therefore, is that the decrease of WESEs observed hauling-out on the fast-ice at Cape Royds between the 30th of October and 28th of December 2017 is not due to a decreased propensity for individuals to haul-out, but due to regional movements of WESEs causing the haul-out location to be out of the frame of reference of the three cameras set up used to inform my model. This is an important caveat for my model, as it suggests that the effect of date is unique and specific to the Cape Royds population I observed. Different locations in McMurdo Sound and elsewhere on the continent will experience fast-ice break-out at different points in time, and different populations may experience different predation pressures. Therefore, such a strong seasonal decrease may occur at a different point in time, or not at all. This is in contrast with the other covariates in my model which may be more universally experienced by WESEs in the Ross Sea region or beyond.

Diurnal variation

My results suggest a haul-out cycle in the Cape Royds population of WESEs (Fig. 9), supporting previous work whom all confirm the general principle that more WESEs haul-out in the afternoon than in the morning, local time (Banner, 2012; Lake et al., 1997; Siniff et al., 1971; Smith, 1965; Stirling, 1969a; J. A. Thomas & DeMaster, 1983). This haul-out cycle does not appear to be the strongest effect on haul-out behaviour as suggested by a chi-sq value compared to temperature and date (Table 6) and size of the effect in comparison to other covariates (Fig. 9). The raw data seems to indicate the haul-out cycle is quite pronounced, with a peak of 2.5 and a trough of 1.1 individuals (Fig. 8) (a range of 1.4 individuals). However, the model suggests a gentler haul-out cycle, with a range of effect of only 0.8 individuals (Fig. 9). This is probably due to some of the diurnal variation being attributed by the GAM to other environmental covariates that may have a cyclical daily component, such as temperature which follows a clear diurnal pattern (Fig. 5).

The presence of a haul-out cycle is to be expected considering the wealth of knowledge documenting this phenomenon in other WESE populations. (Smith, 1965) conducted a 24-hour ground census of WESEs hauled-out on the fast-ice due south of Scott Base on two separate days in February 1963 and 1964, at this point in the year fast-ice has mostly broken out, leaving only open water, multi-year land-fast sea-ice, and the Ross Ice Shelf. A distinct daily pattern is visible in the raw data from this study, with maximum haul-out at 1600 NZST and minimum haul-out between 0100-0400 NZST in both years. This pattern is made particularly clear by the large number of individuals counted across the 24-hour period, with a peak of 700 and 450 individuals in 1963 and 1964 respectively. However, these data are only used to inform the remainder of the research by (Smith, 1965). The daily pattern was not modelled with respect to other environmental covariates. It is possible that the effect would be lessened after accounting for factors such as temperature in the same way as in my model. (Stirling, 1969a) also described a clear diurnal pattern in WESE haul-out, with a similar peak at 1600 NZST. This was again not modelled with respect to environmental covariates. Instead, the haul-out pattern was used directly to calibrate census data, by adjusting aerial fly-over counts by the time of day, to achieve a better estimate of WESE counts. Such methodology seems justified since in both cases the objective of recording the haul-out cycle was to standardise future counts at the same location, whether by only sampling at peak haul-out, or adjusting by the estimated proportion of population haul-out by the time of data collection. The underlying assumption of this method is that the haul-out cycle remains the same between its identification and the time of the following study. This is reasonable if the research informed by the haul-out cycle is conducted at the same location within the same season.

Previous work by (Banner, 2012) focused specifically on WESE haul-out in order to generate a more accurate understanding of the percentage of WESEs hauled-out onto the fast-ice at a given time. Thus allowing for the adjustment of satellite images by time of day to provide more accurate satellite census data. Trail camera counts were collected for a pupping WESE population at Big Razorback Island by McMurdo Station in 2010, and compared with estimates generated from satellite images taken at exactly the same time. After correction for temperature, tide, and wind speed, the diurnal haul-out cycle persisted with peak haul-out around 1700 NZST. Due to higher daily counts of seals at Big Razorback (around 20 a day), (Banner, 2012) was able to generate a separate haul-out cycle for each day of the study. This was not something I felt would be appropriate in my study, where a mean of 1.7 individuals per photograph would create a much less reliable haul-out pattern from a single day of data. However, the similarity in haul-out pattern, where my data had peak haul-out between 1200-2000 NZST (Fig. 9) is encouraging. A key point of distinction between the research of (Banner, 2012) and my study is that I looked at non-reproductive WESEs, in contrast to reproductive female adults. The fact that this haul-out cycle persists between both demographics drives home the point that it is not present purely as a result of females needing to balance the acts of foraging and weaning their pups. The presence of this cycle in non-reproductive WESEs implies that it is a more wide-ranging phenomenon governing WESE foraging strategy.

Although difficult to study (due to their preference for pack-ice and the marginal ice zone as a habitat (Wege et al., 2021)), there is evidence that such a haul-out cycle is present in other Antarctic phocids such as crabeater seals (*Lobodon carcinophagus*), which also display a peak haul-out in the afternoon, between 1200 and 1400 hrs local time (Bengtson & Stewart, 1992). To address similar questions, crabeater seals are harder to study due to their association with pack-ice leading to a much wider range and lack of stable populations near the shore such as with fast-ice obligate Weddell seals. Even less observational data has been collected for the elusive Ross seal, but again, the little evidence there is does seem to indicate a preference for spending more time on pack-ice during the afternoon, and more time in the ocean during the early morning (Southwell, 2003), though notably the Ross seal data was collected from only two individuals. This is clearly not representative of their entire population, however, the methods of this study (using radio transmitting tags to monitor an individual) is a powerful technique as it allows for the full tracking of a seal's behaviour over a period of time, in contrast to relying on placing cameras. In my study, it is uncertain whether a lack of seals in an image is due to a lack of haul-out, or a haul-out in a different location. With tagging data, these questions are easier to understand, as these tags largely record behaviours up to several times per second (Goetz, 2015).

My findings support the work of (Siniff et al., 1971). They tracked adult female WESEs in McMurdo Sound with radio-tags, and found them to be most active in the water between 0000 and 1000 NZST, and mostly inactive and hauled-out in the afternoon. regarding haul-out cycles and activity/behaviour, they also reaffirm the suggestion that WESEs haul-out on fast-ice in order to recover from foraging. The presence of a diurnal haul-out cycle persists in my model after accounting for the environmental covariates of temperature, pressure, and wind speed. This implies that the time of day cycle is inherent in WESE life history regardless of weather variables. It is possible that the haul-out cycle in WESEs evolved in response to a diurnal pattern of prey availability. In other non-Antarctic phocid species such as Arctic ringed seals (*Pusa hispida*) there is an observable relationship between diurnal haul-out cycle and plankton movements (T. G. Smith, 1973) or grey seals (*Halichoerus grypus*) that show a diurnal cycle in foraging behaviour linked to diurnal movements of sand eels (Photopoulou et al., 2014). It is well documented that motile plankton exhibit a vertical diurnal migration up and down the water column driven by movements in temperature gradients and sunlight availability (Kamykowski & Zentara, 1976; Wirtz & Smith, 2020). In McMurdo Sound, ocean dynamics tend to be dominated by High Salinity Shelf Water production from the Ross Ice Shelf, as opposed to a surface-thermocline (Lewis & Perkin, 1985) (a lack of which is common in polar waters due to surface cooling from cold air promoting mixing of the top layer). However, there still exists a diurnal variation in under-ice radiant flux due to shifting in sunlight angle (Matthes et al., 2019) which could drive vertical plankton movement even in the 24-hour sunlight of austral summer. (Stirling, 1969b) suggest that the activity of WESE prey may be higher during the "night" cycle, leading to increased hunting activity. Time-depth recording of eight adult WESEs supports the potential relationship between prey availability and haul-out (Plötz et al., 2001). Foraging dives increased in depth across the night, with the deepest dives occurring between 0800-1000 local time before diving depth reduced and individuals haul-out on the fast-ice. The depth of dives appears to be a behavioural response to the stratification of prey species at different depth layers (McIntyre et al., 2013). Such behaviour is consistent with a diurnal cycle of WESE prey availability within the water column, as a similar behaviour would be present if different foraging strategies were required at different times of the day. Therefore, I believe it is likely that the modelled diurnal WESE haul-out cycle is at least partially, the above-surface consequence of a foraging pattern driven by diurnal variation in prey availability. However, it does seem that temperature influenced this diurnal pattern, it is unsurprising that a species adapted to live in such a harsh environment would change its behaviour in response to changes in temperature. As the WESE haul-out cycle persists the implication is that time of day captures diurnal variation in some other environmental variable (abiotic or otherwise) that I did not record in this study.

Whilst generally considered as a large Antarctic predator, WESEs are also preyed upon by Type-B killer whales and leopard seals, where the taking of pups or juveniles contributes heavily to non-reproductive mortality rates (Fenwick, 1973). We know that WESEs have co-evolved with such predation pressure as we can observe various anti-predator responses such as the adjusting rate of calls rate and social behaviours based on perceived predation risk (J. Thomas et al., 1987). Given how common adjusting diurnal patterns as a tactic to reduce predation pressure are (Lima & Dill, 1990), it is possible that such a haul-out cycle forms part of an evolved anti-predatory strategy. However, the relationship between WESEs and their potential predators requires more attention, and I do not think there is conclusive evidence to support or reject this hypothesis.

Environmental covariates

One large advantage of Generalised Additive Models is that by using shrinkage base functions I can account for the near-collinearity between variables such as the seasonal variation in temperature in my dataset (Fig. 3 & 4), (Marra & Radice, 2010). This relationship is important to elucidate as it is clear from my data that temperature also follows a cyclical diurnal, and seasonal pattern (Fig. 5). This relationship is repeatedly noted in other studies, such as (Lake et al., 1997) observing peak WESE haul-out rates in the Vestfold Hills also coinciding with the warmest time of day.

My GAM shows a relationship between temperature and seal count, indicating that as temperature increases, the number of WESEs on the ice increases (Fig. 9). Secondly, with increasing wind speed, the number of seals decreases. It is important to take both into account simultaneously due to their influence on thermoregulation of Antarctic species. Wind speed has a significant impact on the perceived temperature an individual experiences, and it has been demonstrated that increases in windspeed can increase temperature flux due to the continuous removal of warmed air maintaining a steep temperature gradient (Beltran et al., 2016).

WESEs have evolved in conjunction with the extreme temperatures of the Antarctic, (Stirling, 1977; Zapol, 1987). Consequently, a reduced WESE haul-out in colder conditions could be a behavioural response to supplement their physiological adaptations to the cold weather. They have already developed a high thermoregulatory buffer, as their thick layer of blubber can simultaneously act as an effective insulator and deep store of metabolic energy (J. A. E. Mellish et al., 2011), which allows them to spend time hauled-out on the sea-ice surface for extended periods of time despite negative air temperatures. They also utilize the variation in temperature over seasonal scales for maximum ecological benefit, as the temperature in the Ross Sea Region begins increasing in October through November, which coincides with WESE pups being born. This warming combined with the subsequent plankton blooms may have impacted the evolution of pupping timing in WESEs, as pups being smaller, with fewer reserves of metabolic energy have stricter thermodynamic requirements (Stirling, 1969b). The fewer hauled-out WESEs in colder temperatures as implied by my model support the work of (Boehme et al., 2016) who found that haul-out patterns in WESEs tend to be seasonally bimodal, with individuals spend a larger percentage of the day in the ocean during winter than in summer. The authors suggesting this could be a response to a threshold temperature where energy losses to lower air temperature (which can reach upward of -70°C in winter) outweigh energy losses to cold water. However, it is equally likely that such a change in haul-out pattern, as identified in their paper, is due to the increased foraging demands on female WESEs that need to build mass to support gestation costs (Shero et al., 2018).

Like most polar waters, the sub-ice water in McMurdo Sound tends to lack a thermocline and maintain temperatures of around -1.5°C (Madden et al., 2014). In winter, and even across my dataset, air temperatures in the Antarctic get much colder than McMurdo Sound. However, the dramatically higher thermal conductivity of water leads to larger thermal losses in the ocean than on ice at a given temperature. Whilst temperature and wind-speed are both shown to impact thermoregulatory capacity, (J. A. Mellish et al., 2015) the complexity of Weddell seal thermoregulatory systems, and different behavioural strategies in water and on ice, contribute to the difficulty of determining where exactly such a threshold temperature lies, and how it can vary between individuals and across time.

There is a tendency in ecology to view all individuals within a population as homogenous, being subject to the same pressures and making the same decisions in response to environmental stimuli. However, in reality, all individuals within a population are different and have unique preferences and responses to the environment. I think that the non-linear relationship of WESE haul-out to both the diurnal cycle and environmental stimuli like temperature and wind speed is an excellent example of this. Early research attempted to elucidate the effect of temperature on WESE haul-out to mixed success. (Smith, 1965) found the effect of temperature was limited outside of “bad weather”, however wind speed seemed to explain most of the variance the effect they observed varied on demographics, with only nursing individuals remaining on the ice. Furthermore, they observed a small scale variation in habitat use, with nursing females hauling out nearer to broken ice-ridges than males. The argument presented is that this variation in habitat use offered females more protection from the adverse weather effects they had to endure since they could not simply retreat under the ice and leave their pups alone.

A subsequent study by (Siniff et al., 1971) supported the argument that WESEs would prefer staying in the water during “bad weather”. With environmental variables primarily modifying behaviour during the peak haul-out times between 1700-2100. A hypothesis for this could be that warm weather would not make a WESE haul-out whilst foraging, but cold weather could encourage some seals to take shelter in the ocean instead of staying exposed on the sea ice. (Siniff et al., 1971) defined “bad weather” by a wind-chill index threshold to obtain a more objective proxy of bad weather. Such a definition could be followed up using a similar GAM analysis to the one I performed that includes an interactive effect between temperature and wind speed, instead of interpreting pressure as a proxy for bad weather.

In Queen Maud Land, East Antarctica (Sato et al., 2003) conducted ground counts of WESEs in the early afternoon (intentionally counting at peak haul-out). They found that the number of WESEs on fast-ice decreased under higher wind speeds and lower temperatures. However, even on relatively calm and warm days, there was a lot of variation in exact WESE numbers, indicating that there were still independent decisions being undertaken by individual seals. Further research in the Vestfold Hills found that wind speed and temperature were the strongest environmental descriptors of WESE winter haul-out with decreasing numbers of individuals at lower temperatures, and higher wind speeds (Andrews-Goff et al., 2010). Further research of reproductive WESEs at McMurdo used infra-red cameras to monitor body heat-flux (Mellish et al., 2015). This research was comprehensive, covering pups, juveniles, post-weaning females, and skip-breeding females. Across all four demographics, the biggest environmental contributor to loss of body temperature was wind speed. Higher winds contributed to a larger heat loss, as the air surrounding an individual is continually replaced by fresh colder air, maintaining a steep temperature gradient between the warm skin and cool air. Furthermore, this behaviour of retreating into the water in bad weather conditions appears to be present in other seal species such as Crabeater seals, which prefer spending more time hauled-out when it is warmer (Bengtson & Cameron, 2004). It seems reasonable to suggest that both species experience similar thermoregulatory pressures as part of their daily life in the Antarctic.

It is clear that temperature, wind speed and thermoregulation are intrinsically linked. The need for reduced model complexity prevented the exploration of interactive terms between temperature and wind speed in this model, but that is certainly something that could be explored in subsequent analyses. It seems probable that there is some level of thermoregulatory incentive to haul-out variation, but this certainly does not explain all the variation and is just a component. Whilst I have assumed that less heat loss will occur on ice partially due to a decreased metabolic rate, it is certainly the case that male Weddell seals can also rest under the sea-ice (Stirling, 1969b), as well as perform other behaviours not related to foraging, such as the vicious defence of underwater territories (Brusa et al., 2020). This could theoretically increase the critical threshold temperature at which Weddell seals lose less energy to the environment in the ocean vs hauled-out, thus providing a mechanism by which a wind speed-temperature complex would be a motivating factor in seal behaviour.

The perceived effect of temperature and wind speed seems in contrast to some earlier research. Which has found these factors to be less important than loosely defined "bad weather" (Siniff et al., 1970), or (Smith, 1965) who found that non-pupping WESEs; freed from their responsibilities of caring for less robust young, would flee into the water to escape local blizzards. In my study, I interpret the role of pressure as a more quantitative measure of weather quality. GAM output seems to suggest that there is a threshold pressure of around 980 kPa below which you get fewer seals, and above there are more (Fig. 9). This is in line with early observations of "bad weather" if we treat pressure as a proxy for such. Low-pressure systems tend to be associated with atmospheric phenomena often viewed as "bad weather", such as the drop in temperatures and increased windspeed already accounted for in the model, but also variables that were unaccounted for, such as increased precipitation, reduced visibility, or increased cloud cover (Speer et al., 2009). Indeed, lower pressure systems are associated with higher snow-fall events in Ross Island too (Cohen et al., 2013). Precipitation is a fairly significant determinant of bad weather and not something that was recorded by the AWS systems used in my study. As such, the relationship between haul-out and pressure in my model can be interpreted as WESEs appearing to haul-out in greater numbers during fine weather conditions.

Generalised Additive Model

My model identifies a large variation in WESE count between the three trail cameras (Fig. 9), which were placed in the same location but at slightly different angles viewing the fast ice. While the absolute number of seals recorded by each camera is different, the actual impact of model covariates should be consistent across all three sites given their proximity to each other, and to the AWS at Marble Point which provided the environmental data that informs my model. If I did not define camera as a random effect, the model would underestimate the dependency of the WESE count observations within each camera and the shrinkage smoothing functions would not be able to account for the correlation between some variables in the dataset, such as between temperature and date (Fig. 2). This would lead to an over-fitted model. At this point, it is worth noting that all variables have highly significant p-values (Table 6). This is in part due to the nature of GAMs, where the p-value is associated with the distribution of the response in association with a smoothing parameter, instead of the choice of the actual smoothing term (Bradshaw et al., 2004). In simpler terms, the p-values indicate how well the modelled relationship fits the data, however, the relationship could still have no biological effect (such as a linear relationship with a gradient of zero).

Assumptions and limitations

The two largest assumptions I make with my modelling are: that the environmental covariates collected at Marble Point relate to the environmental conditions at Cape Royds, and that sampling effort across the data set is consistent. Despite Marble Point being approximately 60 km away, the GAM performance is reasonable, with 56.9% of deviance explained (Table 6). This indicates that between the 30^{th} of October and 28^{th} of December 2017, weather at Marble Point is at least somewhat consistent with Cape Royds. Secondly, the visual comparison of weather data at 3 separate AWS (Cape Bird, Willie Fields, and Marble Point) triangulated around Cape Royds, implied broad consistencies. I think it is justified to use the weather data at Marble Point as an inference point, however, this is clearly a limitation; if geographically closer data were available, a more accurate model of WESE haul-out behaviour could be built.

There is a potential that a systematic difference in sampling effort across the dataset exists. The number of low-quality photographs varies by time of day, with the highest percentage of low-quality photographs having been taken in the early afternoon, between 1200-1600 NZST (Fig. 6). Such a pattern of low-quality photographs is consistent with the sun generating lens glare in the afternoon in a set of west-facing cameras. As low-quality photographs represent my decreased confidence in spotting all individuals that were hauled-out in an image, it also suggests that some under-sampling of WESE counts may be occurring in the afternoon. I decided against including this as a parameter within my model, as I felt that my rating of perceived overexposure of each image was very subjective, especially between medium and high-quality photographs. While being able to identify white-outs was fairly straightforward, trying to get a measure of how overexposed an image of already white sea-ice was more challenging. Furthermore, photograph quality depended quite heavily on the camera, with camera #2 being at the highest vantage-point, it experienced the least overexposure from sunlight reflection due to its higher angle relative to the fast-ice surface, whilst camera #3 experienced the most over-exposure, and consequently the most low-quality photographs since its proximity to the ice-surface lead to more light-flux hitting the lens. The fact that quality measure was so subjective and camera-specific, meant I was more comfortable using camera as a random factor to also account for this variability in photo quality, rather than use my measure of photo quality directly. Finally, since most low-quality photographs, and therefore under-sampling, occurs in the early afternoon, this would imply that I detected fewer seals in the afternoon than there were actually present. Consequently, the haul-out cycle I detected might be slightly stronger than I calculated as by under-sampling in the afternoon I suppressed the number of seals at peak haul-out. However, future research could account for variation in sampling effort by measuring the quality of an image in a more objective way

Conclusions

In summary, my study echo's the vast body of literature in identifying a diurnal cycle in WESE haul-out. Critically, this haul-out pattern remains even once accounting for the environmental variables of temperature, windspeed, and pressure. Unsurprisingly, WESEs are less likely to haul-out onto the fast-ice if the weather is unpleasant. The fact that non-reproductive WESEs also display a haul-out cycle is interesting and worth exploring further, as it implies that the presence of haul-out cycle is not entirely linked to the demands of raising young in Antarctica. To conduct this research I only used trail cameras from one location, but the methods used could be reasonably reproduced with cameras covering a wider range of WESE colonies. If in the future, data are collected from multiple locations or multiple seasons, more complex models could be constructed to further elucidate the roles of various environmental parameters. The biggest effects that could be looked at further are certainly interactive ones between wind-speed and temperature, certainly no-one can dispute the impact windchill can have in the Antarctic.

This study has implications for remote sensing surveys of ice-obligate seals and other Antarctic animals. Firstly, it demonstrates the importance of trail cameras as a remote sensing technology. In this case, three Cuddeback trail cameras were opportunistically set up at a field site where researchers conducted studies on a completely different species, the Adélie penguin. These cameras were left unattended for two months before recovery. Combined with long-term monitoring of environmental conditions provided by the University of Wisconsin, it has been possible to tease out clear behaviours of ecological significance. There are obvious limitations to a camera set-up like this, such as the limited field of view covered, or lens flair generated by a low-angle sun. However, these are not challenges that can't be solved by increasing the number of cameras and using UV filters to limit to prevent glare. Trail cameras have already been used to great effect in the Antarctic, such as the Penguin Watch project (Jones et al., 2018), where over 70,000 photographs from 15 cameras at penguin colonies in the Antarctic peninsula have created a deluge of data from which ecological information can be teased. With the continually increasing quality of battery and data storage devices, there has never been a better time for supplementing Antarctic data collection with trail camera technology.

Remote sensing can also be performed by satellite-based imagery, as it is being increasingly used within ecology to monitor populations (Moxley et al., 2017). However, satellite imagery presents a single snapshot in time. As is clear by the presence of a WESE haul-out cycle, satellite imagery would likely contain count discrepancies caused by differences in time of day of photographs taken (LaRue et al., 2011). Thus far, the majority of studies conduct their own estimates of daily haul-out in order to calibrate their work. However, this needs to be conducted repeatedly with each new population observed. The methods of my study could be extended further to build a comprehensive model used to predict the proportion of WESEs hauled-out at a given time, given certain environmental conditions such as weather, wind speed, and pressure. When paired together these two remote sensing techniques could prove powerful tools for generating population estimates at a much larger scale.

Better satellite census data is a critical step in understanding the wide-scale ecology of WESEs in both the Ross Sea region and Antarctica as a whole. As WESEs exhibit a circumpolar distribution (Langley et al., 2018; J. A. E. Mellish et al., 2011) they will experience the full range of changing environmental conditions from a warming peninsula, marine ice-sheet collapse, to reduced fish-stock in the Ross Sea (Ainley et al., 2015; Joughin et al., 2014; Vaughan et al., 2003). Monitoring how WESEs react to these changes will be a critical step in understanding the impact humanity is having on the planet and what this means specifically for the Antarctic continent and its associated ecosystems.

References

Ainley, D. G., & Ballard, G. (2012). Trophic interactions and population trends of killer whales (Orcinus orca) in the southern Ross Sea. *Aquatic Mammals*, *38*(2), 153–160. https://doi.org/10.1578/AM.38.2.2012.153

Ainley, D. G., Ballard, G., Karl, B. J., & Dugger, K. M. (2005). Leopard seal predation rates at penguin colonies of different size. *Antarctic Science*, *17*(3), 335–340. https://doi.org/10.1017/S0954102005002750

Ainley, D. G., Cziko, P. A., Larue, M., Nur, N., Rotella, J. J., Eastman, J. T., Stirling, I., & Abrams, P. A. (2020). *Perspective Further evidence that Antarctic tooth fish are important to Weddell seals*. *13*, 1–13. https://doi.org/10.1017/S0954102020000437

Ainley, D. G., Larue, M. A., Stirling, I., Stammerjohn, S., & Siniff, D. B. (2015). An apparent population decrease, or change in distribution, of Weddell seals along the Victoria Land coast. *Marine Mammal Science*, *31*(4), 1338–1361. https://doi.org/10.1111/mms.12220

Ainley, D. G., Lindke, K., Ballard, G., Lyver, P. O. B., Jennings, S., Toniolo, V., Pennycook, J., Massaro, M., & Santora, J. A. (2017). Spatio-temporal occurrence patterns of cetaceans near Ross Island, Antarctica, 2002–2015: implications for food web dynamics. *Polar Biology*, *40*(9), 1761–1775. https://doi.org/10.1007/s00300-017-2100-9

Ainley, D. G., & Siniff, D. B. (2009). The importance of antarctic toothfish as prey of Weddell seals in the ross sea. *Antarctic Science*, *21*(4), 317–327. https://doi.org/10.1017/S0954102009001953

Albrecht, A. R. T. (2014). *Six priorities for Antarctic science*. 5–7.

Andrews-Goff, V., Hindell, M. A., Field, I. C., Wheatley, K. E., & Charrassin, J. B. (2010). Factors influencing the winter haulout behaviour of Weddell seals: Consequences for satellite telemetry. *Endangered Species Research*, *10*(1), 83–92. https://doi.org/10.3354/esr00257

Andrews, R. D., Pitman, R. L., & Ballance, L. T. (2008). Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. *Polar Biology*, *31*(12), 1461–1468. https://doi.org/10.1007/s00300-008-0487-z

Banner, K. M. (2012). *Correcting for Time-of-Day to Compare Satellite Images and Ground Counts of Weddell Seals in Big Razorback Haul-Out (Erebus Bay, Antarctica)*. http://www.math.montana.edu/grad/writing-projects/12banner.pdf

Beltran, R. S., Testa, J. W., & Burns, J. M. (2016). An agent-based bioenergetics model for predicting impacts of environmental change on a top marine predator, the Weddell seal. *Department of Biology* *and Wildlife, University of Alaska Fairbanks*.

Bengtson, J. L., & Cameron, M. F. (2004). Seasonal haulout patterns of crabeater seals (Lobodon carcinophaga). *Polar Biology*, *27*(6), 344–349. https://doi.org/10.1007/s00300-004-0597-1

Bengtson, J. L., & Stewart, B. S. (1992). Diving and haulout behavior of crabeater seals in the Weddell Sea, Antarctica, during March 1986. *Polar Biology*, *12*(6–7), 635–644. https://doi.org/10.1007/BF00236986

Blanchet, M. A., Lydersen, C., Ims, R. A., & Kovacs, K. M. (2015). Seasonal, oceanographic and atmospheric drivers of diving behaviour in a temperate seal species living in the high arctic. *PLoS ONE*, *10*(7), 1–28. https://doi.org/10.1371/journal.pone.0132686

Boehme, L., Baker, A., Fedak, M., Årthun, M., Nicholls, K., Robinson, P., Costa, D., Biuw, M., & Photopoulou, T. (2016). Bimodal winter haul-out patterns of adult Weddell seals (Leptonychotes weddellii) in the southern Weddell Sea. *PLoS ONE*, *11*(5), 1–19. https://doi.org/10.1371/journal.pone.0155817

Bradshaw, C. J. A., Higgins, J., Michael, K. J., Wotherspoon, S. J., & Hindell, M. A. (2004). At-sea distribution of female southern elephant seals relative to variation in ocean surface properties. *ICES Journal of Marine Science*, *61*(6), 1014–1027. https://doi.org/10.1016/j.icesjms.2004.07.012

Brusa, J. L., Rotella, J. J., Garrott, R. A., Paterson, J. T., & Link, W. A. (2020). Variation of annual apparent survival and detection rates with age, year and individual identity in male Weddell seals (Leptonychotes weddellii) from long-term mark-recapture data. *Population Ecology*, *62*(1), 134–150. https://doi.org/10.1002/1438-390X.12036

Burns, J. M., Castellini, M. A., & Testa, J. W. (1999). Movements and diving behavior of weaned Weddell seal (Leptonychotes weddellii) pups. *Polar Biology*, *21*(1), 23–36. https://doi.org/10.1007/s003000050329

Cameron, M. F., Siniff, D. B., Proffitt, K. M., & Garrott, R. A. (2007a). Site fidelity of Weddell seals: The effects of sex and age. *Antarctic Science*, *19*(2), 149–155. https://doi.org/10.1017/S0954102007000223

Cameron, M. F., Siniff, D. B., Proffitt, K. M., & Garrott, R. A. (2007b). Site fidelity of Weddell seals: The effects of sex and age. *Antarctic Science*, *19*(2), 149–155. https://doi.org/10.1017/S0954102007000223

Ciannelli, L., Fauchald, P., Chan, K. S., Agostini, V. N., & Dingsør, G. E. (2008). Spatial fisheries ecology: Recent progress and future prospects. *Journal of Marine Systems*, *71*(3–4), 223–236. https://doi.org/10.1016/j.jmarsys.2007.02.031

Cohen, L., Dea, S., & Renwick, J. (2013). Synoptic weather types for the ross sea region, Antarctica. *Journal of Climate*, *26*(2), 636–649. https://doi.org/10.1175/JCLI-D-11-00690.1

Croxall, J. P., & Hiby, L. (1983). Fecundity , Survival and Site Fidelity in Weddell Seals , Leptonychotes weddelli. *British Ecological Society*, *20*(1), 19–32.

Curtis, C., Stewart, B. S., & Karl, S. A. (2011). Genetically effective population sizes of Antarctic seals estimated from nuclear genes. *Conservation Genetics*, *12*(6), 1435–1446. https://doi.org/10.1007/s10592-011-0241-x

Cutler, T. L., & Swann, D. E. (1999). Using remote photography in wildlife ecology: A review. *Wildlife Society Bulletin*, *27*(3), 571–581.

Davis, R. W., Fuiman, L. A., Williams, T. M., Collier, S. O., Hagey, W. P., Kanatous, S. B., Kohin, S., & Horning, M. (1999). Hunting behavior of a marine mammal beneath the antarctic fast ice. *Science*, *283*(5404), 993–996. https://doi.org/10.1126/science.283.5404.993

Fenwick, G. D. (1973). Breeding Biology and Population Dynamics of the Weddell Seal, Leptonychotes weddelli: A Review. *Department of Zoology, University of Canterbury*, *Mauri Ora*, 29–36.

Forcada, J., Trathan, P. N., Boveng, P. L., Boyd, I. L., Burns, J. M., Costa, D. P., Fedak, M., Rogers, T. L., & Southwell, C. J. (2012). Responses of Antarctic pack-ice seals to environmental change and increasing krill fishing. *Biological Conservation*, *149*(1), 40–50. https://doi.org/10.1016/j.biocon.2012.02.002

Fretwell, P. T., Scofield, P., & Phillips, R. A. (2017). Using super-high resolution satellite imagery to census threatened albatrosses. *Ibis*, *159*(3), 481–490. https://doi.org/10.1111/ibi.12482

Fuiman, L. A., Williams, T. M., & Davis, R. W. (2020). Homing tactics of Weddell seals in the Antarctic fast-ice environment. *Marine Biology*, *167*(8), 1–16. https://doi.org/10.1007/s00227-020-03730-w

Garrott, R. A., Rotella, J. J., Siniff, D. B., Parkinson, C. L., & Stauffer, G. E. (2012). Environmental variation and cohort effects in an Antarctic predator. *Oikos*, *121*(7), 1027–1040. https://doi.org/10.1111/j.1600-0706.2011.19673.x

Goetz, K. T. (2015). Movement, Habitat, and Foraging Behaviour of Weddell Seals (Leptonychotes Weddellii) in the Western Ross Sea, Antarctica. *UC Santa Cruz*, 1920–2020. https://escholarship.org/uc/item/0jx2107r

Griffiths, M., & Van Schaik, C. P. (1993). Camera-Trapping: A new Tool for the study of Elusive Rain Forest. *Animals Tropical Biodiversity*, *1*(June), 131–135.

Gurarie, E., Bengtson, J. L., Bester, M. N., Blix, A. S., Cameron, M., Bornemann, H., Nordøy, E. S., Plötz, J., Steinhage, D., & Boveng, P. (2017). Distribution, density and abundance of Antarctic ice seals off Queen Maud Land and the eastern Weddell Sea. *Polar Biology*, *40*(5), 1149–1165. https://doi.org/10.1007/s00300-016-2029-4

Hastings, K. K., & Testa, J. W. (1998). Maternal and birth colony effects on survival of Weddell seal offspring from McMurdo Sound, Antarctica. *Journal of Animal Ecology*, *67*(5), 722–740. https://doi.org/10.1046/j.1365-2656.1998.00242.x

Jones, F. M. (2019). *Using the Penguin Watch network to examine phenology and breeding success in Pygoscelis penguins By*.

Jones, F. M., Allen, C., Arteta, C., Arthur, J., Black, C., Emmerson, L. M., Freeman, R., Hines, G., Lintott, C. J., Machkov, Z., Miller, G., Simpson, R., Southwell, C., Torsey, H. R., Zisserman, A., & Hart, T. (2018). Data Descriptor: Time-lapse imagery and volunteer classifications from the Zooniverse Penguin Watch project. *Scientific Data*, *5*, 1–13. https://doi.org/10.1038/sdata.2018.124

Joughin, I., Smith, B. E., & Medley, B. (2014). Marine ice sheet collapse potentially under way for the Thwaites Glacier Basin, West Antarctica. *Science*, *May*, 735–739.

Kamykowski, D., & Zentara, S.-J. (1976). The diurnal vertical migration of motile phytoplankton through temperature gradients. *University of Texas Marine Science Institute*, *18*, 99–112. https://doi.org/10.31392/iscs.2021.18.099

Kennicutt, M. C., Bromwich, D., Liggett, D., Njåstad, B., Peck, L., Rintoul, S. R., Ritz, C., Siegert, M. J., Aitken, A., Brooks, C. M., Cassano, J., Chaturvedi, S., Chen, D., Dodds, K., Golledge, N. R., Le Bohec, C., Leppe, M., Murray, A., Nath, P. C., … Chown, S. L. (2019). Sustained Antarctic Research: A 21st Century Imperative. *One Earth*, *1*(1), 95–113. https://doi.org/10.1016/j.oneear.2019.08.014

Kim, S., Saenz, B., Scanniello, J., Daly, K., & Ainley, D. (2018). Local climatology of fast ice in McMurdo Sound, Antarctica. *Antarctic Science*, *30*(2), 125–142. https://doi.org/10.1017/S0954102017000578

Lake, S. E., Burton, H. R., & Hindell, M. A. (1997). Influence of time of day and month on Weddell seal haul-out patterns at the Vestfold Hills, Antarctica. *Polar Biology*, *18*(5), 319–324. https://doi.org/10.1007/s003000050194

Landres, P. B., Verner, J., & Thomas, J. W. (1988). Ecological Uses of Vertebrate Indicator Species: A Critique. *Conservation Biology*, *2*(4), 316–328. https://doi.org/10.1111/j.1523-1739.1988.tb00195.x

Langley, I., Fedak, M., Nicholls, K., & Boehme, L. (2018). Sex-related differences in the postmolt distribution of Weddell seals (Leptonychotes weddellii) in the southern Weddell Sea. *Marine Mammal Science*, *34*(2), 403–419. https://doi.org/10.1111/mms.12461

LaRue, M. A., Ainley, D. G., Pennycook, J., Stamatiou, K., Salas, L., Nur, N., Stammerjohn, S., & Barrington, L. (2020). Engaging 'the crowd' in remote sensing to learn about habitat affinity of the Weddell seal in Antarctica. *Remote Sensing in Ecology and Conservation*, *6*(1), 70–78. https://doi.org/10.1002/rse2.124

LaRue, M. A., Rotella, J. J., Garrott, R. A., Siniff, D. B., Ainley, D. G., Stauffer, G. E., Porter, C. C., & Morin, P. J. (2011). Satellite imagery can be used to detect variation in abundance of Weddell seals (Leptonychotes weddellii) in Erebus Bay, Antarctica. *Polar Biology*, *34*(11), 1727–1737. https://doi.org/10.1007/s00300-011-1023-0

Larue, M. A., Salas, L., Nur, N., Ainley, D. G., Stammerjohn, S., Barrington, L., Stamatiou, K., Pennycook, J., Dozier, M., Saints, J., & Nakamura, H. (2019). *Physical and ecological factors explain the distribution of Ross Sea Weddell seals during the breeding season*. *612*, 193–208.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, *68*(4), 619–640. https://doi.org/10.1139/z90-092

Lynch, T. P., Foster, S., Devine, C., Hegarty, A., McEnnulty, F., Burton, M., & Lyle, J. M. (2020). Trail camera video systems: Investigating their utility in interpreting patterns of marine, recreational, trailer-boat fishers' access to an offshore Marine Park in differing weather conditions. *ICES Journal of Marine Science*, *77*(7–8), 3110–3126. https://doi.org/10.1093/icesjms/fsaa209

Madden, K. M., Fuiman, L. A., Williams, T. M., & Davis, R. W. (2014). Weddell seal foraging dives: Comparison of free-ranging and isolated-hole paradigms. *Antarctic Science*, *27*(1), 57–68. https://doi.org/10.1017/S0954102014000297

Mannas, J. M. (2011). *Assessing Weddell seal maternal investment in offspring*. *May*.

Marra, G., & Radice, R. (2010). Penalised regression splines: Theory and application to medical research. *Statistical Methods in Medical Research*, *19*(2), 107–125. https://doi.org/10.1177/0962280208096688

Marvin, D. C., Koh, L. P., Lynam, A. J., Wich, S., Davies, A. B., Krishnamurthy, R., Stokes, E., Starkey, R., & Asner, G. P. (2016). Integrating technologies for scalable ecology and conservation. *Global Ecology and Conservation*, *7*, 262–275. https://doi.org/10.1016/j.gecco.2016.07.002

Matthes, L. C., Ehn, J. K., Girard, S. L., Pogorzelec, N. M., Babin, M., & Mundy, C. J. (2019). Average cosine coefficient and spectral distribution of the light field under sea ice: Implications for primary production. *Elementa*, *7*(1). https://doi.org/10.1525/elementa.363

McIntosh, R. R., Kirkwood, R., Sutherland, D. R., & Dann, P. (2015). Drivers and annual estimates of marine wildlife entanglement rates: A long-term case study with Australian fur seals. *Marine Pollution Bulletin*, *101*(2), 716–725. https://doi.org/10.1016/j.marpolbul.2015.10.007

McIntyre, T., Stansfield, L. J., Bornemann, H., Plötz, J., & Bester, M. N. (2013). Hydrographic influences on the summer dive behaviour of Weddell seals (Leptonychotes weddellii) in Atka Bay, Antarctica. *Polar Biology*, *36*(11), 1693–1700. https://doi.org/10.1007/s00300-013-1384-7

Mellish, J. A. E., Hindle, A. G., & Horning, M. (2011). Health and condition in the adult Weddell seal of McMurdo Sound, Antarctica. *Zoology*, *114*(3), 177–183. https://doi.org/10.1016/j.zool.2010.11.007

Mellish, J. A., Hindle, A., Skinner, J., & Horning, M. (2015). Heat loss in air of an Antarctic marine mammal, the Weddell seal. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *185*(1), 143–152. https://doi.org/10.1007/s00360-014-0868-2

Monaghan, A. J., Bromwich, D. H., Powers, J. G., & Manning, K. W. (2005). The climate of the McMurdo, Antarctica, region as represented by one year of forecasts from the Antarctic Mesoscale Prediction System. *Journal of Climate*, *18*(8), 1174–1189. https://doi.org/10.1175/JCLI3336.1

Moxley, J. H., Bogomolni, A., Hammill, M. O., Moore, K. M. T., Polito, M. J., Sette, L., Sharp, W. B., Waring, G. T., Gilbert, J. R., Halpin, P. N., & Johnston, D. W. (2017). Google haul out: Earth observation imagery and digital aerial surveys in coastal wildlife management and abundance estimation. *BioScience*, *67*(8), 760–768. https://doi.org/10.1093/biosci/bix059

Nylen, T. H., Fountain, A. G., & Doran, P. T. (2004). Climatology of katabatic winds in the McMurdo dry valleys, southern Victoria Land, Antarctica. *Journal of Geophysical Research: Atmospheres*, *109*(3), 1–9. https://doi.org/10.1029/2003jd003937

Photopoulou, T., Fedak, M. A., Thomas, L., & Matthiopoulos, J. (2014). Spatial variation in maximum dive depth in gray seals in relation to foraging. *Marine Mammal Science*, *30*(3), 923–938. https://doi.org/10.1111/mms.12092

Plötz, J., Bornemann, H., Knust, R., Schröder, A., & Bester, M. (2001). Foraging behaviour of Weddell seals, and its ecological implications. *Polar Biology*, *24*(12), 901–909. https://doi.org/10.1007/s003000100297

Robinson, E. S. (1963). Geophysical investigations in McMurdo Sound, Antarctica. *Journal of Geophysical Research*, *68*(1), 257–262. https://doi.org/10.1029/jz068i001p00257

Rotella, J. J., Link, W. A., Chambert, T., Stauffer, G. E., & Garrott, R. A. (2012). Evaluating the demographic buffering hypothesis with vital rates estimated for Weddell seals from 30years of mark-recapture data. *Journal of Animal Ecology*, *81*(1), 162–173. https://doi.org/10.1111/j.1365-2656.2011.01902.x

Salas, L., Nur, N., Ainley, D., Burns, J., Rotella, J., & Ballard, G. (2017). Coping with the loss of large, energy-dense prey: A potential bottleneck for Weddell Seals in the Ross Sea: A. *Ecological Applications*, *27*(1), 10–25. https://doi.org/10.1002/eap.1435

Sato, K., Tsuchiya, Y., Kudoh, S., & Naito, Y. (2003). Meteorological factors affecting the number of Weddell seals hauling-out on the ice during the molting season at Syowa Station, East Antarctica. *Polar Bioscience*, *16*, 98–103.

Shero, M. R., Goetz, K. T., Costa, D. P., & Burns, J. M. (2018). Temporal changes in Weddell seal dive behavior over winter: Are females increasing foraging effort to support gestation? *Ecology and Evolution*, *8*(23), 11857–11874. https://doi.org/10.1002/ece3.4643

Shero, M. R., Krotz, R. T., Costa, D. P., Avery, J. P., & Burns, J. M. (2015). How do overwinter changes in body condition and hormone profiles influence Weddell seal reproductive success? *Functional Ecology*, *29*(10), 1278–1291. https://doi.org/10.1111/1365-2435.12434

Siniff, D. B., DeMaster, D. P., Hofman, R. J., & Eberhardt, L. L. (1977). An Analysis of the Dynamics of a Weddell Seal Population. *Ecological Society of America*, *31*(4), 337–367.

Siniff, D. B., Tester, J. R., & Kuechle, V. B. (1971). Some observations on the activity patterns of Weddell seals as recorded by telemetry. In *Antarctic Pinnipedia* (Vol. 18). https://doi.org/10.1029/ar018p0173

Siniff, Donald B., Garrott, R. A., Rotella, J. J., Fraser, W. R., & Ainley, D. G. (2008). Opinion: Projecting the effects of environmental change on Antarctic seals. *Antarctic Science*, *20*(5), 425–435. https://doi.org/10.1017/S0954102008001351

Smith, M. S. R. (1965). *Seasonal Movements of the Weddell Seal in McMurdo Sound, Antarctica*. *29*(3), 464–470.

Smith, T. G. (1973). Population Dynamics of the Ringed Seal in the Canadian Eastern Arctic. *Fisheries Research Board of Canada*, *181*.

Southwell, C. (2003). Haul-out behaviour of two Ross seals off eastern Antarctica. *Antarctic Science*, *15*(2), 257–258. https://doi.org/10.1017/S0954102003001251

Speer, M. S., Wiles, P., & Pepler, A. (2009). Low pressure systems off the New South Wales coast and associated hazardous weather: Establishment of a database. *Australian Meteorological and Oceanographic Journal*, *58*(1), 29–39. https://doi.org/10.22499/2.5801.004

Stearns, C. R. (1988). Research Results from Antarctic Automatic Weather Stations. *Deparment of Meteorology, University of Wisconsin, Madison*, *26*(1), 45–61.

Stirling, I. (1969a). Distribution and abundance of the Weddell seal in the western Ross Sea, Antarctica. *New Zealand Journal of Marine and Freshwater Research*, *3*(2), 191–200. https://doi.org/10.1080/00288330.1969.9515288

Stirling, I. (1969b). Ecology of the Weddell Seal in McMurdo Sound, Antarctica. *Ecology*, *50*(4), 573–586. https://doi.org/10.2307/1936247

Stirling, I. (1977). Adaptations of Weddell and ringed seals to exploit the polar fast ice habitat in the absence or presence of surface predators. *Adaptations within Antarctic Ecosystems. Proceedings of the 3rd SCAR Symposium on Antarctic Biology*, *January*, 741–748.

Testa, J. W., & Siniff, D. B. (1987). POPULATION DYNAMICS OF WEDDELL SEALS (LEPTONYCHOTES WEDDELLI) IN McMURDO SOUND, ANTARCTICA'. *Ecological Monographs*, *57*(2), 149–165.

Thomas, J. A., & DeMaster, D. P. (1983). Diel haul-out patterns of Weddell seal (Leptonychotes weddelli) females and their pups . *Canadian Journal of Zoology*, *61*(9), 2084–2086. https://doi.org/10.1139/z83-273

Thomas, J., Ferm, L., & Kuechle, V. (1987). Silence as an antipredation strategy by Weddell seals. *Antartic*

Journal, *808*, 232–234. http://oai.dtic.mil/oai/oai?verb=getRecord&metadataPrefix=html&identifier=ADA208289

Tin, T., Fleming, Z. L., Hughes, K. A., Ainley, D. G., Convey, P., Moreno, C. A., Pfeiffer, S., Scott, J., & Snape, I. (2009). Impacts of local human activities on the Antarctic environment. *Antarctic Science*, *21*(1), 3–33. https://doi.org/10.1017/S0954102009001722

Vaughan, D. G., Marshall, G. J., Connolley, W. M., Parkinson, C., Mulvaney, R., Hodgson, D. A., King, J. C., Pudsey, C. J., & Turner, J. (2003). Recent rapid regional climate warming on the Antarctic Peninsula. *Climate Change*, *60*, 243–274. https://doi.org/10.1017/S0016756800021464

Wege, M., Bornemann, H., Blix, A. S., Nordøy, E. S., Biddle, L., & Bester, M. N. (2021). Distribution and Habitat Suitability of Ross Seals in a Warming Ocean. *Frontiers in Marine Science*, *8*(May), 1–15. https://doi.org/10.3389/fmars.2021.659430

Wirtz, K., & Smith, S. L. (2020). Vertical migration by bulk phytoplankton sustains biodiversity and nutrient input to the surface ocean. *Scientific Reports*, *10*(1), 1–12. https://doi.org/10.1038/s41598-020-57890-2

Wood, S. N. (2008). Fast stable direct fitting and smoothness selection for generalized additive models. *Journal of the Royal Statistical Society. Series B: Statistical Methodology*, *70*(3), 495–518. https://doi.org/10.1111/j.1467-9868.2007.00646.x

Zapol, W. M. (1987). Diving Adaptations of the Weddell Seal. *Scientific American*, *256*(6), 100–105.

Zappes, I. A., Fabiani, A., Sbordoni, V., Rakaj, A., Palozzi, R., & Allegrucci, G. (2017). New data on Weddell seal (Leptonychotes weddellii) colonies: A genetic analysis of a top predator from the Ross Sea, Antarctica. *PLoS ONE*, *12*(8), 1–20. https://doi.org/10.1371/journal.pone.0182922

Appendices

Appendix A:

Automated Weather Station specifications as presented at: https://amrc.ssec.wisc.edu/aws/index.html

University of Wisconsin-Madison AWS Specifications

From Technical Manual for Automatic Weather Stations, by George A. Weidner, Department of Meteorology (now Atmospheric and Oceanic Sciences), University of Wisconsin-Madison, 1985.

Variable Sensor Specifications

Air Pressure	Paroscientific Model 215 A	Range: 0 to 1100 hPa Resolution: 0.050 hPa Accuracy: +/- 0.2 hPa (0.2 hPa/year long term drift)
Air Temperature	Weed PRT Two-wire bridge	Range: to -100 C minimum Resolution: 0.125 C Accuracy: +/- 0.5 C
Humidity	Vaisala HMP-35A (and other models)	Range: 0 to 100% Resolution: 1.0 % Accuracy: +/- 5.0 % down to -55 C Corrections possible for lower temperatures
Wind Direction	10 K Ohm pot.	Range: 0 to 355 Degrees Resolution: 1.5 Degrees Accuracy: +/- 3.0 Degrees
Wind Speed	Bendix/Belfort RM Young Hydro-Tech	Resolution/Accuracy: 0.25 +/- 0.5 m/s Resolution/Accuracy: 0.20 +/- 0.5 m/s Resolution/Accuracy: 0.33 +/- 2%
Temperature String	Thermocouple Two junction Copper-Cons.	Resolution: 0.06 C Accuracy: +/- 0.125 C