Distribution and diving behaviour of crabeater seals (*Lobodon carcinophaga*) in the Weddell Sea

Bachelorarbeit

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Summary

The crabeater seal (*Lobodon carcinophaga*) is the most abundant seal worldwide and inhabits the circumpolar pack ice zone of the Southern Ocean. Around half of its population is found in the Weddell Sea. By now, information on important environmental factors which affect their distribution as well as on geographic and seasonal differences in diving and foraging behaviour is limited due to the inaccessibility of their habitat.

In austral summer 1998, a heterogeneous group of 12 crabeater seals belonging to both sexes and different age classes was equipped with satellite-linked time-depth recorders (SDRs) at Drescher Inlet (72.85°S, 19.26°E) in the eastern Weddell Sea. The transmitters provided data for a duration between 7 and 117 days ($\bar{x}$ = 54.9 d). During this time the tagged seals dispersed radially in the Weddell Sea and covered large distances ($\bar{x}$ = 1,763 km). To identify environmental variables which influence the distribution of crabeater seals and to predict suitable habitats, a maximum entropy (Maxent) modelling approach was implemented. It revealed that sea ice concentration mattered most in modelling species distribution with increasing probabilities of presence towards the ice edge. However, seals spent an unusually high amount of 64.4% in open waters and were only occasionally found in ice-covered zones during the study period. This is likely to be related to the comparatively low sea ice cover of the Weddell Sea in summer 1998. Although crabeater seals are generally closely associated with pack ice, it seemed to be that they can deal better with open water conditions than previously thought. Further important factors identified by Maxent were surface temperature, water depth and distance to the shelf break. All these four environmental variables are known to influence and determine the distribution of Antarctic krill (*Euphausia superba*), the preferred prey of crabeater seals. In general, predicted suitable habitats were congruent with probable habitats of krill.

Beside geographic locations, satellite-linked data logger record dive data. Diving behaviour in this thesis was characterized by short (>90% = 0 – 5 min) and shallow (>80% = 0 – 72 m) dives. This pattern reflects the typical summer and autumn diving and foraging behaviour of crabeater seals since krill is abundant in the upper 150 m of the water column during summer. Differences between age classes were not evident. In contrast, diving behaviour showed seasonal differences with dives becoming shorter and shallower in autumn. This behaviour corresponds to the biology and ecology of krill which inhabits the under ice habitat during autumn and winter. This shows that both the vertical and horizontal distribution of crabeater seals is closely related to its primary prey.

Zusammenfassung

Die Krabbenfresserrobbe (*Lobodon carcinophaga*) ist die häufigste Robbenart der Welt und bewohnt die zirkumpolare Packeiszone des Südlichen Ozeans. Über die Hälfte der Population ist im Weddellmeer zu finden. Aufgrund der Unzugänglichkeit ihres Lebensraums sind bis dato nur wenige Informationen über wichtige Umweltfaktoren, welche die Verbeitung der Tiere beeinflussen, sowie über geographische und saisonale Unterschiede des Tauch- und Jagdverhaltens verfügbar.

Im Südsommer 1998 wurde eine heterogene Gruppe aus 12 Krabbenfresserrobben, bestehend aus beiden Geschlechtern und unterschiedlichen Altersklassen, mit satellitengestützen Tauchrekordern im Drescher Inlet (72.85°S, 19.26°E) im östlichen Weddellmeer besendert. Während der Sendezeit zerstreuten sich die Tiere sternförmig im Weddellmeer und legten dabei weite Strecken zurück ($\bar{x}$ = 1,763 km). Um Umweltvariabeln zu identifizieren, welche die Verteilung von Krabbenfresserrobben beeinflussen, und geeignete Habitate vorherzusagen, wurde ein modellierender Maximum-Entropie-Ansatz (Maxent) implementiert. Das Modell zeigte, dass die Meereiskonzentration den wichtigsten Beitrag zur Modellierung der Robbenverteilung leistete. Besonders hohe Wahrscheinlichkeiten des Vorkommens waren zum Eisrand hin zu entdecken. Allerdings verbrachten die Robben im Untersuchungszeitraum einen ungewöhnlich hohen Anteil von 64.4% im offenen Wasser und suchten nur gelegentlich eisbedeckte Gebiete auf. Dieses Verhalten ist wahrscheinlich mit der vergleichsweise geringen Meereisbedeckung des Weddellmeeres im Sommer 1998 verbunden. Obwohl Krabbenfresserrobben generell eng mit dem Packeis assoziiert sind, scheinen sie doch besser im offenen Wasser zurecht zu kommen als bisher vermutet. Weitere wichtige Faktoren, welche von Maxent identifiziert wurden, sind Meeresoberflächentemperatur, Wassertiefe und Distanz zum Kontinentalrand. Diese vier Umweltvariabeln sind bekannt dafür, dass sie die Verbreitung des Antarktischen Krills (*Euphausia superba*), der bevorzugten Beute von Krabbenfresserrobben, beeinflussen und bestimmen. Im Allgemeinen waren die modellierten, geeigneten Habitate deckungsgleich mit dem wahrscheinlichen Verbreitungsgebiet des Krills.

Neben geographischen Positionen nehmen satellitengestützte Datenlogger auch Tauchdaten auf. Das Tauchverhalten in dieser Arbeit war charakterisiert durch kurze (>90% = 0 – 5 min) und flache (>80% = 0 – 72 m) Tauchgänge. Dieses Muster spiegelt das typische Sommer- und Herbsttauchverhalten von Krabbenfresserrobben wider, da der Krill im Sommer vor allem in den oberen 150 m der Wassersäule zu finden ist. Unterschiede zwischen den Altersklassen waren nicht belegbar. Im Gegensatz dazu gab es jedoch saisonale Unterschiede im Tauchverhalten mit immer kürzer und flacher werdenden Tauchgängen. Dieses Verhalten entspricht der Biologie und Ökologie des Krills,

der im Herbst und Winter die Unterseite des Meereises als Habitat nutzt. Dies zeigt, dass sowohl die horizontale als auch vertikale Verteilung von Krabbenfresserrobben maßgeblich mit seiner Hauptnahrung zusammenhängt.

1. Introduction

The crabeater seal (*Lobodon carcinophaga*) is the most abundant pinniped species worldwide (Laws 1984) comprising an estimated population size between 7.3 and 12.3 million individuals of which approximately 50% are found in the Weddell Sea (Erickson & Hanson 1990, Bester & Odendaal 2000, Forcada & Trathan 2008, Southwell et al. 2012). The range of 5 million within the estimates shows that reliable abundance estimates are difficult to obtain since crabeater seals inhabit the hardly accessible Antarctic pack ice zone (Joiris 1991, Bester et al. 2002, Ackley et al. 2003, Southwell et al. 2012). Their life cycle is tightly coupled to the availability of sea ice that they occupy for breeding, mating and resting (Siniff et al. 1979, Bengtson & Cameron 2004, Southwell 2004). By now, only a few studies are available for giving an insight into distribution and habitat use of crabeater seals. They tend to be associated with medium to high sea ice concentrations throughout the year (Nordøy et al. 1995, Burns et al. 2004, Wall et al. 2007). Moreover, crabeater seals favor certain bathymetric features. They seem to be attracted by the continental shelf break and areas with ocean depths ranging between 2,500 and 5,000 m off the shelf (Nordøy et al. 1995, Ackley et al. 2003, Southwell et al. 2005, Wall et al. 2007). Nevertheless, there is still limited information about seasonal and geographic variation of distribution and habitat use of crabeater seals.

A common way to obtain such data is satellite telemetry. Animals are tagged with transmitting data loggers which are connected to polar orbiting satellite systems as the Argos System (Argos 1996, Read 2009). During an overpass the satellite receives uplinked messages and can determine the position of the transmitter using the Doppler shift algorithm (Costa 1993). As a result, the animal's movements can be tracked. Additionally, these loggers are able to record a variety of data. For example, the application of satellite-linked time-depth recorders (SDRs) in marine mammal studies led to an improved understanding of migrations and movement patterns (Costa 1993). Since this type of transmitters was available and affordable, they were used increasingly in multiple studies, especially in inaccessible areas like the Antarctic, but to only a limited extent in crabeater seals (Nordøy et al. 1995, Burns et al. 2004, Wall et al. 2007).

The aim of this thesis is to enhance knowledge about which environmental factors influence the distribution and movements of crabeater seals in the Weddell Sea. The dependence on sea ice will be highlighted. Several studies found a close relationship between seal occurrence and sea ice concentration (Joiris 1991, Nordøy et al. 1995, Burns et al. 2004, Wall et al. 2007). However, during the study period in 1998 the sea ice cover of the Weddell Sea was comparatively low with pack ice virtually absent in the eastern Weddell Sea (Bester & Odendaal 2000, Cavalieri & Parkinson 2008, Schwegmann 2012). Thus, it will be investigated how crabeater seals deal with such open water conditions by connecting each seal location with corresponding satellite observation data of sea ice concentration. Furthermore, a presence-only habitat modelling approach will be conducted called maximum entropy (Maxent). Maxent predicts the probability of presence of a certain species in the study area on the basis of known environmental variables by identifying the probability distribution of maximum entropy (Phillips et al. 2006). Environmental factors which are essential for their distribution will be detected and suitable habitats in the Weddell Sea will be revealed. Identifying favored habitat conditions is especially important in the context of a recent initiative led by Germany for creating a large marine protected area in the Weddell Sea (Teschke et al. 2013). By the help of Maxent modelling the following hypotheses will be investigated:

Suitable habitats for crabeater seals are associated with:

1) medium to high sea ice concentration.
2) ocean depths ranging between 2,500 and 5,000 m.
3) proximity to the continental shelf break.

Satellite-linked data logger can also provide information on activities at sea, e.g. diving and foraging behaviour (Costa 1993). Several studies documented the diving behaviour of crabeater seals in different areas around Antarctica and during different seasons. They perform short and shallow dives lasting less than 5 min and penetrating the upper 50 m of the water column which constitute up to 90% of the diving activity (Bengtson & Stewart 1992, Nordøy et al. 1995, Wall et al. 2007). This pattern is congruent with the vertical distribution of their primary prey (Siegel 2005). Despite their name crabeater seals feed almost exclusively on Antarctic krill (*Euphausia superba*) which represents about 90% of their diet (King 1961, Øritsland 1977, Lowry et al. 1988, Hückstädt et al. 2012). In summer a diel pattern in diving behaviour is evident when crabeater seals are diving and foraging during darkness and haul out during daylight due to diel vertical migrations of krill (Bengtson & Stewart 1992, Nordøy et al. 1995, Siegel 2005). In this context, Bengtson and Cameron (2004) reported that juveniles hauled out twice as long as adults (Bengtson & Cameron 2004). However, diving and haul out behaviour shift with seasons (Nordøy et al. 1995, Bengtson & Cameron 2004, Burns et al. 2004).

This thesis will investigate possible differences in diving behaviour of crabeater seals in terms of age which has not been examined by now. Furthermore, it will mainly review known results with a focus on seasonal changes in diving behaviour as well as variations between geographic areas. In this context, the following hypotheses will be tested:

Diving behaviour of crabeater seals

4) differs between age classes.
5) shows seasonal differences.

2. Material and Methods

2.1 Seal tagging site and animal handling

During the ANT XV/3 (PS 48), EASIZ (Ecology of the Antarctic Sea Ice Zone) II, research expedition of RV *Polarstern* into the Weddell Sea in austral summer 1998, a seal satellite-tagging project was carried out from a field camp at Drescher Inlet (72.85°S, 19.26°E), a 25-km long funnel-shaped crack in the Riiser-Larsen ice shelf, Antarctica (Fig. 1). The Inlet is characterized by a stable sea ice cover with an underlying platelet ice layer up to 30 m thick. Tidal cracks along the foot of the ice cliff and across the entire inlet provided breathing holes for Weddell seals (*Leptonychotes weddellii*) during the austral summer 1998. The inlet's fast-ice is flanked by floating ice cliffs of up to 30 m above and 80 m below the sea surface. The topography of the inlet's seabed is irregular with water depths ranging from 360 m to 430 m, and the seabed extends for ca. 100 km under the ice shelf. The Drescher Inlet is usually covered with fast-ice during summer and therefore not a typical habitat for crabeater seals (Fig. 2). However, end January 1998 a major part of the outer sea ice had disintegrated into pack-ice due to strong wind and gales. During this time a number of crabeater seals belonging to both sexes and different age classes entered the inlet, and fifteen were equipped with satellite-linked dive recorders (SDR) between 28 January and 6 February 1998 (Table 1). Prior to tagging seals were immobilized with a combination of 500 mg xylazine, 400 mg ketamine and 50 I.U. hyaluronidase known as "Hellabrunner Mischung" (HM). Doses of 2 – 3 ml HM were supplemented by 2 – 3 ml ketamine (100 mg/ml) and injected by using Telinject®-blowpipe darts. Maintenance of narcosis was guaranteed by manual follow-up doses of ketamine, and/or xylazine and/or diazepam on demand. Immobilization procedure is described explicitly in Bornemann et al. (1998; see Bornemann & Plötz 2006 for data). While seals were immobilized, body length measurements were taken and SDRs were attached to the fur on the animal's back by using quick-setting epoxy glue (Fig. 3b). After completion of the tagging procedure the seals could recover from narcosis and were released.

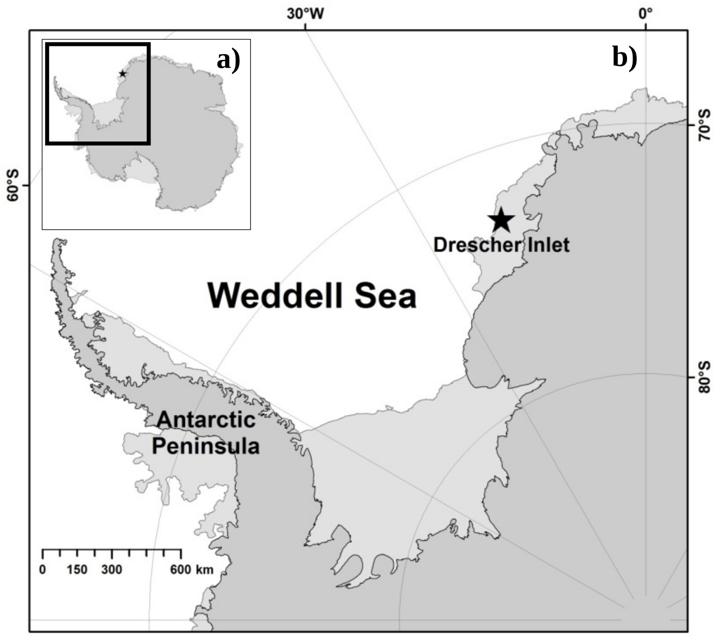


Fig. 1: Drescher Inlet (star) in the eastern Weddell Sea. a) Antarctica (dark grey) with grounding line (solid grey) and ice shelves (light grey). b) Excerpt of (a) Weddell Sea and Antarctic Peninsula.

Fig. 2: Drescher Inlet from above with typical fast ice situation inside, and ice free entrance. Photo: Joachim Plötz.

2.2 SDR settings

The animals were tagged with 0.5-W, microprocessor controlled satellite-linked time-depth recorders (SDR-T6; Wildlife Computers, Redmond, WA, USA; Fig. 3a) which deliver at-sea locations through communication with the Argos System via polar-orbiting satellites (CLS / Service Argos, Toulouse, France). Thus, it is possible to record the seals' geographical dispersal. The SDRs included a seawater conductivity sensor to record whether the seal was in the water or hauled out on the ice at a certain location. The at-sea transmission interval was set to 44 - 51.5 s, whereas on-land transmissions repeated only every 84 - 91.5 s. The recorder changed into on-land mode after 3 consecutive "dry" transmissions. If the seal hauled out for longer than 6 hours the SDR stopped transmitting. After 4 successive "wet" transmissions the recorder changed back into at-sea mode. The number of transmissions per day was limited to 300 to achieve a long lifespan of the battery package. Hereafter, this separate dataset of at-sea and on-land transmissions is called DSB (Dive, at Surface Behaviour; hdl:10013/epic.26929.d001) dataset. In addition to a geographical position, all transmissions carried temporal information as well. Date and time were given in Greenwich Mean Time + 1 h (GMT+1:00).

Furthermore, SDRs collected information about the diving behaviour of each seal. Several parameters were recorded in this context. Dive depth and dive duration were measured in 10 s intervals, processed and encoded in 14 user-defined intervals onboard the SDR in for 6 hourly cumulative histograms which were finally transmitted to the Argos satellites. Dive depth measurements were restricted by the upper limit of the pressure transducer of the transmitter. Thus, the unit covered a depth range of 0 – 741 / 747 / 750 / 753 / 756 m respectively depending on the individual SDR. The minimum depth to be considered as a dive was set to 6 m and the transducer measured dive depths with a resolution of ± 3 m. The upper limits of the histogram bins for dive depth were: 9 m, 21 m, 30 m, 42 m, 51 m, 60 m, 72 m, 81 m, 90 m, 102 m, 150 m, 201 m, 252 m, > 252 m, and needed to be set as even multiples of the transducer resolution (3 m). Since the histogram's bin steps were not equidistant, data were processed before to avoid misinterpretations. Therefore, the final histogram values were corrected by dividing them through the corresponding interval length. Finally, data were converted to relative values in order to achieve an improved comparability.

Upper limits for dive duration histogram bins were: 1 min, 2 min, 3 min, 4 min, 5 min, 6 min, 7 min, 8 min, 9 min, 10 min, 11 min, 12 min, 13 min, > 13 min. These intervals were chosen since previous studies at that time revealed that crabeater seals are generally shallow divers with only short dive durations (Bengtson & Stewart 1992, Nordøy et al. 1995). Since the histogram's bin steps of dive duration were equidistant, they did not need special processing. Again, relative values were given for better comparison.

Additionally, the absolute maximum dive depth of a day was post-hoc processed for the preceding 24 h and transmitted together with technical information in a status message. Beside all dive parameters, the SDR recorded also information on diving and haul out behaviour, e.g. time spent at certain depths and absolute and relative time spent outside the water. However, due to time gaps in the satellite uplinks these data were too incomplete for systematic analyses and therefore disregarded. Dive data analyses and handling of all spreadsheets were conducted with R version 2.15.2 (R Core Team 2012) as well as Microsoft Office Excel 2010 (© Microsoft Corporation, USA).

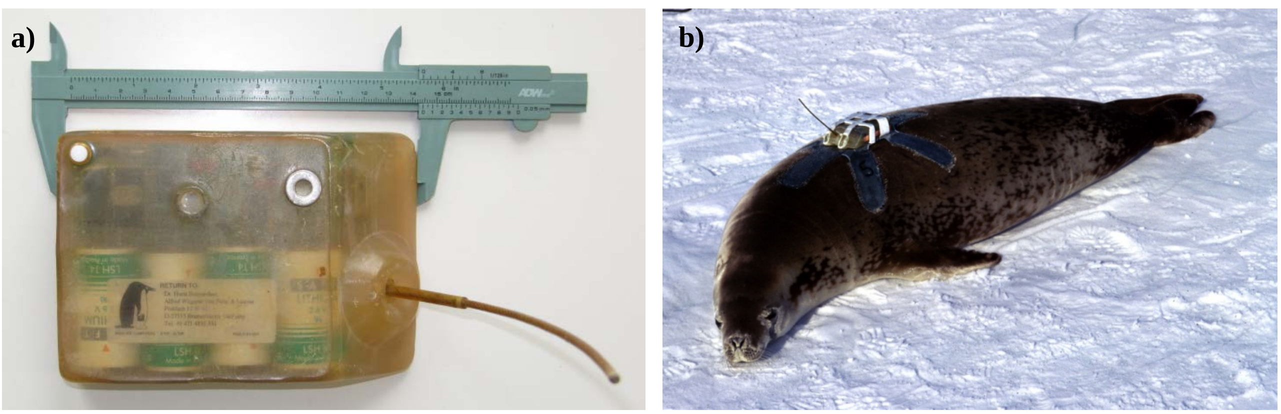


Fig. 3: a) Satellite-linked dive recorder (SDR-T6 manufactured by Wildlife Computers, Redmond, USA; 14.2 cm x 9.8 cm x 3.3 cm, without antenna) which were used for crabeater seal (*Lobodon carcinophaga*) satellite tagging in summer 1998. Photo: Dominik Nachtsheim. b) Immobilized adult crabeater seal equipped with SDR on its back. Photo: Horst Bornemann.

2.3 Argos location classes and SDA-filter

Location data supplied by CLS/ Argos Service are generally divided into different location classes (LC = 3, 2, 1, 0, A, B and Z) depending on the estimated accuracy of the position (Argos 1996). LC Z stands for invalid locations, whereas LC A and B are valid but no accuracy estimation was possible due to an insufficient number of uplinks to the satellite. A minimum of 4 successive uplinks is needed to estimate a position with known precision which applies to LC 0, 1, 2 and 3. Their estimated location accuracy ranges from > 1500 m (LC 0) to ≤ 150 m (LC 3) (Argos 1996). As marine mammals spend only limited time at the surface or outside the water, a high amount of locations have a low or unknown accuracy due to a restricted number of uplinks during a satellite overpass (Nordøy et al. 1995, Folkow et al. 1996, Freitas et al. 2008). This results in numerous biologically and physiologically unrealistic positions. A way to remove these positions is to filter the data under certain aspects. For example, McConnell et al. (1992) developed a velocity filter which removes all locations exceeding a defined maximum mean swimming speed of the seal. Locations of dive depth, dive duration and maximum dive depth transmissions were processed with this filter within the workflow of data acquisition and archival storage, using a conservatively estimated maximum mean velocity of 3.5 $m \cdot s^{-1}$ (12.6 $km \cdot h^{-1}$) (McConnell et al. 1992). Thus, only the filtered dive data were available for this thesis. By contrast, the DSB dataset was present as raw data and therefore a modified filter could be applied. Freitas et al. (2008) designed a track-filtering algorithm called SDA-filter (Speed-Distance-Angle-filter) on the basis of the velocity filter by McConnell et al. (1992). In addition, they included distance between consecutive positions and turning angle as further parameters. The SDA-filter removes similar proportions of locations with low accuracy (LC A and B) but keeps significantly more good-quality locations (LC 1, 2 and 3) than the simple velocity filter (Freitas et al. 2008) Interpolated locations (LC Z) are completely rejected (Freitas et al. 2008). This results in a more realistic track of the animal without unlikely spikes or incorrect on-land positions. The SDA-filter algorithm is freely available within the R package 'argosfilter' in the R environment (R Core Team 2012). Filtered seal tracks were plotted in ArcGIS for Desktop 10.2 (© ESRI, Inc., USA) for visualization (Fig. 5).

2.4 Environmental data

A set of 16 environmental variables was used to investigate how these parameters potentially influence the dispersal of crabeater seals in the Weddell Sea. As certain physical and biological factors may affect occurrence and habitat use of this pinniped species (Nordøy et al. 1995, Burns et al. 2004, Wall et al. 2007, Friedlander et al. 2011) the following parameters were chosen for analysis: sea ice concentration [%], sea ice thickness [m], sea ice freezing rate [cm d^{-1}], water surface and bottom temperature [°C], surface and bottom salinity (provided as psu), surface and bottom zonal current velocity [m s^{-1}], surface and bottom meridional current velocity [m s^{-1}], bathymetry [m], slope [°], distance to coastline [m], distance to shelf break (defined as 1000 m isobath) [m] and geomorphology (provided in 17 geomorphological categories including sediment types). SeaWiFS chlorophyll *a* data from NASA and NOAA has been disregarded due to very large data gaps in the study area. Sea ice, temperature, salinity and velocity data were derived from the Finite Element Sea ice-Ocean Model FESOM (Timmermann et al. 2009, Haid 2013, Haid & Timmermann 2013) as monthly mean values from January to May 1998 with a resolution of 5 km x 5 km. However, for sea ice concentration additionally satellite observation data recorded by the Special Sensor Microwave/Imager (SSM/I) of the Defense Meteorological Satellite Program (DMSP) at the National Snow and Ice Data Center (NSIDC), Boulder, Colorado, USA with a resolution of 25 km x 25 km were acquired. They were available as daily mean ice concentrations ranging from 0% (open water) to 100% (closed ice cover) after being processed with the NASA-Team-Algorithm (Cavalieri et al. 1984). The locations of the DSB dataset were matched with these data to achieve on spot information about the current ice concentration on a seal's position. Additionally, ice conditions within the first six pixels away in each direction from a seal's central position (in total 169 pixels, each having a size of 25 km x 25 km) were analyzed. This distance was chosen as a heuristic maximum daily distance a seal theoretically could move, in order to provide a measure for potential scattering of the surrounding ice concentrations. Analyses of these data can be seen in the chapter 3.5. Bathymetric data were derived from The International Bathymetric Chart of the Southern Ocean (IBCSO) with a resolution of 0.5 km x 0.5 km (Arndt et al. 2013). On the basis of the IBCSO bathymetric raster Jerosch et al. (in prep.) derived maps on geomorphology and slope for the Atlantic sector of the Southern Ocean with the same grid size. All environmental variables were available as raster layers and were imported into ArcGIS.

2.5 Processing of data for Maxent

Since the DSB dataset was filtered with an improved filter algorithm, only these data were used for dispersal analyses. Then, filtered seal locations were separated into respective months and also plotted in ArcGIS. Positions were assigned to the environmental raster files from respective sampling months. Values at each seal location were extracted from the rasters using the "Extract Values to Points" tool in ArcGIS and added to the species location table. Final table handling and transformation to CSV files required for the Maxent analysis was done with Microsoft Office Excel 2010. Eventually, only respective data from February, March and April were used for Maxent modelling as January and May contained insufficient numbers of location records for a solid statistical analysis.

Values from all environmental raster files were resampled with a resolution of 5 km x 5 km because this size corresponded with FESOM rasters which contributed 11 of 16 variables. The remaining parameters had a higher spatial resolution. Additionally, 5 km x 5 km is a more conservative determination for a seal's position since Argos locations with low accuracy are abundant in marine mammal studies (Vincent et al. 2002, Freitas et al. 2008), and hence allow for a better reconciliation between seal locations and environmental parameters. Furthermore, the extent of all new raster layers matched the study area for Maxent analyses which was defined as part of the Atlantic sector of the Southern Ocean since the available FESOM data were only processed for this region. Unfortunately, this led to a removal of seal locations east of 30°E. The extent of the study region ranged from 65°W to 30°E and from 62°S to the edge of the shelf ice and the continent, respectively, and covered an area of 4,760,426 km^2 (Fig. 5). The whole study area, even the eastern part, is influenced by the Weddell Gyre (Schröder & Fahrbach 1999), and determines oceanographically the Weddell Sea. Finally, the new environmental raster files were converted from ArcGIS rasters to ASCII raster format for further usage in Maxent.

2.6 Subsampling locations

For model calculations the processed DSB dataset was subsampled in two steps to diminish potential biases. All locations within a radius of 30 km around Drescher Inlet were removed to avoid a possible influence of clustered positions near the tagging site as recommended by Edrén et al. (2010). Referring to Edrén et al. (2010) and Friedlander et al. (2011), only one transmission per day of each animal was used for a consistent representation of each individual within the Maxent analysis since the Argos system delivered different numbers of transmissions per day and animal. If more than one transmission has been received on the same day then the first location was selected.

2.7 Maxent modelling

Commonly, maximum entropy (Maxent) is used to model species geographic distribution on the basis of environmental conditions at known occurrence sites (Phillips et al. 2006). Thus, it needs presence-only data which is extremely helpful when absence records are not available (Phillips et al. 2006). For example, natural history museums and herbarium collections possess data about locations where species exist or were found but usually not where they are absent (Phillips et al. 2006, Phillips

& Dudík 2008). Therefore, Maxent is often used for modelling the distribution of terrestrial organisms e.g. plants, birds and insects concerning biogeographic, conservation biological and ecological issues (Elith et al. 2011). Only recently, it was applied to marine top predators using satellite telemetry datasets, too (e.g. Edrén et al. 2010, Friedlander et al. 2011, Ballard et al. 2012). Since these data also contain opportunistic presence-only records and Maxent works perfectly with small sample sizes (Phillips et al. 2006, Wisz et al. 2008) as well as imprecise locations (Graham et al. 2008), it is a good tool for reasonably modelling distribution and suitable habitats for marine mammals (Edrén et al. 2010). Additionally, it provided better results than many established modelling methods such as Generalized Linear Models (GLM), Generalized Additive Models (GAM) and Genetic Algorithm for Rule-set Prediction (GARP) regarding predictive power (Elith et al. 2006, Phillips et al. 2006).

The program Maxent version 3.3.3k (Phillips et al. 2006, Phillips & Dudík 2008) was run in SWD (samples-with-data) format, i.e. the imported CSV file contained both species locations and values of all environmental variables at the specific location. As environmental layers 1,000 random background sample points of all environmental data raster were used instead of the original ASCII raster. This reduces the runtime of Maxent significantly without losing much predictive power (Phillips et al. 2006). For each month 20 model replicates were conducted using the auto-features setting of Maxent which supplies a quite good model performance in comparison to elaborated manual tuning (Phillips & Dudík 2008). By default Maxent randomly divides the species occurrence dataset in training and test data. While most data points are used for training, which means creating a species distribution model, some remaining data evaluate the performance of the training model (Phillips et al. 2006). In this thesis a random test percentage was set to 20% to achieve an improved evaluation result. Thus, the remaining 80% of species occurrence data were selected to create Maxent models in accordance to Edrén et al. (2010). Model performance was evaluated by creating receiver operating characteristic (ROC) curves using both test and training data. The area under the curve (AUC) gives information about the quality of model prediction (Phillips et al. 2006). The AUC can range between 0 and 1 where an area of 0.5 means a random prediction (Phillips et al. 2006). Thus, the closer AUC approaches 1 the higher is the predictive power of the model (Fielding & Bell 1997).

Moreover, Maxent indicates to which proportion an environmental variable contributes to the model and identifies the variable which matters most concerning species distribution. Furthermore, a jackknife test was implemented on training data to check the importance of each variable by another approach. On that account, Maxent builds and compares individual models by using only one environmental variable in isolation on the one hand and all variables except one on the other hand. Thus the jackknife analysis reveals in which extent a variable can solely explain the model and how much gain is lost when it is absent.

For February, March and April Maxent was run with 20 replications providing the logistic output which supplies species probability of presence in a range between 0 and 1 (Phillips & Dudík 2008, Elith et al. 2011). All model results are given as average of 20 replicates.

3. Results

3.1 Tag performance

Fifteen crabeater seals were tagged with SDRs but 12 provided sufficient data for further analyses (Table 1). Since tags of seal 3, 4 and 13 transmitted for a maximum of two days only, these animals were completely neglected in the course of the analyses. Seals were divided into three age classes on the basis of standard body length after Laws et al. (2003). Adults were defined as individuals that have already reached age of maturity. Usually, female crabeater seals become reproductively active between 3 and 4 years (Bengtson & Siniff 1981). Thus, the group consisted of 7 yearlings (≤ 1 year), 1 subadult (2 - 3 years) and 4 adults (> 3 years). However, yearlings and subadults were pooled together to a new ‘subadult’ group to simplify statistical comparisons between age classes. Additionally, seals can be divided by sex resulting in 10 males and 2 females.

The 12 remaining transmitters provided data for a duration between 7 and 117 days ($\bar{x}$ = 54.9 d) which ideally means until end of May. In total, 3,425 transmissions were received within the DSB dataset and 4,200 transmissions of dive data were available which had already passed the velocity filter by McConnell et al. (1992) shortly after data acquisition. This resulted in an overall average of 5.6 positions per animal and day. The mean temporal distance between two DSB transmissions was 4 h 16 min.

3.2 Argos location classes and SDA-filter

Nearly half of unfiltered DSB data consisted of LC A and B with unknown accuracy (48.1%) (Table 2). Invalid values (LC Z) had already been manually removed before. LC 0 represented 16.7% and LC 1 contributed 18.4% while only 16.8% had an estimated location accuracy of 350 m and better (LC ≥ 2). Then, the SDA-filter algorithm developed by Freitas et al. (2008) was applied resulting in more likely and realistic seal tracks (Fig. 4). In total, the filter removed 47.7% of all locations leaving 1,791 positions. The amount of LC A and B was reduced to 40.2% while the relative frequency of accurate positions (LC ≥ 2) increased to 23%. LC 0 and 1 contributed 13.2% and 23.6%, respectively. After application of the SDA-filter an average of 2.8 locations per day and animal were available and the mean distance between transmissions dropped to 8 h 32 min.

Table 1: Overview about 15 crabeater seals (*Lobodon carcinophaga*) tagged with satellite-linked dive recorders (SDRs) at Drescher Inlet in 1998. Age class was determined on the basis of standard body length (Laws et al. 2003). Track length was calculated with ArcGIS based on filtered DSB locations.

Seal No.	Sex	Age class	Body length [cm]	SDR deployment date	SDR longevity [d]	Last location	Track length [km]
1	male	adult	225	28/01/1998	35	71.963°S, 33.167°W	932
2	male	adult	223	29/01/1998	7	73.611°S, 38.257°W	211
3*	female	adult	236	29/01/1998	0	72.877°S, 19.131°W	N/A
4*	male	yearling	182	01/02/1998	0	no data	N/A
5	male	yearling	178	01/02/1998	17	71.926°S, 27.855°W	921
6	male	yearling	188	01/02/1998	117	66.874°S, 45.762°E	4438
7	male	yearling	189	01/02/1998	59	70.794°S, 32.414°W	1751
8	male	yearling	186	01/02/1998	103	65.449°S, 24.551°W	3406
9	female	subadult	204	02/02/1998	73	65.698°S, 55.483°E	3648
10	male	adult	227	03/02/1998	60	71.705°S, 24.601°W	1379
11	male	yearling	193	03/02/1998	39	70.416°S, 37.236°W	973
12	male	yearling	184	03/02/1998	38	72.334°S, 44.679°W	1193
13*	male	subadult	208	04/02/1998	2	72.830°S, 19.844°W	N/A
14	female	adult	N/A	04/02/1998	96	69.205°S, 15.771°W	1531
15	male	yearling	188	06/02/1998	15	67.108°S, 14.889°W	777

* Since SDRs of seal 3, 4 and 13 transmitted for maximally 2 days, these animals were completely neglected for further analyses.

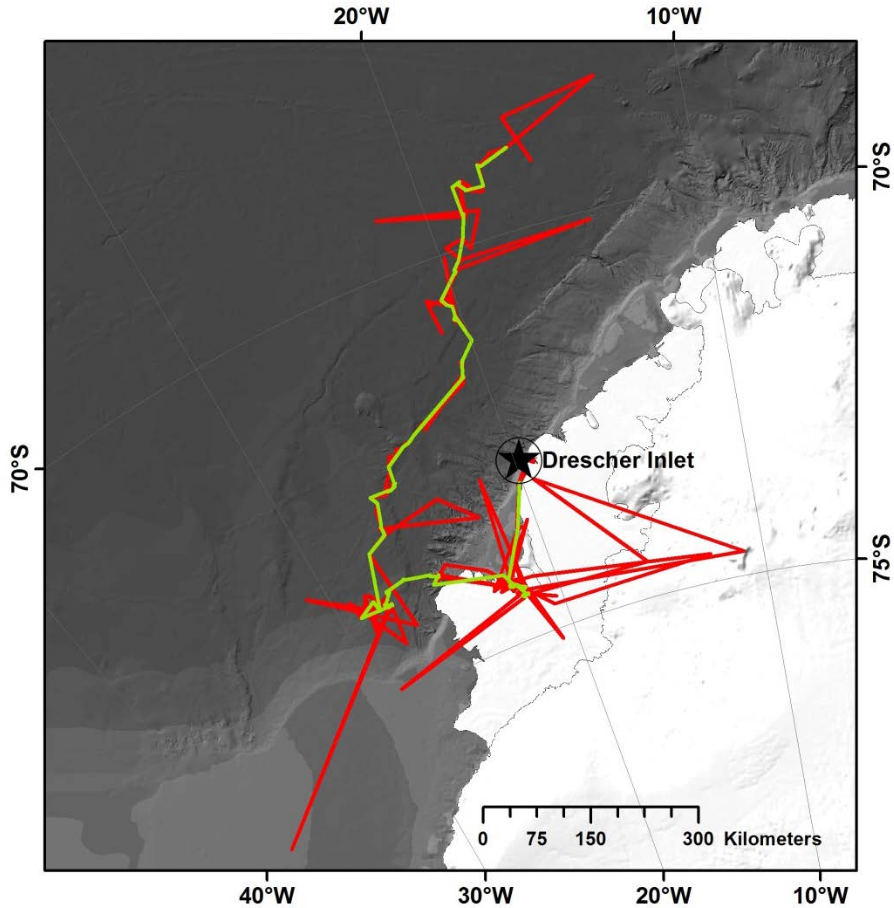


Fig. 4: Example of unfiltered (red line) and filtered (green line) track data for seal 14.

Table 2: Distribution of Argos locations classes on unfiltered and filtered DSB data. Values are given in absolute and relative numbers. Additionally, the estimated location accuracy of each location class is listed (Argos 1996).

Argos location class	Estimated location accuracy	Unfiltered		Filtered	
		Frequency of locations	Frequency of locations [%]	Frequency of locations	Frequency of locations [%]
Z	invalid	0	0	0	0
B	no estimate	932	27.2	333	18.6
A	no estimate	714	20.9	387	21.6
0	> 1000 m	572	16.7	236	13.2
1	350 m – 1000 m	631	18.4	423	23.6
2	150 m – 350 m	366	10.7	256	14.3
3	≤ 150 m	210	6.1	156	8.7
	sum:	3425	100	1791	100

3.3 Distribution

3.3.1 Description of individual seal movements

All geographic terms used in the following description are based on The International Bathymetric Chart of the Southern Ocean (Arndt et al. 2013, doi.pangaea.de/10.1594/PANGAEA.805735, see Appendix Fig. A.1). Tracks of each of the seals are available (see Appendix Fig. A.2)

Generally, the seals dispersed radially from Drescher Inlet shortly after tagging (Fig. 5). Most of the time they moved and only area restricted movements in a circumscribed area. Ten seals explored the eastern and central Weddell Sea while 2 animals migrated far eastwards along the coast. These animals covered a distance of 4,438 km and 3,648 km in 117 and 73 days, respectively. Generally, the track length ranged from 211 km to 4,438 km ($\bar{x}$ = 1,763 km) (Table 1). Averaged mean speed of all animals was 1.42 $km \cdot h^{-1}$ after filtering (range: 0.66 – 2.26 $km \cdot h^{-1}$). Thus, a defined maximum mean speed of 12.6 $km \cdot h^{-1}$ for the SDA-filter was appropriate and well conservative.

Seal 1 (Fig. 5, coral line)

The seal left Drescher Inlet in southern direction after staying there for two days. It swam along the edge of the Riiser-Larsen Ice Shelf until it reached a large promontory of the ice shelf. The seal stayed there from 2nd to 9th February until it headed out northwest into the Weddell Sea. On its way seal 1 passed the Polarstern Canyon and the Deutschland Canyon. At 71.483°S, 29.146°W on 22nd February it reached the northernmost point of its movement. Shortly after it turned and travelled steadily in southwesterly direction. Between 1st and 4th March the seal stayed in a quite restricted area until transmission ended.

Seal 2 (Fig. 5, yellow line)

Seal 2 directly left Drescher Inlet and headed west where it passed Polarstern Canyon. After 7 days the recording ceased.

Seal 5 (Fig. 5, dark red line)

The seal also left Drescher Inlet after the tagging procedure and moved northwestwards. On 4th February at 71.960°S, 23.129°W seal 5 sharply turned to northeast and continued this direction for 6 days. At 69.775°S, 18.526°W it turned again and swam west and to southwest, respectively. This direction was maintained until transmissions ended on 18th February at 71.926°S, 27.855°W.

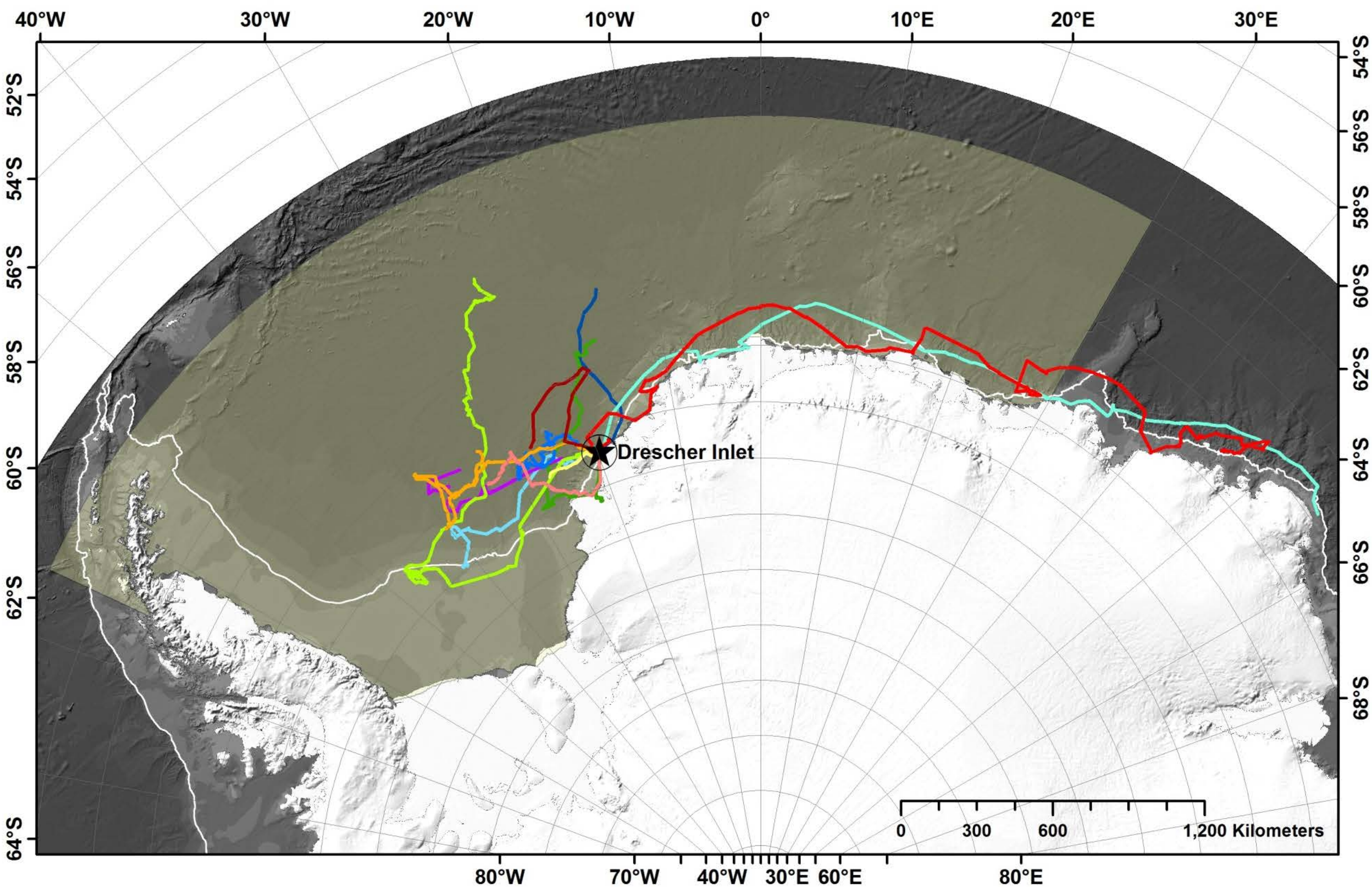


Fig. 5: Tracks of 12 crabeater seals (*Lobodon carcinophaga*) in the Weddell Sea and further to the east dispersing from Drescher Inlet (star). Each different colored line represents an individual. Bathymetry is indicated by various shades of grey (light = shallow, dark = deep). The white line shows the 1000 m isobath of the continental shelf defined as shelf break. The transparent yellow polygon illustrates the study area used for Maxent analyses, corresponding with the FESOM data.

Seal 6 (Fig. 5, red line)

Seal 6 left Drescher Inlet to remain for a few days on the eastern side of the inlet's mouth. On 5th February it moved away in westerly direction and approached the ice shelf edge. It followed the ice shelf contour and the coastline to the northeast for 3 days until it reached 71.089°S, 11.342°W where it stayed outside the water for several hours. Hereafter, it continued travelling eastwards in a distance to the coastline and ice shelf, respectively. During this movement it passed the Bungenstock Plateau and Sanae Canyon and entered the Lazarev Sea. The next time it approached the ice shelf was near Astrid Ridge on 14th March at 69.529°S, 15.436°E. Then, seal 6 moved straight away from the continent into the Riiser-Larsen Sea and turned eastwards again to swim along the coast in a certain distance. Between 31st March and 7th April seal 6 in a small area over the margin of the continental shelf before, it swam away from the ice shelf again and continued its movement eastwards. The next stop at the ice shelf occurred after crossing Gunnerus Ridge close to the Japanese Showa Station on 20th April at 68.579°S, 40.833°E. Hereafter, it returned offshore into the Cosmonaut Sea and travelled east again. Seal 6 migrated to 65.795°S, 48.147°E (19th May) but then turned 180° and swam back in the opposite direction. On 29th May at 66.874°S, 45.762°E transmission stopped.

Seal 7 (Fig. 5, orange line)

After staying in the Drescher Inlet for one day, seal 7 moved first northwest and then westwards within the Weddell Sea. It crossed Polarstern Canyon and spent nearly four days south of the Polarstern Plateau. It passed the Deutschland Canyon and Akademik Fedorov Canyon to reach the central Weddell Sea. At 71.615°S, 37.367°W on 26th February it entered the Uruguay Canyon where it stayed until 18th March. Seal 7 migrated south towards the continental slope to 72.425°S, 40.152°W but then turned to the opposite direction. It swam down the canyon again and passed the adjacent Antarctic Canyon. As it reached 70.229°S, 39.024°W it turned south again and travelled upwards the canyon. When the seal left the Uruguay Canyon on 18th March it followed nearly the same way back to the Akademik Fedorov Canyon but then changed to a more northerly direction. On 1st April the transmitter stopped.

Seal 8 (Fig. 5, light green line)

Seal 8 was tagged on 1st February and left Drescher Inlet directly afterwards in western direction. After nearly one week a gap of 3.5 day occurred without satellite contact. The next location was situated at 73.895°S, 32.674°W right at the outflow of the Filchner Trough outflow. During 4.5 days seal 8 swam up to the continental shelf slope but then turned west again over the Berkner Bank. From this area it continued moving northwestwards until it reached the margin of the General Belgrano Bank (74.071°S, 44.490°W) on 20th February. Seal 8 stayed within this region for more than one month until 24th March. During this time it remained in an area not deeper than 1,000 m water depth. Seal 8 moved eastwards into deeper waters, where it stayed until 3rd April. Then, seal 8 headed north-northeast continuously till the end of transmissions on 15th May at 65.449°S, 24.551°W above the central Weddell Abyssal Plain and north of the Antarctic Circle.

Seal 9 (Fig. 5, turquoise line)

After being tagged on 2nd February seal 9 remained in the Drescher Inlet until it left the area on 4th February in northeasterly direction in a certain distance to the ice shelf. The seal made a short rest close to the Neumayer III Station at the Ekström Ice Shelf from 14th to 16th February. Seal 9 continued travelling eastwards and stayed near the Fimbul Ice Shelf for four days. Seal 9 then resumed its eastward movement, passed Astrid Ridge and entered the Riiser-Larsen Sea. Finally, it also crossed Gunnerus Ridge and reached its terminal easternmost position at 65.698°S, 55.483°E on 16th April ahead of Enderby Land.

Seal 10 (Fig. 5, blue line)

Seal 10 left Drescher Inlet in northeastern direction. It crossed the Polarstern Canyon and migrated in an area south of the Polarstern Plateau where it stayed for 10 days. Then it travelled westwards into the Deutschland Canyon and remained there from 4th to 23rd March. Seal 10 headed back to the Polarstern Plateau where last transmissions took place were received on 4th April.

Seal 11 (Fig. 5, purple line)

Seal 11 was tagged on 3rd February but the first locations could be calculated only on 8th February. During this 5-day period the animal has moved westwards to the Polarstern Canyon and further west until it had reached the Akademik Fedorov Canyon, where it stayed from 15th to 24th February. Afterwards, it continued its westward movement but turned in northern direction along the Uruguay Canyon after one week. Finally, it changed direction to east with last transmissions on 14th March.

Seal 12 (Fig. 5, light blue line)

Seal 12 stayed in the vicinity of the Drescher Inlet for one day until it left in western direction. After nearly two weeks it turned to southwest and headed towards the Filchner Trough outflow. It changed direction at 73.624°S, 32.450°W to the west again and crossed the Akademik Fedorov Canyon. Between 25th February and 5th March seal 12 swam a loop and moved up the continental slope. On 8th March it reached the northwestern edge of the Berkner Bank with water depths around 1,000 m. The seal remained in this quite restricted area for several days when transmissions stopped on 13th March.

Seal 14 (Fig. 5, dark green line)

Seal 14 left the Drescher Inlet one day after tagging in southwestern direction close to the ice shelf. It apparently entered another ice shelf crack between Lyddan Island and the Stancomb-Wills Ice Tongue on 7th February and stayed herein until 27th March. After seven weeks seal 14 finally left the inlet in western direction and remained in an area with water depths between 2,500 and 3,000 m for one week. Hereafter, it headed straight northeast through Polarstern Canyon into the eastern part of the Weddell Abyssal Plain with last transmission at 69.205°S, 15.771°W on 11th May.

Seal 15 (Fig. 5, dark blue line)

Three days after tagging seal 15 left the area around the Drescher Inlet northeastwards along the continental shelf margin. At 71.926°S, 16.116°W it turned to north and swam down the continental slope into deeper regions of the eastern Weddell Sea. It followed this direction for 11 days and finally nearly reached the Antarctic Circle. Last transmissions were recorded at 67.108°S, 14.889°W on 21st February.

3.3.2 Categorization of similar distributional patterns between age classes and sexes

Subadult seals (n = 8) were more mobile than adults (n = 4) (Fig. 6). They travelled on longer distances ($\bar{x}$ = 2,138 km vs. 1,013 km) although mean transmitter longevity did not differ strongly ($\bar{x}$ = 57.6 d vs. 49.5 d). While adults mainly stayed in the eastern part of the Weddell Sea, subadults also moved into the central and northern Weddell Sea near the Antarctic Circle. Only one adult seal moved far northwards after it remained in a circumscribed area for seven weeks. Two subadult seals migrated far eastwards to 45° E off Enderby Land. However, these differences between age classes were not tested statistically due to too small sample sizes.

Since females were clearly underrepresented in this study (n = 2) a comparison between sexes was not performed (Fig. 7).

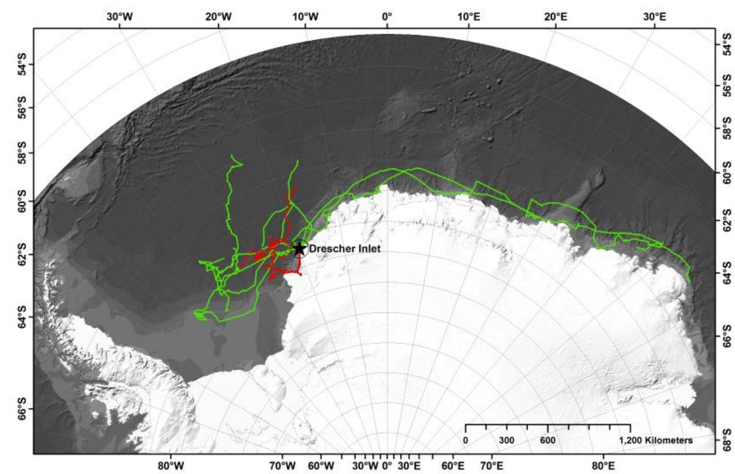


Fig. 6: Tracks of all subadult (green) and adult (red) crabeater seals dispersing from Drescher Inlet (star).

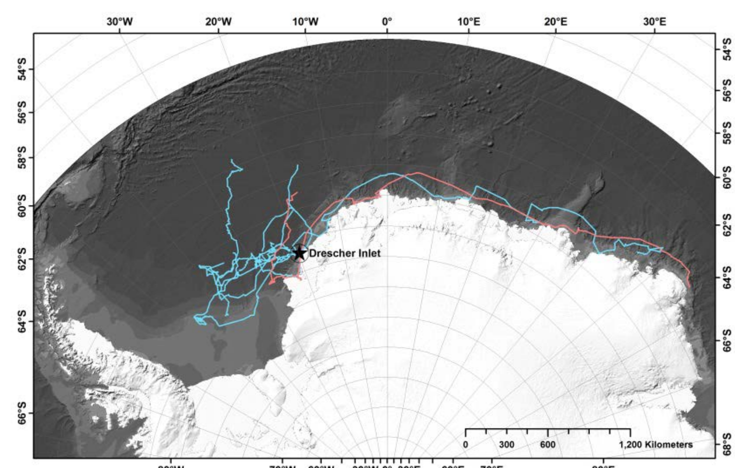


Fig. 7: Tracks of all female (pink) and male (blue) crabeater seals dispersing from Drescher Inlet (star).

3.4 Maxent modelling

Sixteen different environmental factors were used in a maximum entropy modelling approach to create geographic distribution maps of crabeater seals in the Weddell Sea for three different months during 1998. It was investigated which factors primarily influence their movements. It was tested to which proportion each parameter contributes to the model. All following results are given as mean values of 20 model replications.

3.4.1 Model evaluation

First, AUC values were used to examine the predictive power of each model. Values close to 1 indicate a high model quality. Generally, Maxent performed very well in generating models from occurrence data. AUC values of test data were quite high ranging between 0.927 and 0.963 whereas standard deviations were low between 0.013 and 0.006 (Table 3). Thus, the created Maxent models distinctly differ from a random prediction (Fig. 8).

Table 3: Total number of seal locations for each month as well as Maxent model sample size used for either training or test purpose. Average AUC (Area Under the Curve) values obtained by using the test data and their standard deviation (SD) are listed.

	Total locations	Training (test) locations	Average test AUC	Test AUC SD
February	223	147 (36)	0.927	0.013
March	173	117 (29)	0.930	0.009
April	64	52 (12)	0.963	0.006

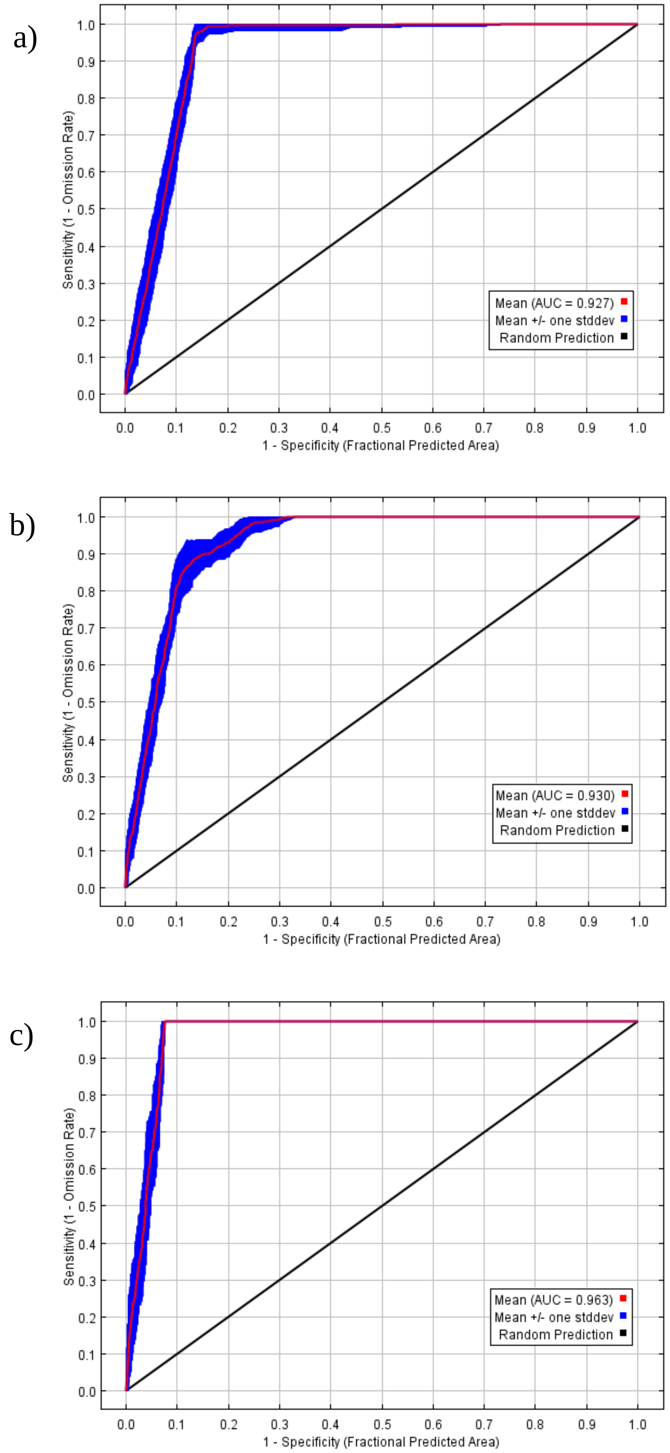


Fig. 8: Receiver Operator Characteristic (ROC) curves for 20 replicated Maxent models of February (a), March (b) and April (c). The Area Under the Curve (red) is called AUC. Standard deviation is shown in blue. The black line illustrates a random prediction.

3.4.2 February

Generally, the Maxent model for February showed large areas with zero probability of presence (Fig. 9). However, there were well defined regions especially in the central and western Weddell Sea where the model predicted high occurrence rates. Additionally, three spots in the eastern part as well as in the Lazarev Sea between 0° and 10° E including Maud Rise seemed to be important due to intermediate presence probability values. Highest values around 0.8 occurred on the continental shelf margin between the General Belgrano Bank and Berkner Bank. This area was extensively used by one seal from end of February until begin of April.

The environmental variable which contributed most to the February model was sea ice concentration with an input of 44.9% (Table 4). Furthermore, surface water temperature (29.7%) and distance to shelf break (14.6%) were also detected as important parameters. All remaining factors seemed to be less crucial for the Maxent model. This order was confirmed by the jackknife analysis (Fig. 12a). Additionally, it showed that an omission of ice concentration for model building leads to a strong decrease in model gain which underlines the importance of this single factor. Isolation of surface temperature results in a less pronounced decline. The jackknife test revealed that distance to shelf and water depth may also be important contributors but without these variables the full model gain can still be achieved (Fig. 12a).

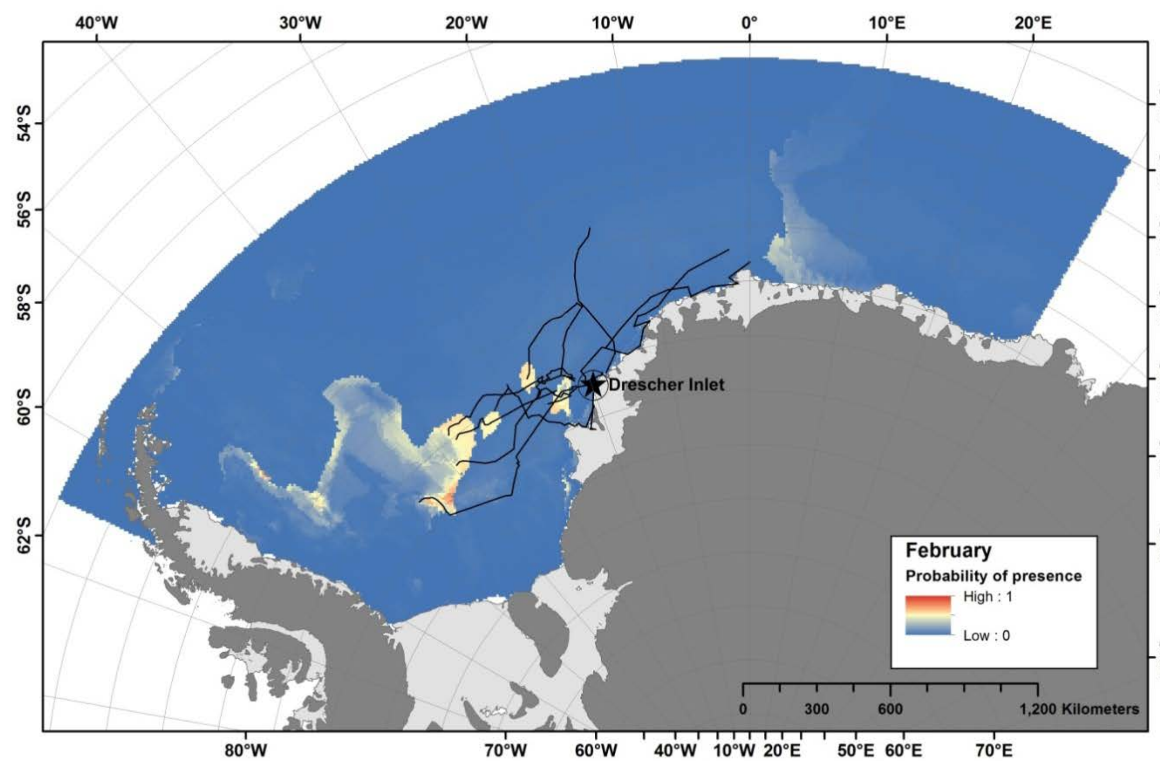


Fig. 9: Probability of presence of crabeater seals modeled by Maxent for February. Black lines illustrate seal tracks during that month. Drescher Inlet is represented by a star. Dark grey = Antarctic continent; light grey = ice shelves.

3.4.3 March

The Maxent model for March revealed high occurrence probabilities in the western Weddell Sea with values greater than 0.9, especially between depths of 1,000 and 4,000 m and above the continental shelf east of the Antarctic Peninsula (Fig. 10). Only one patch with medium probabilities around 0.4 extended into the eastern Weddell Sea. Then, the model predicted similar presence rates along the coast in the Lazarev and Riiser-Larsen Sea comprising Maud Rise again. As indicated in Fig. 10 two seals migrated through these seas in March. Large areas of the study region did not seem to be important for crabeater seals as predicted by the model.

Sea ice concentration was reconfirmed as the most important environmental variable (34.1%) but closely followed by depth (28.4%) (Table 4). Furthermore, surface temperature and salinity as well as distance to shelf break contributed small proportions to the model. The jackknife analysis reflected these results in large parts (Fig. 12b). The best explanatory factor was sea ice concentration again but surface salinity seemed to be nearly equally important. However, there had been no loss in model gain if this variable was rejected in contrast to ice concentration. All other above mentioned factors contributed strongly to the model and reduced model quality apparently when omitted.

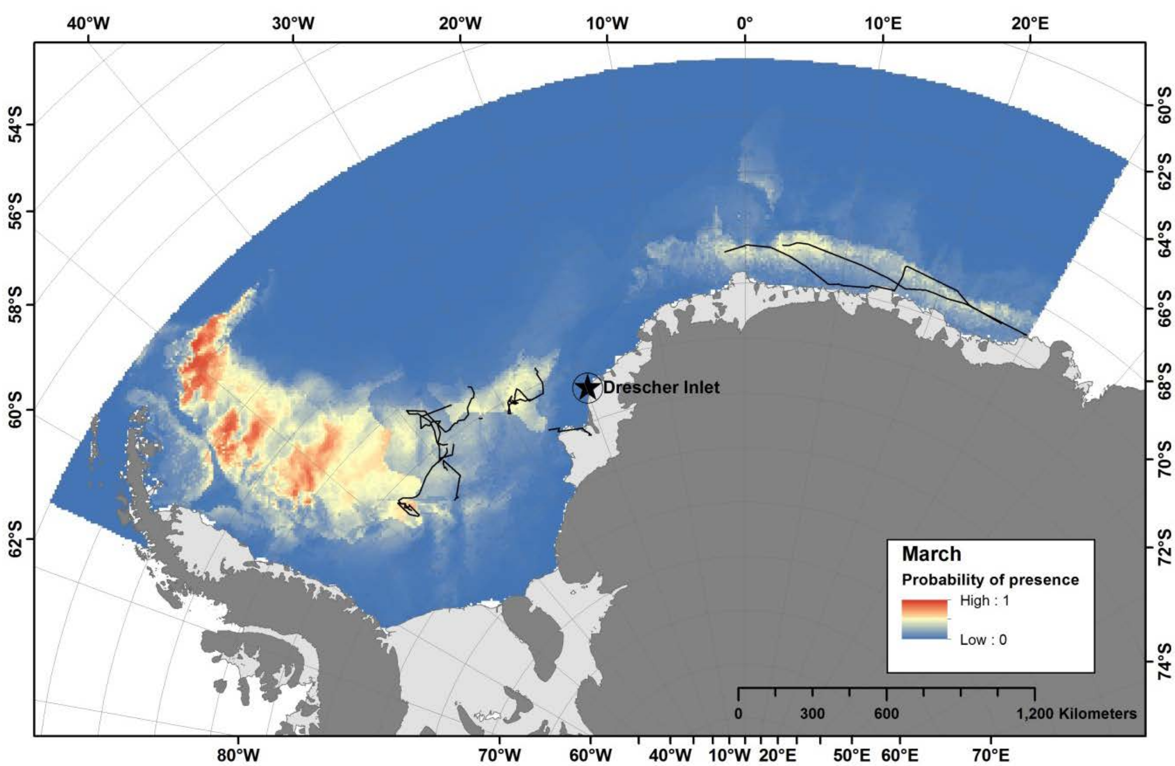


Fig. 10: Probability of presence of crabeater seals modeled by Maxent for March. Black lines illustrate seal tracks during that month. Drescher Inlet is represented by a star. Dark grey = Antarctic continent; light grey = ice shelves.

3.4.4 April

For April, the predicted species distribution looked diffuse and patchy (Fig. 11). Again, the model showed spots with high probability of presence in the western Weddell Sea, especially on the continental shelf break of the General Belgrano Bank. Even higher values (> 0.9) were visible near the coast between 15°W and 30°E. In contrast to February and March, this time large areas displayed low to medium probabilities of occurrence. Scattered spots also appeared in the open ocean far off land. Generally, the model predicted that seals frequently occurred above the continental slope between 500 and 4,000 m water depth throughout the whole study area.

By far, sea ice concentration was once more the most important variable and contributed nearly three quarters to the model (72.9%) (Table 4). Second greatest contributor was again surface temperature with 20.3%. However, the jackknife analysis showed another result (Fig. 12c). Here surface temperature had the strongest input. Other very important parameters were sea ice thickness, sea ice freezing rate, sea ice concentration and distance to shelf in descending order. The absence of none environmental variable but surface temperature led to a loss in training model gain.

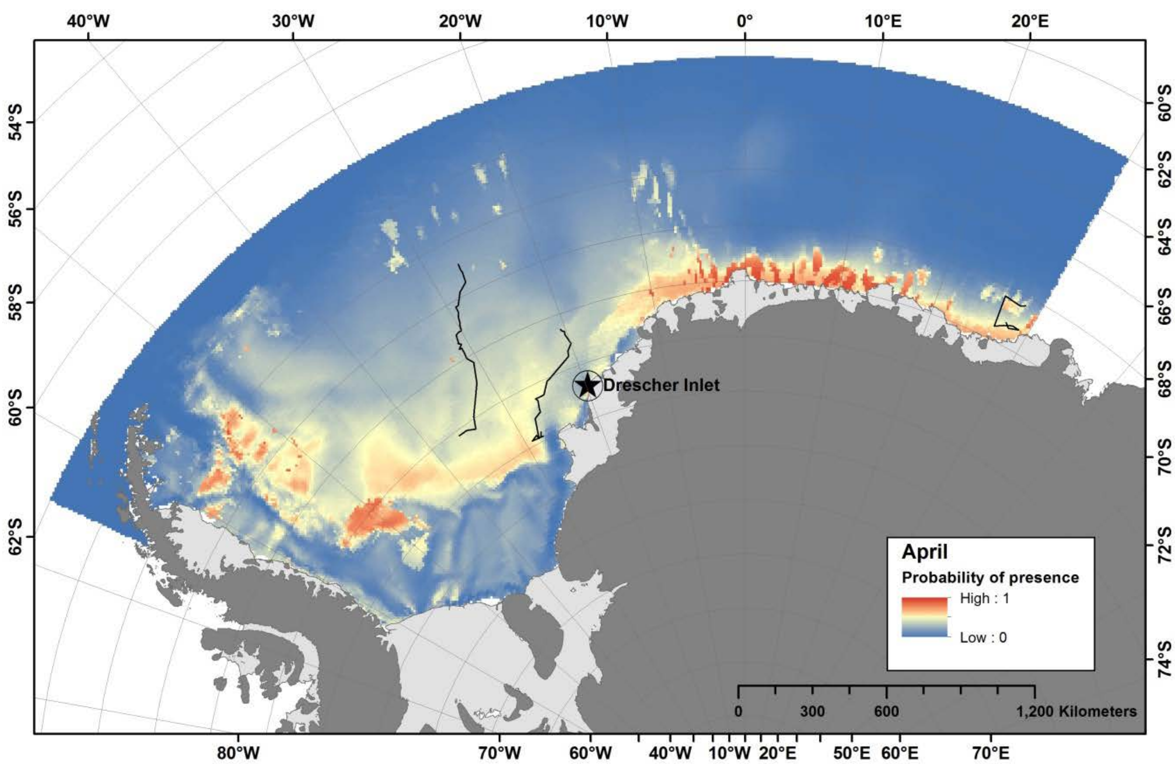


Fig. 11: Probability of presence of crabeater seals modeled by Maxent for April. Black lines illustrate seal tracks during that month. Drescher Inlet is represented by a star. Dark grey = Antarctic continent; light grey = ice shelves.

Table 4: Percent contribution of each environmental variable to the Maxent model in February, March and April.

	February	March	April
Water depth	0.9	28.4	0.6
Distance to coast	1.1	1.4	0.2
Distance to shelf	14.6	7.1	1.3
Sea ice freezing rate	0.1	0.0	2.3
Geomorphology	0.5	1.1	0.5
Sea ice thickness	0.2	0.2	0.1
Sea ice concentration	44.9	34.1	72.9
Salinity, bottom	0.2	0.7	0.8
Salinity, surface	1.2	10.7	0.2
Slope	0.1	0.5	0.0
Water temperature, bottom	5.5	0.6	0.2
Water temperature, surface	29.7	13.5	20.3
Velocity, meridional, bottom	0.1	0.2	0.0
Velocity, meridional, surface	0.8	0.1	0.4
Velocity, zonal, bottom	0.0	0.2	0.0
Velocity, zonal, surface	0.2	1.2	0.2

3.4.5 General results of Maxent modelling analysis

Across all three months the model predicted high probabilities for the occurrence of crabeater seals in the western and partially central Weddell Sea. To some extent also the coast of the Lazarev and Riiser-Larsen Seas seem to be an important habitat whereas the eastern Weddell Sea was of less importance. Generally, areas near the continental shelf break and above the continental slope were predicted as suitable habitats, e.g. the edge of the General Belgrano and Berkner Banks during all three months. This is consistent with the result that the variables water depth and/ or distance to shelf break influenced all Maxent models. Furthermore, surface temperature always contributed a large proportion to the model. However, the greatest contributor in all cases was sea ice concentration. By contrast, many other variables such as salinity, current velocities, geomorphology, distance to coast and slope gradient did not play an important role for model building.

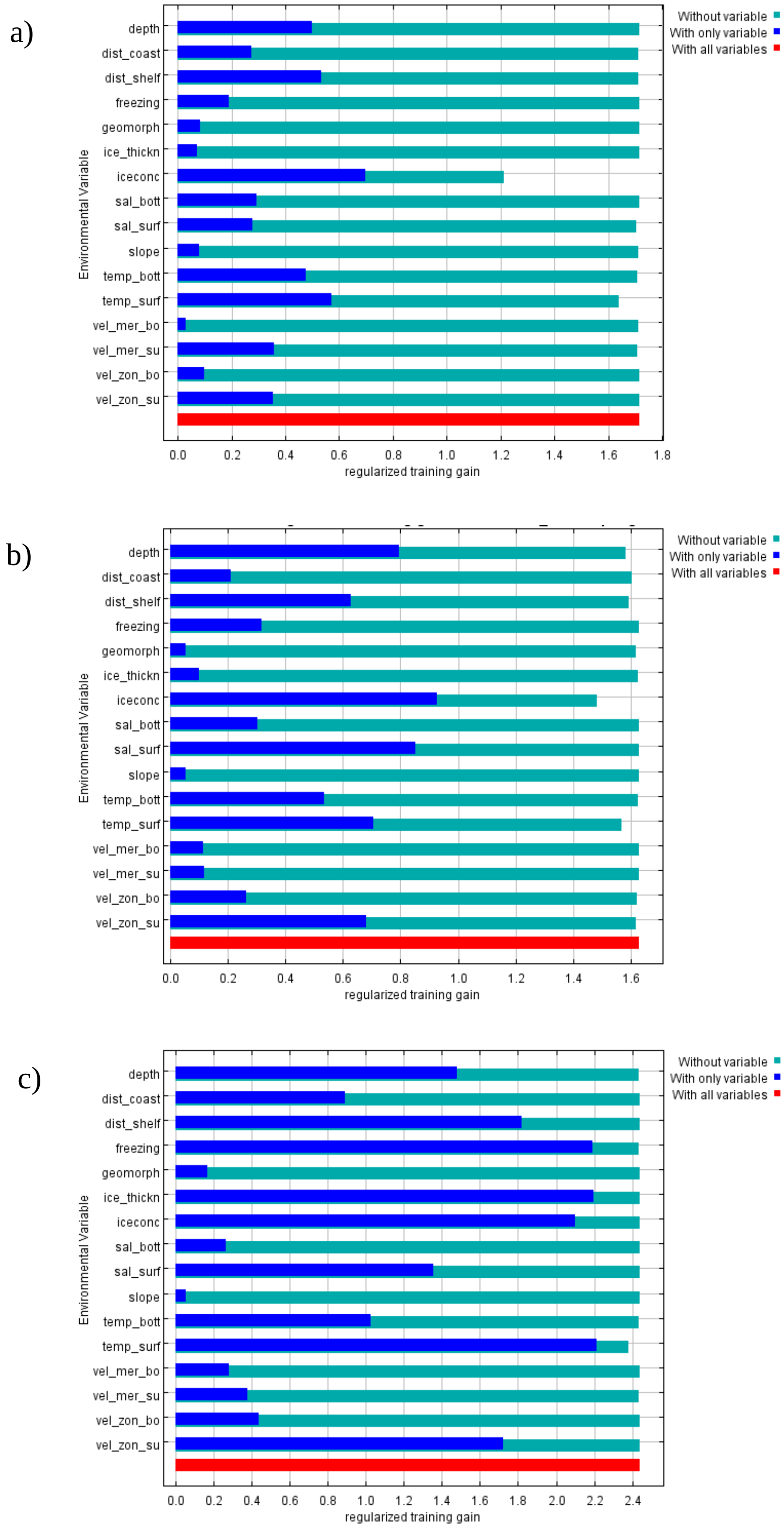


Fig. 12: Results of jackknife analyses on Maxent training models for February (a), March (b) and April (c). Blue bars show gain when only this variable was used for a separate model creation. In contrast, green bars illustrate the resulted gain if all variables but this one were used to build a model. The red bar shows the gain achieved with all parameters.

3.5 Sea ice concentration

Sea ice concentration played an important role in modelling crabeater seal distribution. An analysis of the ice conditions at the seals' locations was conducted over the whole tagging period. To this end, satellite observation data was matched with each seal's position to get on spot information about preferences for certain sea ice concentrations.

Seals extensively used the open water or marginal ice fringes which correspond to sea ice concentration between 0% and 15% (Fig. 13). The amount of positions in totally ice-free waters (0%) was mainly responsible for the height of the first bar and represented more than 50% of all seal locations (Appendix Fig. A.3). The frequency spent between 0% and 15% ranged from 44.6% to 91.6% ($\bar{x}$ = 64.4%) between seals excluding two extreme cases of seal 14 and 15, respectively[1]. Ice concentrations higher than 30% represented only an average of 21.8%. However, some seals were present in areas with quite high ice concentrations e.g. seal 6, 8 and 14 but these regions were frequented only from mid of April onwards, and thus represent only these animals.

Additionally, ice conditions in the vicinity of each seal position were analyzed to review these findings. An area of 325 km x 325 km around each location was examined according to half of the maximally possible travel distance for seals per day. It revealed the same pattern that seals spent most of their time in areas with open water (Appendix Fig. A.4).

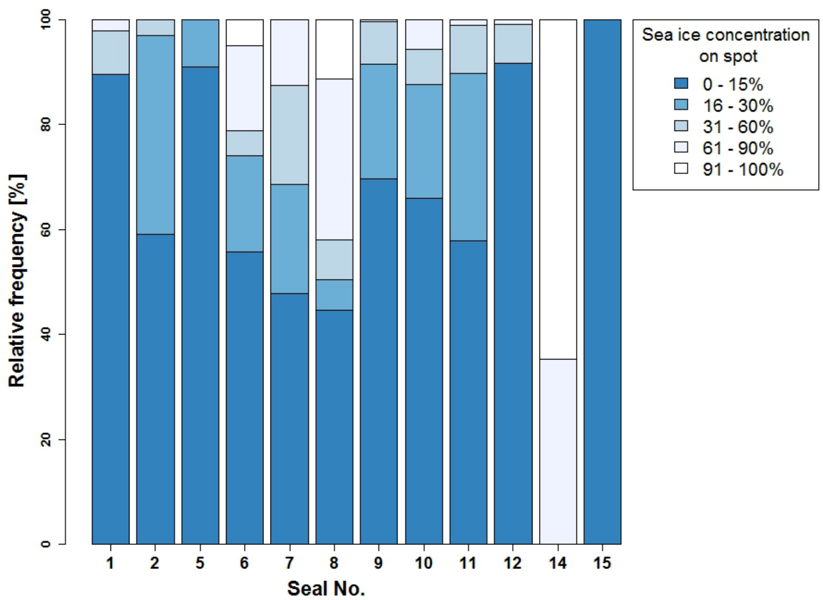


Fig. 13: Relative frequency of sea ice concentration present on individual seal locations. Ice concentration is given in 5 classes.

[1] Seal 14 remained in an ice shelf crack for seven weeks which was recorded as 'on land' by the satellite and is not displayed in Fig. 13. As the seal left the area, it faced heavy pack ice conditions which explain the high ice concentrations. The SDR of seal 15 transmitted for only 17 days. During this time the seal did not encounter aggregations of sea ice.

3.6 Diving behaviour

The analyses of diving behaviour in this thesis are restricted to a descriptive approach. A reasonable statistical deductive attempt was not feasible as it requires statistical models of time dependent diving behaviour on the basis of individuals, in accordance with the frequency data. For this kind of inverse modelling, data sets on the same individuals appear to be clearly too sparse (e.g. across 4 months).

3.6.1 Dive depth frequency

In total, 130,628 dives were recorded within the dive depth datasets. The dive depth distribution of each seal is provided (Fig. 14). For all animals except seal 15 the highest amount of dives took place in depths between 0 and 9 m, ranging between 18% (seal 15) and 74% (seal 1) with an average frequency of 43.3%. Greater depths were less visited with a general pattern of decreasing frequency towards the maximum depth. There is limited individual variability, e.g. some seals (2, 5, 6, 9, 15) show a bimodal pattern. Nevertheless, more than 80% of all dives of each animal occurred from 0 to 72 m. Great depths under 102 m were rarely visited.

A comparison between age classes revealed a similar pattern (Fig. 15). There are slight differences between subadults and adults. While adults spent an average of 55% in the upper water layer until 9 m, subadults used this interval only to an extent of 37%. They frequented water depths between 22 and 60 m more often than adults. Consistently, the relative amount of dives declined to less than 1% under 102 m.

A comparison between sexes was disregarded due to a too low sample size (females n = 2).

Dive depth frequency differed between months (Fig. 16). A strong unimodal pattern was observed where the first bin was prominent during all months. The average amount of dives between 0 and 9 m increased strongly and continuously from 37% to 78% as the season progressed while visits to deeper water layers nearly disappeared.

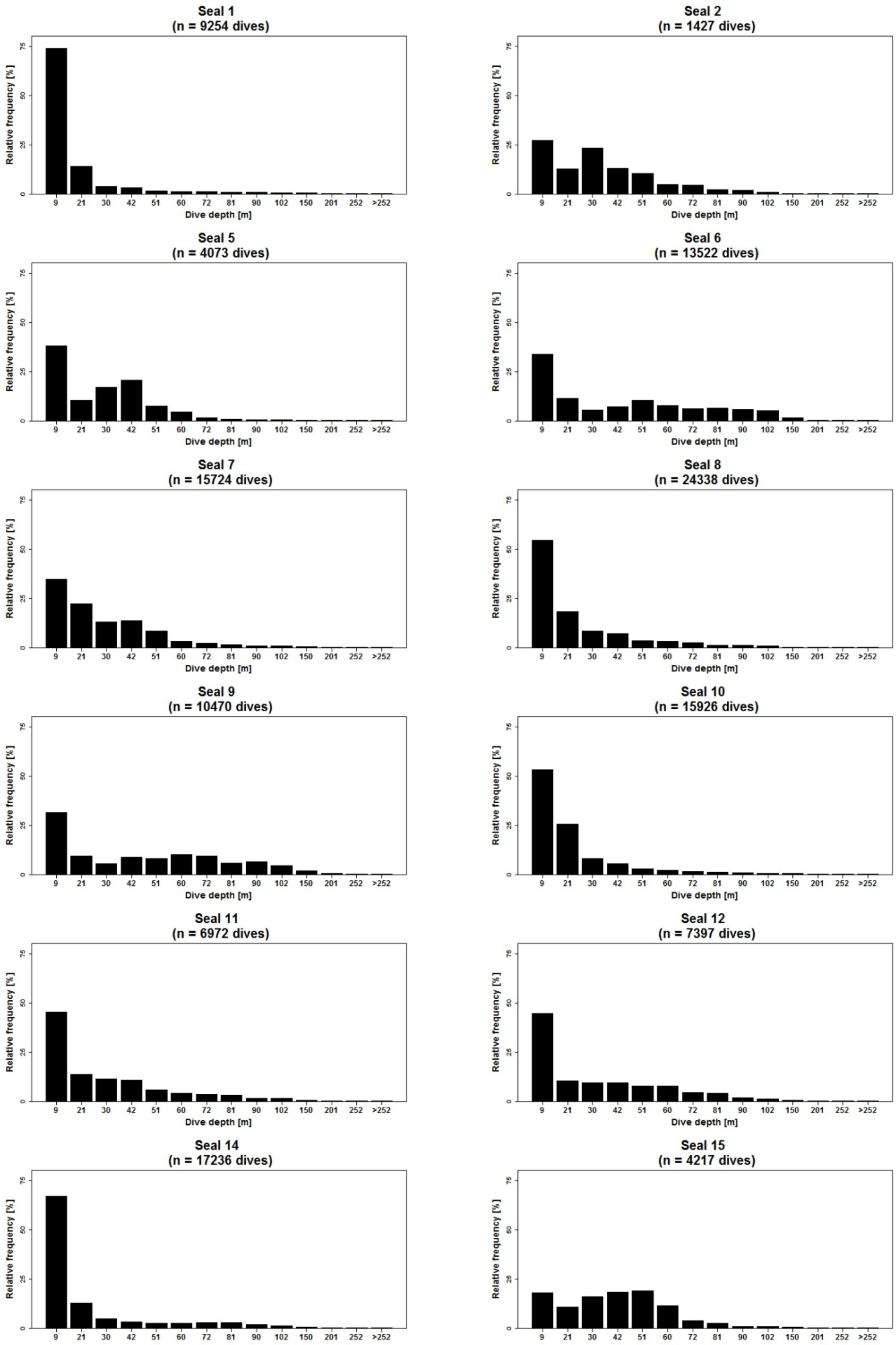


Fig. 14: Dive depth distribution of each individual crabeater seal. Each bar represents the relative amount of dives spent in a certain depth interval e.g. 0-9 m, 10-21 m etc.; n = total number of dives.

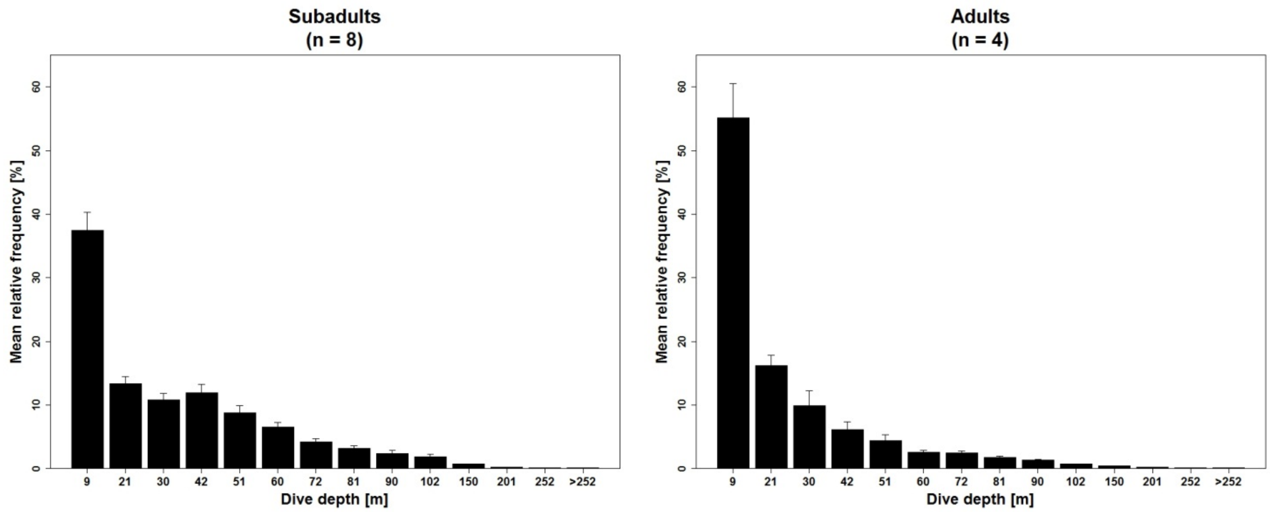


Fig. 15: Dive depth distribution of subadult and adult crabeater seals; n = number of seals belonging to the corresponding age class. Bars represent the mean frequency distribution, error bars (whisker caps) show standard error of the mean (SEM).

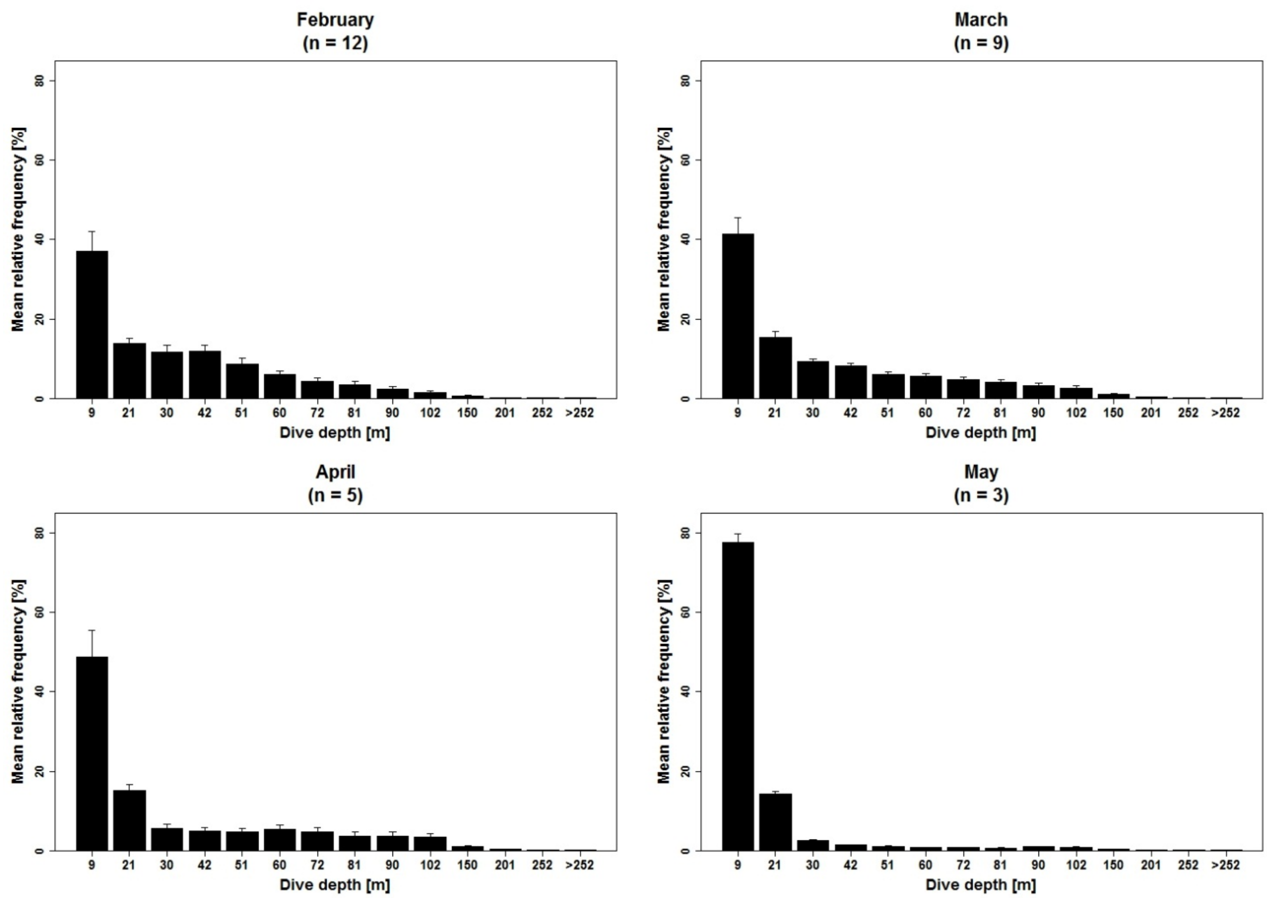


Fig. 16: Dive depth distribution of crabeater seals between months; n = number of seals still transmitting during the corresponding month. Bars represent mean frequency distribution, error bars (whisker caps) show standard error of the mean (SEM).

3.6.2 Maximum dive depth

In total, 403 dives were recorded within the maximum dive depth datasets. The average maximum dive depth of all seals was 247.5 ± 140.8 $_{(SD)}$ m (median = 232 m; SEM = 7.0 m). Maximum dive depth between age classes was 265 m ($\bar{x}$) for subadults vs. 240 m for adults. The deepest dive performed by seal 9 (subadult, female) reached down to 776 m.

3.6.3 Dive duration frequency

Dive recorders collected a total of 134,850 dives within dive duration datasets. Dive duration distribution of each animal is illustrated in Fig. 17. In 8 of 12 seals the first bin representing dives less than 1 min showed the highest frequency. All other remaining animals dived between less than 1 and 3 min with no clear preference for a specific duration. Though a certain degree of individual variability was observed, more than 90% of all dives lasted maximally 5 min. Longer dives were rare.

When comparing age classes a clear unimodal pattern was obvious (Fig. 18). In both subadults and adults dives less than 1 min dominated the diving behaviour but subadults also performed more dives between 1 and 3 min than adults. Dives usually did not last longer than 5 min in both age classes.

A comparison between sexes was disregarded due to a too low sample size (females n = 2).

Similar to dive depth dive duration was also influenced by seasons (Fig. 19). The amount of dives less than 1 min was dominant during all months and increased steadily from 40% to 75%. Simultaneously, dives between 1 and 5 min were reduced.

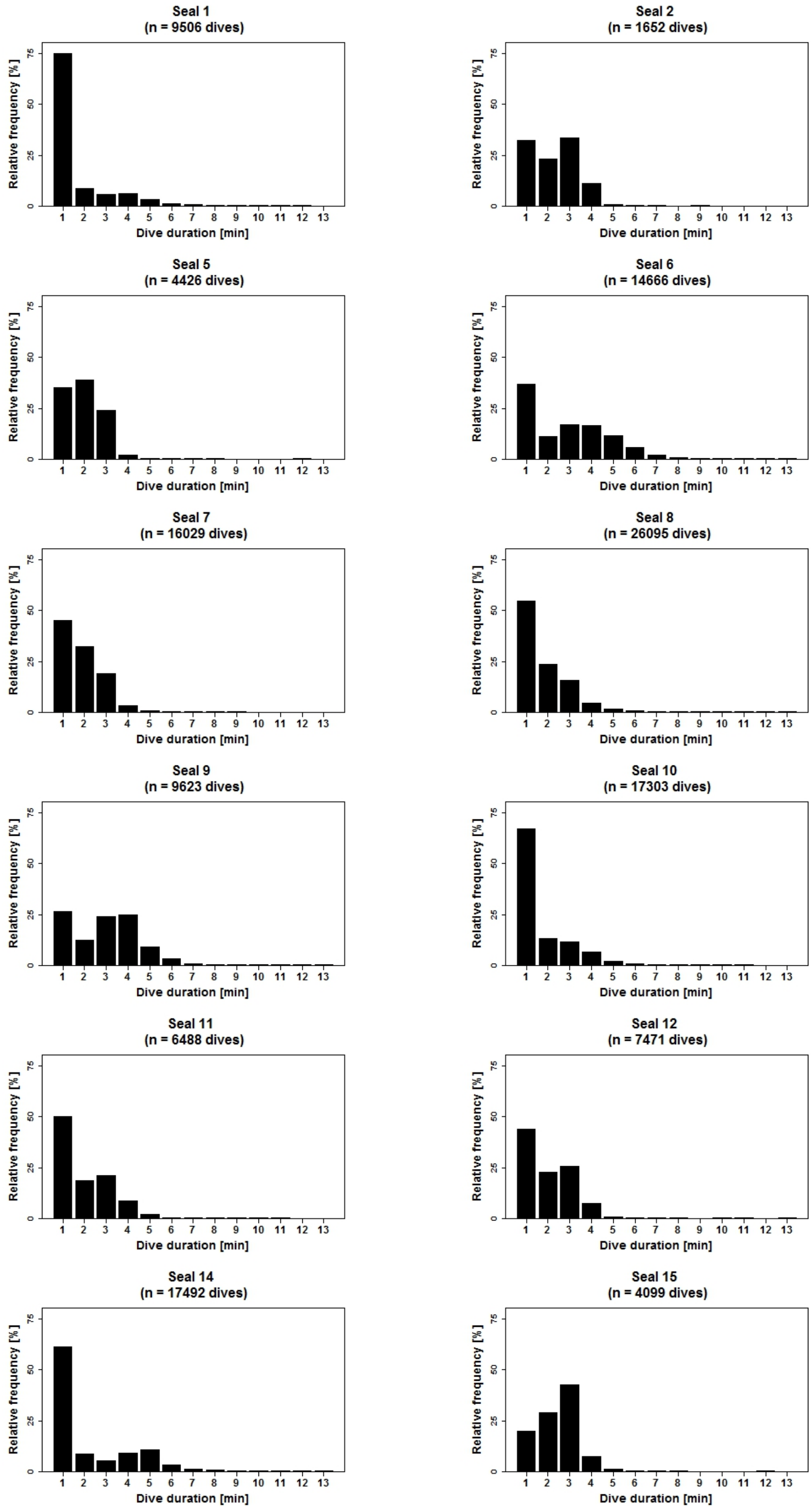


Fig. 17: Dive duration distribution of each individual crabeater seal. Each bar represents the relative amount of dives classified in certain time intervals e.g. 0-1 min, 1-2 min etc.; n = total number of dives.

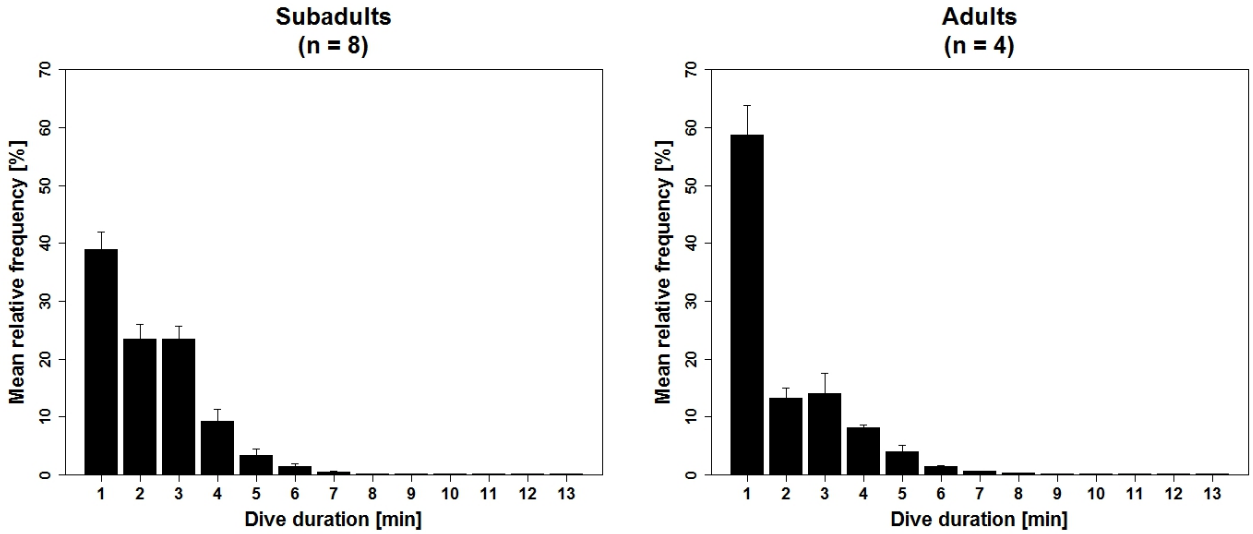


Fig. 18: Dive duration distribution of subadult and adult crabeater seals; n = number of seals belonging to the corresponding age class. Bars represent the mean frequency distribution, error bars (whisker caps) show standard error of mean (SEM).

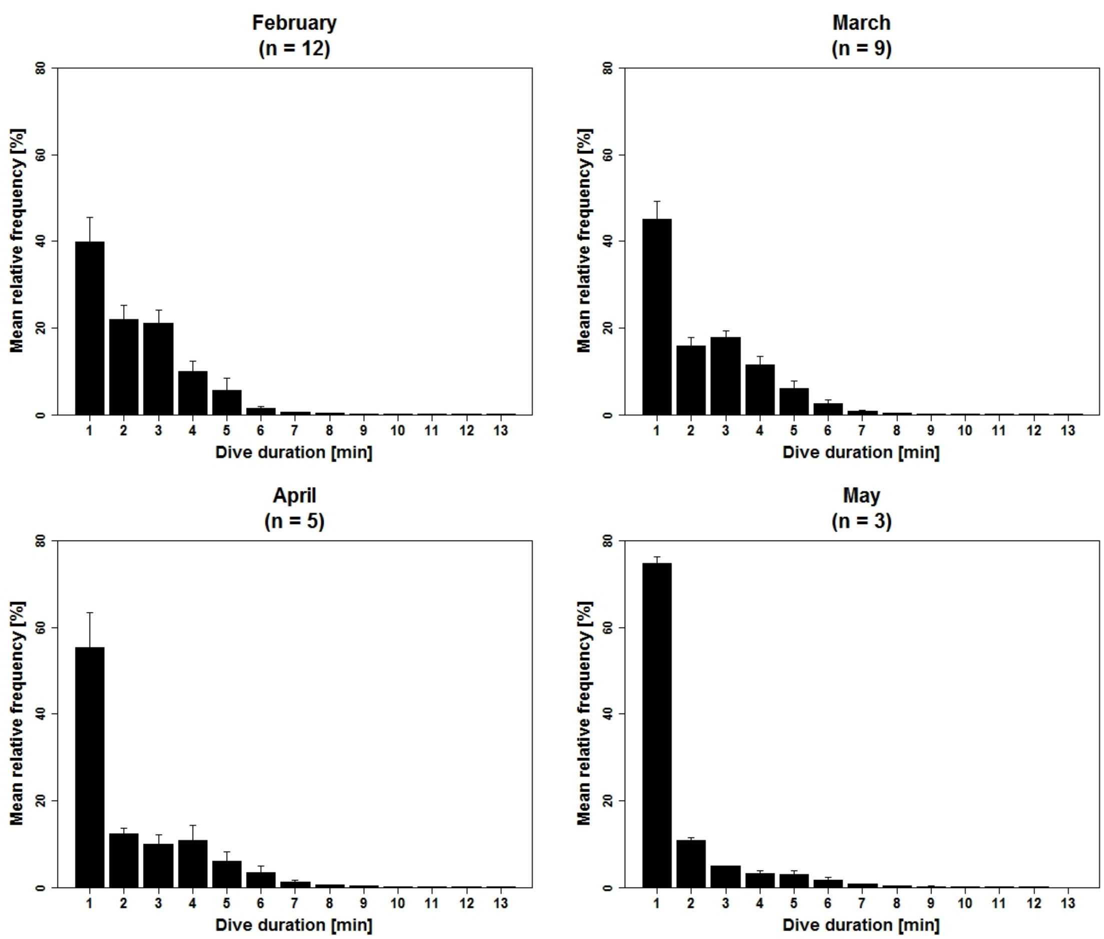


Fig. 19: Dive duration distribution of crabeater seals between months; n = number of seals still recording during the corresponding month. Bars represent the mean frequency distribution, error bars (whisker caps) show standard error of mean (SEM).

4. Discussion

4.1 Tag performance

Average longevity of SDRs and number of transmissions per day were well comparable with other crabeater seal studies (Nordøy et al. 1995, Wall et al. 2007). An early offset of transmissions could be due to tag loss during moult which normally occurs between January and February (Bengtson 2009). Due to a limited availability of crabeater seals at Drescher Inlet in 1998 a special selection of already moulted animals was not possible (H. Bornemann, personal communication). Transmission failure of seals 3, 4 and 13 is considered more likely due to technical malfunction or damage of the antenna through sea ice impact as reported by Burns et al. (2004).

4.2 Distribution

All crabeater seals left Drescher Inlet soon after tag deployment and dispersed radially into the Weddell Sea. Generally, they were not restricted to a certain area (with two exceptions) and performed long migrations. Consistently, Nordøy et al. (1995) reported maximum track lengths of 3,875 km for seals tagged off Queen Maud Land within Weddell Sea. Average travel speed amounted to 1.5 $km \cdot h^{-1}$ which is in accordance with the present investigation ($\bar{x}$ = 1.42 $km \cdot h^{-1}$). Studies conducted at the Antarctic Peninsula revealed that crabeater seals tend to stay in the same region within a radius of 300 – 500 km around the tagging site but also occasionally travel longer distances (Bengtson et al. 1993, Burns et al. 2004). Thus, geographic differences in distributional behaviour of crabeater seals are likely as also suggested by Wall et al. (2007). Moreover, this study discovered that two subadult animals migrated far eastwards along the eastern Weddell Sea and against the Antarctic Coastal Current covering distances of 4,438 and 3,648 km in a few months. This finding is essential in the context of genetic exchange in a metapopulation since crabeater seals occur circumpolar in the Antarctic pack ice zone (Bengtson 2009, Southwell et al. 2012). It is important to know how widespread populations are connected and to which extent genetic heterozygosity and diversity is maintained (Stern 2009). Davis et al. (2008) found little population genetic structure in crabeater seals using microsatellite analyses and concluded that there are high levels of gene flow between different regions around Antarctica. This result is supported by the present observation of long migrations.

4.3 Maxent modelling

A Maxent modelling analysis was conducted using satellite telemetry data to create geographic distribution maps of crabeater seals in the Weddell Sea. Suitable habitats for this species were indicated by high probabilities of presence. A set of 16 environmental variables was used to detect important factors influencing their distribution. The most important factors will be discussed below in connection with the formulated hypotheses.

4.3.1 Sea ice concentration

Contribution of sea ice concentration to the Maxent model was most important and continuously high during all months. The February model predicted some delimited areas where probability of occurrence was medium to high. Interestingly, these areas totally correspond to regions of ice-free water as obtained from the FESOM model for February 1998 (Appendix Fig. A.5). These results match with the observations that seals spent an average of 64.4% in open waters and were only occasionally found in ice-covered zones. Thus, **hypothesis 1** was rejected. This is in contrast to the general scientific opinion that crabeater seals are regarded as typical pack-ice inhabitants which obviously need the ice for breeding, mating and resting (Siniff et al. 1979, Erickson & Hanson 1990, Nordøy et al. 1995, Bester et al. 2002, Ackley et al. 2003, Southwell 2004). Several studies have shown that these seals are closely related to medium and high sea ice concentrations and rarely visit open waters (Nordøy et al. 1995, Ackley et al. 2003, Burns et al. 2004, Wall et al. 2007). However, Wall et al. (2007) reported from eastern Antarctica that tagged seals spent 14.4% of their time in ice-free areas during post-breeding season (after mid-November). Thus, it can be assumed that crabeater seals apparently frequent open waters more than previously thought.

Certainly, one reason for this extensive use of open water was the comparatively low sea ice cover and extent within the whole Weddell Sea area during summer 1998 with a deviation of $-0.25 \cdot 10^6$ km^2 to the mean (Cavalieri & Parkinson 2008, Schwegmann 2012). Thus, the availability of sea ice as haul out platform was limited which was also mentioned by Bester and Odendaal (2000) who conducted helicopter seal censuses in the same season during research expedition (EASIZ II). They concluded that their very high density and abundance estimate was positively biased since seals concentrated on remaining ice floes for hauling out (Bester et al. 1995, Bester & Odendaal 2000). This may be a common problem for surveys in the eastern Weddell Sea because in general nearly all sea ice melts away in this region during summer (Schwegmann 2012). Minimum sea ice cover is usually reached in February (Cavalieri & Parkinson 2008) when the majority of Bester and Odendaal's (2000) observations took place. Tagged seals did not remain for extended time periods in bays or ice shelf cracks like inlets with residual fast ice but instead dispersed widely in the open Weddell Sea (except for seal 14). This distributional pattern is not unusual and was also reported by Nordøy et al. (1995) in a year with regular ice conditions and in the same area. While sea ice cover increased again from March onwards the still transmitting seals in the Weddell Sea swam northwards apparently following the extending ice edge. During that time seals occupied regions with higher ice concentrations (> 50%) for the first time. Both the migration to the north and occurrence within pack ice in autumn are consistent with Nordøy et al. (1995). It can be assumed that crabeater seals can deal quite well with open water conditions and do not necessarily need heavy pack ice in late summer.

Next to sea ice concentration the February Maxent model predicted an increasing probability of presence from open water towards the ice edge (Fig. 9 & Appendix A.5). While the ice edge retreats during summer months, ice algae are released from melting sea ice and build up a phytoplankton bloom (Smith & Nelson 1985, Garrison et al. 1987). Therefore, this zone attracts large aggregations of zooplankton, especially Antarctic krill *Euphausia superba*, which feed on these algae (Stretch et al. 1988, Brierley et al. 2002). As a result, the ice edge may also be attractive for crabeater seals which primarily consume krill (King 1961, Øritsland 1977, Lowry et al. 1988, Burns et al. 2004, Hückstädt et al. 2012). However, results of visual surveys do not support this proposed habitat preference (Southwell et al. 2012).

4.3.2 Bathymetry

Both, water depth and distance to shelf break were identified as important parameters influencing the distribution of crabeater seals. Especially in March, depth contributed evidently to the Maxent model whereas the jackknife analyses confirmed its importance for each month. Predicted favored ocean depths ranged between 500 and 4,000 m with 4,000 m showing highest probabilities of presence which reflects the major range of actual seal occurrences. Therefore, **hypothesis 2** was confirmed. These findings were confirmed by other studies. Southwell et al. (2005) found that seals in eastern Antarctica showed highest occurrence probabilities in water depths around 2,500 m off the continental shelf and were rarely present in depths deeper than 4,000 m. Consistently, crabeater seals off Queen Maud Land generally occupied areas characterized by depths between 3,000 and

5,000 m and only occasionally visited regions with depths less than 500 m in austral autumn (Nordøy et al. 1995).

In addition, Nordøy et al. (1995) mentioned that seals moved near the continental shelf break. For the species distribution model, distance to the shelf break defined as the 1,000 m isobath also seemed to be an important factor. Maxent predicted suitable habitats within a range of 400 km off the shelf margin which covers nearly all seal tracks and is in accordance with results by Wall et al. (2007) so that **hypothesis 3** was confirmed. Beyond that, this area includes the continental slope of the Weddell Sea. It is known that crabeater seals frequent the continental shelf break as well as slope regions and high abundances have been recorded there (Nordøy et al. 1995, Ackley et al. 2003, Southwell et al. 2005, Flores et al. 2008). Also in this study, several seals occurred near the continental shelf break and adjacent slope in late summer and autumn. This matches with the biology and distribution of Antarctic krill, the primary food source of crabeater seals. During summer large aggregations of adult krill are found along the continental shelf break where sufficient food supply is given due to current flows (Siegel 2005, Nicol 2006). Gravid female krill migrate to deeper regions offshore for spawning (Siegel 2005, Nicol 2006). Furthermore, krill is dependent on currents, especially counter-current systems between the Antarctic Circumpolar Current and the Antarctic Coastal Current to transport krill larvae onto the continental shelf (Nicol 2006). High krill concentrations are related to such surface circulations which may occur circumpolar (Marr 1962, Nicol 2006). This may also be a reason why two animals migrated eastwards strictly above the slope for multiple weeks. It can be speculated that it is to some extent favorable for highly mobile planktonic predators to swim against the westward flowing Antarctic Coastal Current which provides them with floating prey, but only two seals followed this concept. During autumn adult krill return onto the continental shelf and overwinter in deeper water layers whereas krill larvae feed on the sea ice community (Siegel 2005, Nicol 2006). However, postlarval krill was also found in locally high densities directly under the winter sea ice (Marschall 1988, Flores et al. 2011, Flores et al. 2012). This seems to be an important food source for crabeater seals occurring in northerly extending pack ice far offshore as seen in this study.

Burns et al. (2004) reported different habitat preferences from the Western Antarctic Peninsula. In winter and spring tagged animals remained on the continental shelf in water depths between 50 m and 450 m and avoided deeper regions. This result matches with observations that adult krill is found above the continental shelf (Siegel 2005, Nicol 2006). These behavioural differences of seals during winter may be due to major geographic and bathymetric differences between study areas. The continental shelf surrounding the Antarctic Peninsula is broad and apparently provides a suitable habitat for crabeater seals e.g. regarding food (Burns et al. 2004, Lawson et al. 2004, Friedlaender et al. 2012). In contrast, the eastern part of the Weddell Sea and other areas in eastern Antarctica are characterized by a narrow continental shelf which may provide less favorable conditions during winter so that seals are following the extending ice edge.

It is noteworthy that Maxent constantly predicted high probabilities of presence for the continental shelf break of the General Belgrano Bank in the central southern Weddell Sea. The model highlighted the continental slope of the Filchner Trough outflow, Berkner Bank and General Belgrano Bank as a suitable habitat in April. Indeed, two crabeater seals visited this region with one animal staying there for more than one month. Tosh et al. (2009) reported that also two adult male southern elephant seals (*Mirounga leonina*) travelled from King George Island into this region. These two animals stayed between Berkner Bank and Akademik Fedorov Canyon for about 100 days until they migrated back to King George Island and South Georgia, respectively. A study on Weddell seals (*Leptonychotes weddellii*) showed that these frequent this area as well (Nicholls et al. 2008). In a comprehensive approach to investigate the Filchner Trough outflow system (Knust 2013), aerial seal census surveys were conducted in the Filchner Trough outflow system to estimate density and abundance of Antarctic seals for this particular region. Crabeater seals were abundant above the continental shelf break and nearly absent above the trough (Bornemann et al., unpublished data). Preliminary results indicate that density in the shelf break area (1.32 km^{-2}) was similar to other aerial seal census studies in the Weddell Sea and adjacent waters (Erickson & Hanson 1990: 0.41 km^{-2}, Bester et al. 2002: 0.72 km^{-2}, Flores et al. 2008: 1.02 km^{-2}, Forcada & Trathan 2008: 2.29 km^{-2}). Interestingly, a significant longitudinal density gradient towards the west was detected which fits well with the model predictions (Bornemann et al., unpublished data). By now, the southern Weddell Sea, especially Berkner and General Belgrano Bank, is poorly studied but generally regarded as biological hotspot due to intensive upwelling and mixing of water masses (Foldvik et al. 2004, Knust 2013). The Filchner Trough outflow contributes strongly to the formation of cold and oxygenated Weddell Sea Deep Water (WSDW) and Weddell Sea Bottom Water (WSBW) which mix with trace-element-rich Ice Shelf Water (ISW) and are transported westwards (Foldvik et al. 2004, Matsumura & Hasumi 2011).

The model characterized regions around the submarine seamount Maud Rise as suitable habitats throughout February and March as well. This is in accordance with ship based observations of high abundances of crabeater seals and other endotherm top predators near Maud Rise (Plötz et al. 1991).

Nordøy et al. (1995) reported that one tagged animal migrated onto the southern slope of the Maud Rise. It is known that an upwelling of warm deep water occurs there which leads to an increased sea ice melting and release of ice algae (Plötz et al. 1991). Thus, also high concentrations of Antarctic krill are found in this region, even in winter under the ice (Plötz et al. 1991, Flores et al. 2012).

4.3.3 Surface temperature

Surface temperature was the second most important factor for modelling the distribution of crabeater seals. By now, no other study found a similar relationship. Solely, Friedlaender et al. (2011) found a connection to deep temperature maximum related to Circumpolar Deep Water (CDW) which may be a sign for enhanced biological productivity. However, in the present study seals seem to favor surface temperatures below 0°C which correspond to Antarctic Surface Water (AASW) (Orsi et al. 1995). AASW is characterized by temperatures less than 0.5°C and salinity values below 34.4 (Orsi et al. 1995). Maxent predicted salinity preferences between 34 and 34.2 which matches the properties of AASW. It ranges quite uniformly between the Polar Front and the Antarctic continent and represents the coldest and freshest water mass within the Weddell Gyre (Orsi et al. 1993, Orsi et al. 1995). Antarctic krill *E. superba* is a typical cold-water species and only occurs south of the Polar Front (Siegel 2005, Mackey et al. 2012). Its optimum temperature range lies between -1 and +1°C (Mackey et al. 2012) which matches the Maxent result well. However, it remains unclear whether the dependence on surface temperature for crabeater seal distribution is real or a pseudo-correlation due to the absence of sea ice and the extensive use of open water in this study.

4.3.4 Regional differences

Although the tagged seals mainly inhabited the eastern and central Weddell Sea, the western part generally seems to be a much more important habitat as predicted by Maxent. Consistently, seal census surveys from the western Weddell Sea revealed high abundance estimates over decades (Erickson & Hanson 1990, Forcada & Trathan 2008). For example, the most recent observation conducted by Forcada and Trathan (2008) under the Antarctic Pack-Ice Seal (APIS) programme estimated a population size of 2,332,505 individuals (95% CI: 1,208,189 – 3,544,511) for this region. This corresponds to around one quarter of the estimated circumpolar population (Southwell et al. 2012). As mentioned above, abundance estimates for the eastern Weddell Sea are difficult to obtain. In general, crabeater seal densities are high in that region, e.g. 3.92 km^{-2} (Erickson & Hanson

1990) and can be even up to 8.01 km^{-2} (Bester & Odendaal 2000), though the latter finding is biased due to very low sea ice concentrations as outlined above. Since surveys mostly take place during summer where sea ice cover is usually very low in this area (Schwegmann 2012), additional surveys early in the season and thus devoid of a potential low ice bias should be conducted. Bester et al. (1995) reported a twofold increase in density with progressing summer (December - February), i.e. as the pack ice rapidly diminished. Thus, observation results can be strongly biased and are also dependent on time of the year. As a result, abundance estimates for the eastern Weddell Sea range between 806,400 (Erickson & Hanson 1990) and 3,564,000 (Bester & Odendaal 2000). As the association between crabeater seals and pack ice was described in many studies (Nordøy et al. 1995, Bester et al. 2002, Ackley et al. 2003, Burns et al. 2004) and the western Weddell Sea provides more stable conditions throughout the year (Schwegmann 2012), it can be assumed that it is indeed a more suitable habitat than the eastern Weddell Sea.

4.4 Diving behaviour

Diving behaviour was generally characterized by short and shallow dives. An average of 43.3% of all dives went down to less than 9 m and more than 80% of all dives for each animal were not deeper than 72 m, and more than 90% of all dives were shorter than 5 min. This reflects the typical summer and autumn diving behaviour of crabeater seals as recorded in other studies conducted in the Weddell Sea and eastern Antarctica, respectively (Bengtson & Stewart 1992, Nordøy et al. 1995, Wall et al. 2007). Usually, crabeater seals use the upper 50 m of the water column and do not dive longer than 5 min. This is in accordance with the vertical distribution of Antarctic krill *E. superba*. It is scientific consensus that krill occurs in the ocean surface layer, generally within the upper 150 m, during summer (Siegel 2005). Recently, a novel fishing trawl was applied during a multiannual and -seasonal field experiment (LAKRIS) in the Lazarev Sea (Flores et al. 2011, Flores et al. 2012, Flores et al. 2014). In the aforementioned studies, only the upper 2 m of the water column were sampled by this device both in open water and also under the ice revealing a krill-dominated community throughout seasons (Flores et al. 2014). During summer and autumn krill was abundant in open water and showed even higher densities compared to under the ice in autumn (Flores et al. 2012). Although densities in the surface layer were generally high in all seasons, epipelagic layer samples (0 – 200 m) mainly exceeded these values (Flores et al. 2012). From these findings it can be assumed that seals in this study found a sufficient amount of prey while they untypically spent most of their time in open water. Since krill is abundant at the surface, crabeater seals do not need to dive deep to achieve this food resource which is energetically efficient (Costa 2009). Consistently, other marine endotherm krill predators show similar diving patterns (Croxall et al. 1985, Boyd & Croxall 1992, Nordøy & Blix 2009).

Bengtson & Stewart (1992) divided crabeater seal dives in four categories on the basis of dive depth and duration fulfilling different ecological functions. They suggested that short and shallow dives (Type I) are connected with travelling although they only used time-depth records (TDRs) which do not provide information about horizontal movements (Bengtson & Stewart 1992). Since diving behaviour in the present study was clearly dominated by this dive type and especially krill predators like the crabeater seal need a regular food intake due to their small-sized prey (Boyd 2002) it is supposed that these dives are also connected with foraging. As mentioned above, seals find food in the surface water layer (Flores et al. 2012).

Diving behaviour did not differ strongly between age classes. Subadults dived slightly deeper than adults so that **hypothesis 4** was rejected. Furthermore, the overall deepest dive was performed by a subadult female seal reaching down to 776 m. This beats the current dive record of 713 m reported by Burns et al. (2004). Thus, an association of increasing dive depths with increasing age due to changing physiological capabilities could not be supported in the same way as for other phocid seals (Bowen et al. 1999, Burns 1999, Jørgensen et al. 2001).

Obviously, diving behaviour of crabeater seals showed seasonal differences. Thus, **hypothesis 5** was confirmed. The average amount of dives within the upper 9 m doubled in the period from February to May (37% vs. 78%). The same pattern holds true for dive durations less than 1 min (40% vs. 75%). This result is confirmed by Nordøy et al. (1995) who observed a similar rise in short, shallow dives between February and June. During this time the sea ice extent of the Weddell Sea is expanding again (Schwegmann 2012) and from mid-March onwards seals already faced heavy pack-ice conditions. It is known that also adult krill inhabits the underside of sea ice during winter (Marschall 1988, Plötz et al. 1991, Siegel 2005, Flores et al. 2012). This would explain the increase of shallow dives since krill spends more time at the surface, and fits with results of Flores et al. (2012) who accounted that krill densities in the surface layer were highest in winter under the ice.

By contrast, Burns et al. (2004) reported a different diving behaviour for crabeater seals during winter. Seals at the Western Antarctic Peninsula dived deeper ($\bar{x}$ = 92 m) and longer ($\bar{x}$ = 5.26 min) compared to all other studies. Additionally, they mainly stayed above the continental shelf and remained in areas with high sea ice concentration (Burns et al. 2004). These behavioural differences can be explained by the distribution of Antarctic krill within this region. During winter adult krill migrates back onto the continental shelf and overwinters in deeper water layers (Siegel 2005, Nicol 2006), which was confirmed by acoustic backscattering and trawling samples during the study period (Burns et al. 2004, Lawson et al. 2004). Therefore, crabeater seals simply had to dive deeper to reach their preferred prey. As a compensation they became locally concentrated where sea ice, bathymetry and prey availability were particularly suitable (Burns et al. 2004). Since no further study about crabeater seal's diving and foraging behaviour in other regions during winter is available, geographic differences cannot be excluded.

4.5 Area restricted movements

Generally, crabeater seals were steadily moving and did not remain at one place for long. However, two seals showed a different behaviour and performed area restricted movements. Seal 14 stayed within a small crack of the Riiser-Larsen Ice Shelf between the Stancomb-Wills Ice Tongue and Lyddan Island for seven weeks. This crack is usually filled with sea ice and situated in a rift of the approximately 100 m thick ice shelf (Humbert et al. 2009, Wuite & Jezek 2009). Since this area restricted movement was an unusual event compared to all other seals, the diving behaviour during that time was analyzed separately. Both dive depth and dive duration frequency differed substantially to the general observed pattern (Appendix Fig. A.6 and Fig. A.7). The amount of dives was more or less evenly distributed from 0 to 81 m and then decreased towards 150 m. Furthermore, dives usually lasted between 3 and 5 min representing 64% of all dives. Thus, seal 14 dived deeper and longer than the average. Since it remained in this area for an extended time, it can be assumed that it found an abundant food source as suggested by Tosh et al. (2009). As a trade-off, seal 14 might have invested more energy into foraging than other seals by diving deeper and longer. Usually, krill is very abundant in the surface layer during February and March (Flores et al. 2012) which questions this different diving behaviour. Nevertheless, krill could have potentially been present in deeper water layers. It is also possible that seals foraged on or even under the ice shelf which was reported for Weddell seals in the Drescher Inlet through seal-mounted cameras (Watanabe et al. 2006) though under shelf ice excursion might require even longer dive durations By now, there is only limited information about composition, distribution and abundance of under-ice-shelf communities. Watanabe et al. (2006) found dense aggregations of invertebrates, e.g. cnidarians and isopods, which may also be a feeding ground for fishes (Bruchhausen et al. 1979).

More importantly, crabeater seals occasionally supplement their krill diet with fish as *Pleuragramma antarcticum*, squid or other zooplankton (Øritsland 1977, Green & Williams 1986). Thus, it is conceivable that seal 14 shifted into a more opportunistic diet and fed on a probably abundant food source which would explain the differences in diving behaviour.

Seal 8 also showed an area restricted movement above the continental shelf break of General Belgrano Bank where it remained about four weeks. In contrast to seal 14, diving behaviour did not reveal any difference to the normal pattern (Appendix Fig. A.8 and Fig. A.9). Since it is known that krill occurs above the continental shelf break during summer (Nicol 2006) and is abundant in the upper 2 m of the water column (Flores et al. 2012), the behaviour of seal 8 is not expected to differ from the observed average.

5. Appendix

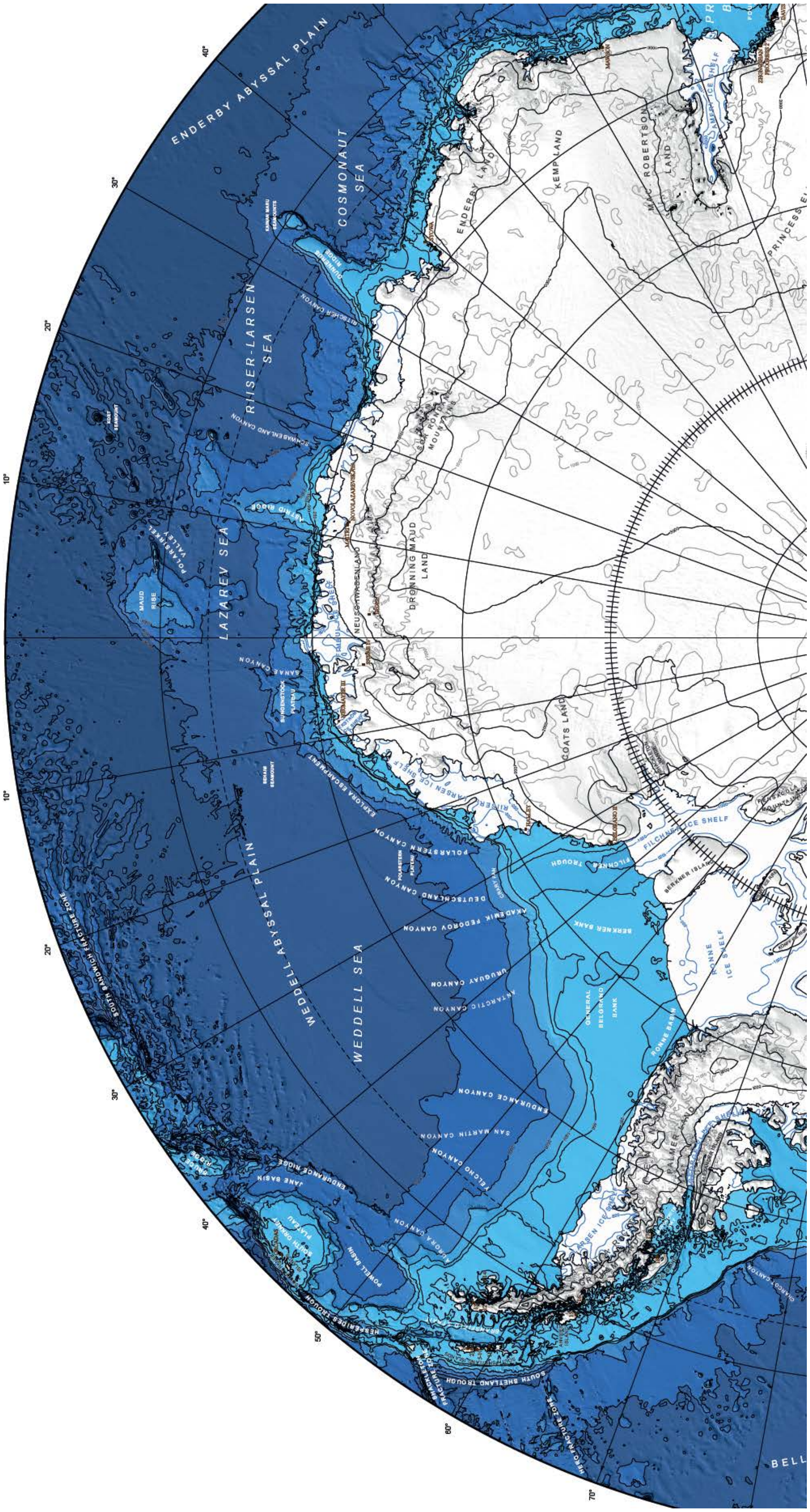


Fig. A.1: Excerpt of the International Bathymetric Chart of the Southern Ocean (IBCSO) (Arndt et al. 2013; doi.pangaea.de/10.1594/PANGAEA.805735). All geographic terms used for describing seal movements in chapter 3.3.1 are indicated on this map.

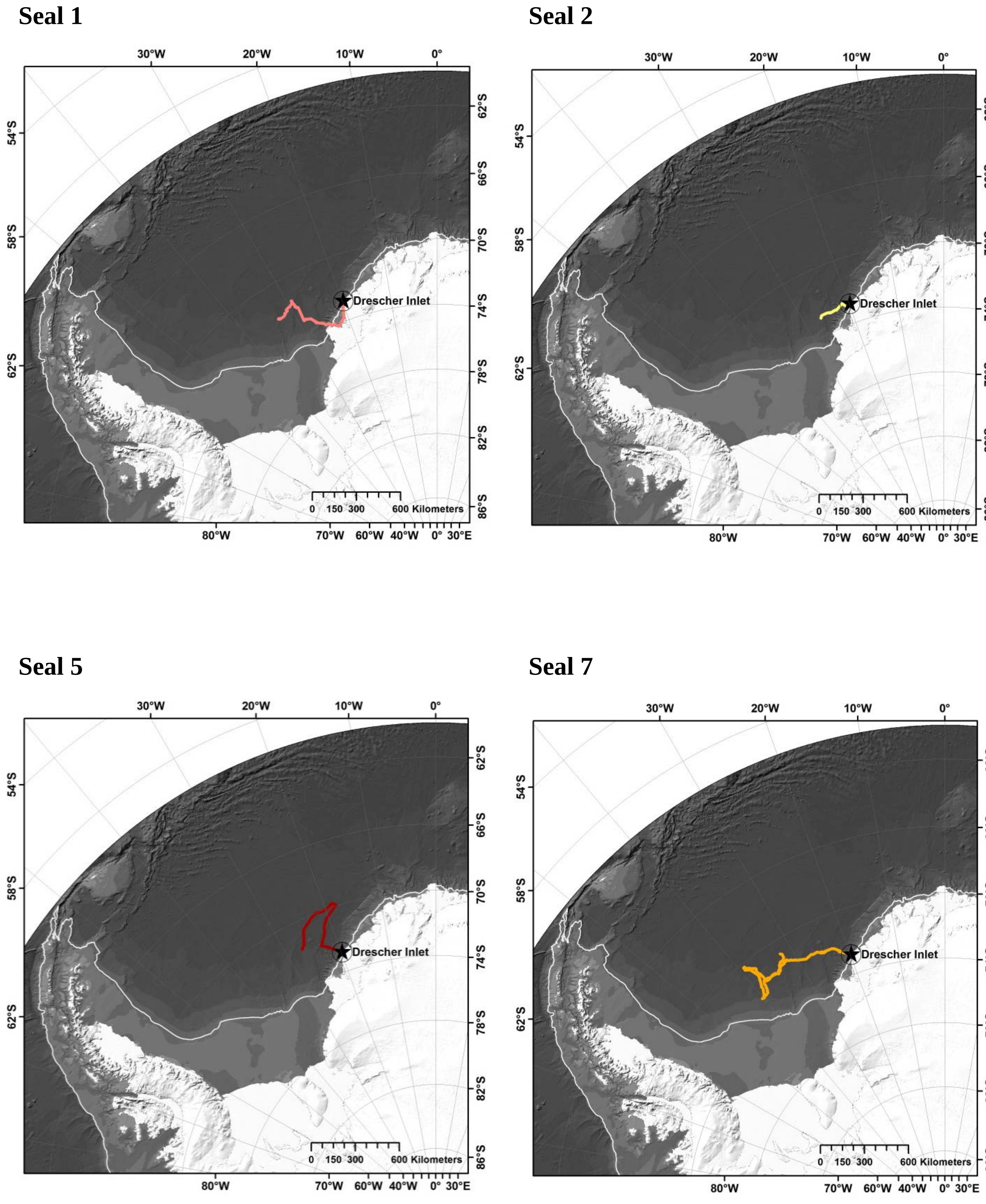
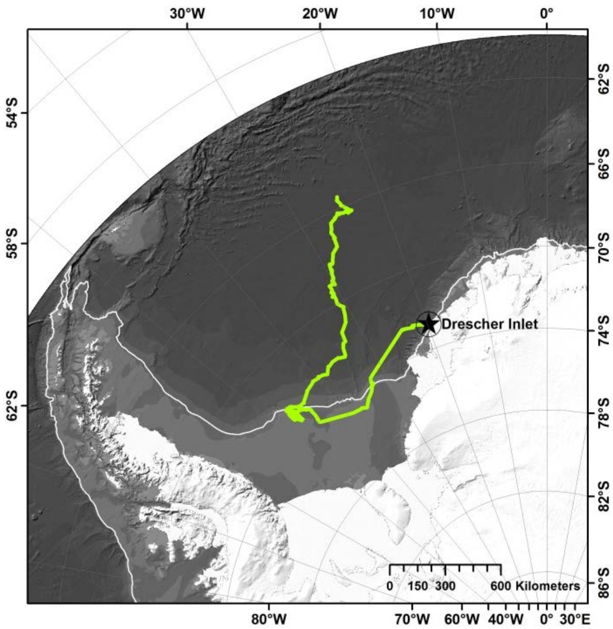
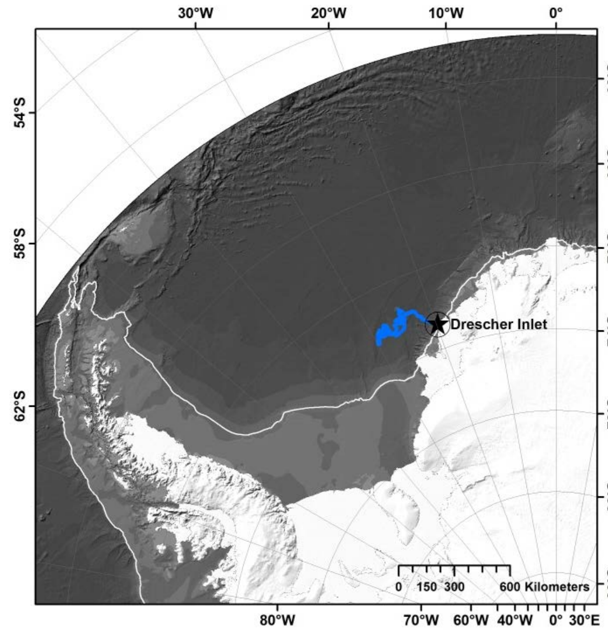


Fig. A.2: Individual tracks of 12 crabeater seals (*Lobodon carcinophaga*) in the Weddell Sea and adjacent waters dispersing from Drescher Inlet (star). Bathymetry is indicated by various shades of grey (light = shallow, dark = deep). The white line shows the 1000 m isobath of the continental shelf defined as shelf break.

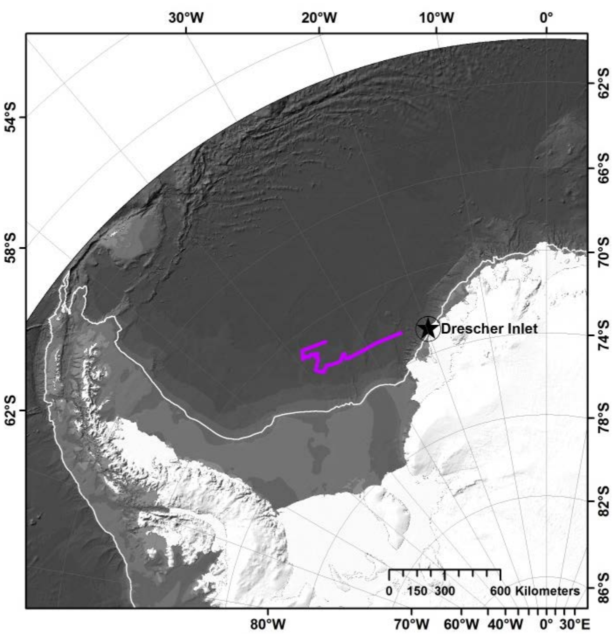
Seal 8



Seal 10



Seal 11



Seal 12

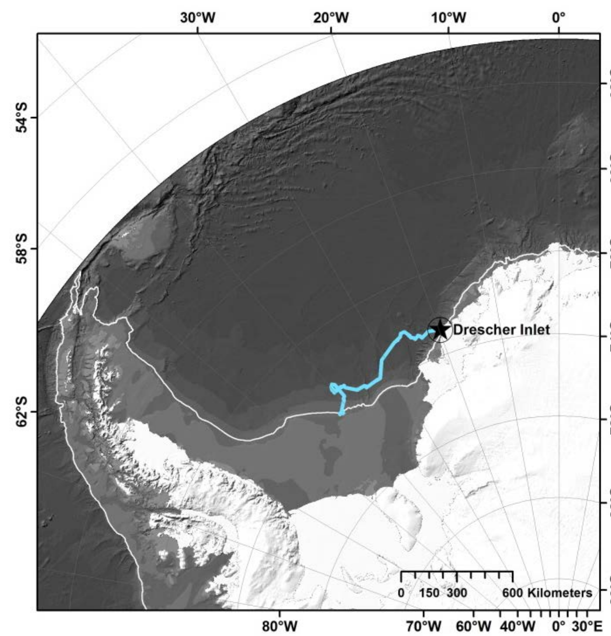
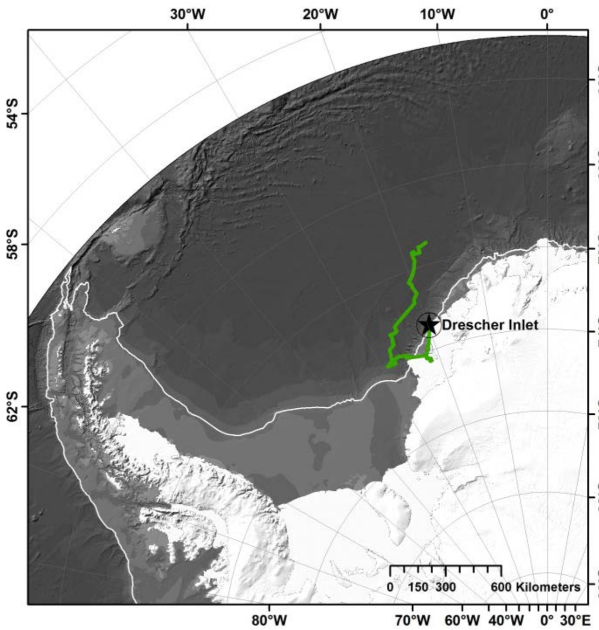
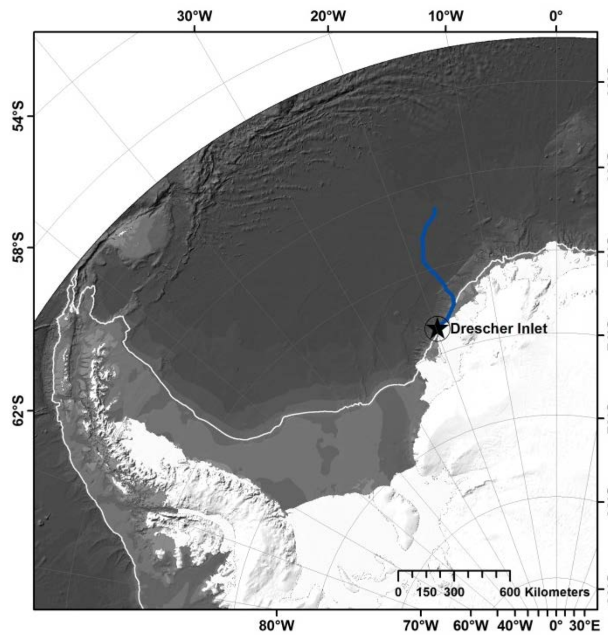


Fig. A.2: (continued)

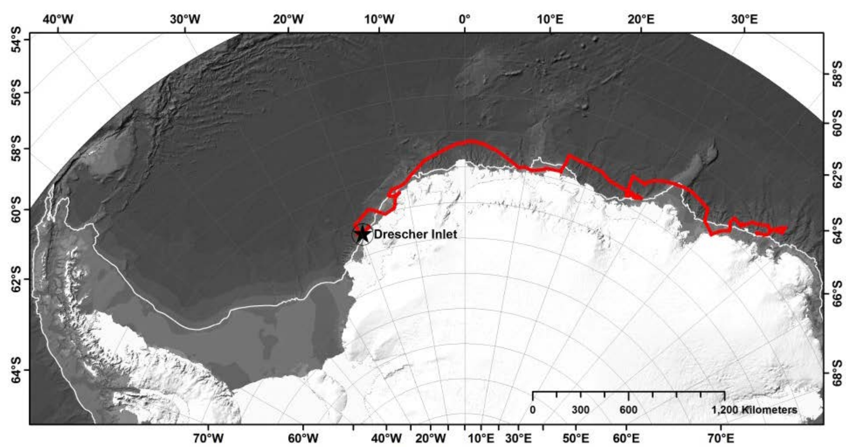
Seal 14

Seal 15





Seal 6



Seal 9

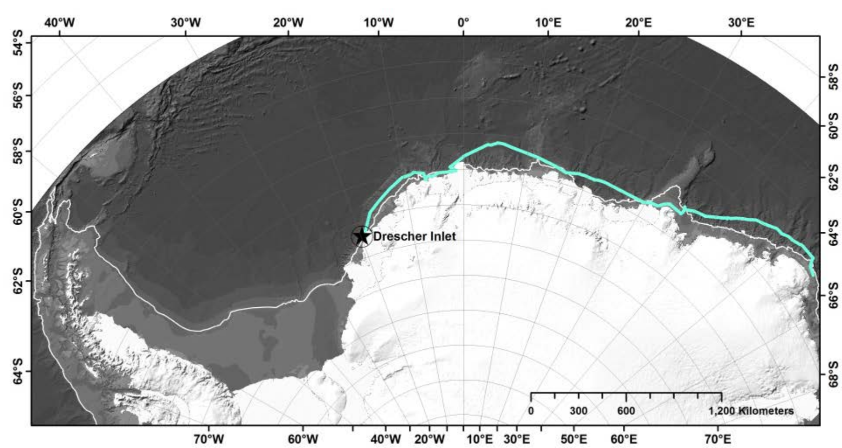


Fig. A.2: (continued)

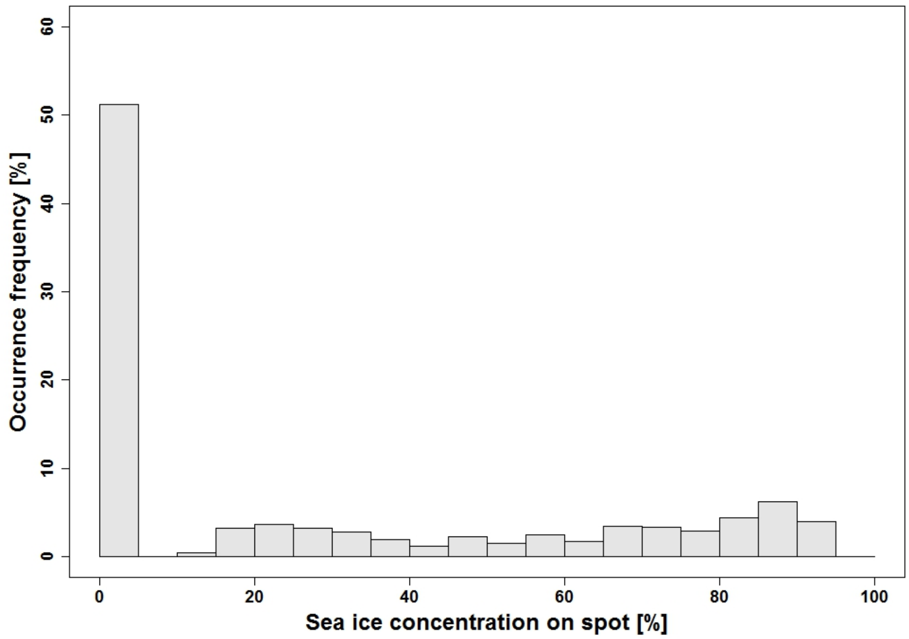


Fig. A.3: Frequency distribution of sea ice concentration present on all seal locations.

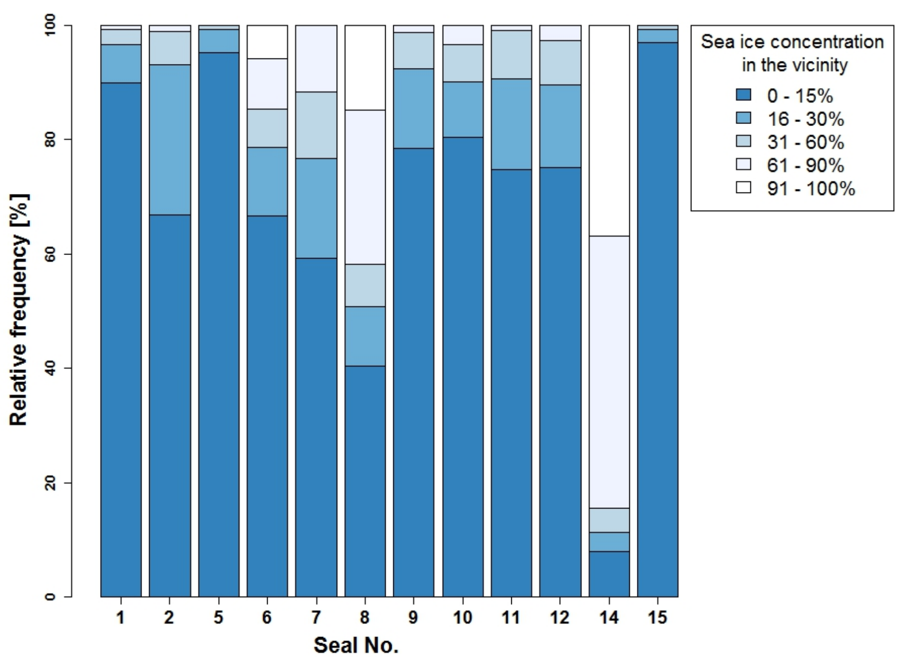


Fig. A.4: Relative frequency of sea ice concentration in 139 pixels surrounding each seal location. Every pixel has a size of 25 km x 25 km resulting in an area of 325 km x 325 km. Ice concentration is given in 5 classes.

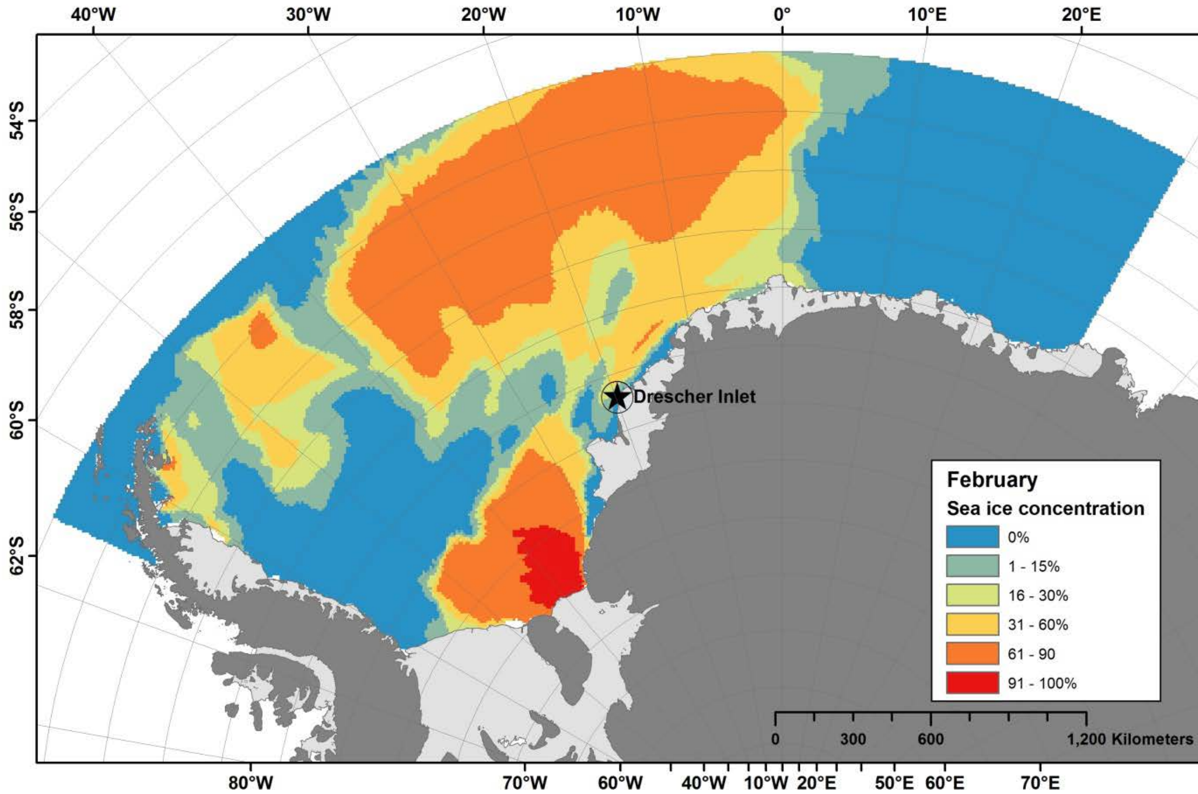


Fig. A.5: Sea ice concentration within the Maxent study area as derived from the FESOM model for February 1998. Blue areas indicate open water and green the ice edge. Red regions illustrate areas with high ice concentrations, i.e. nearly closed ice cover. Drescher Inlet is represented by a star. Dark grey = Antarctic continent; light grey = ice shelves.

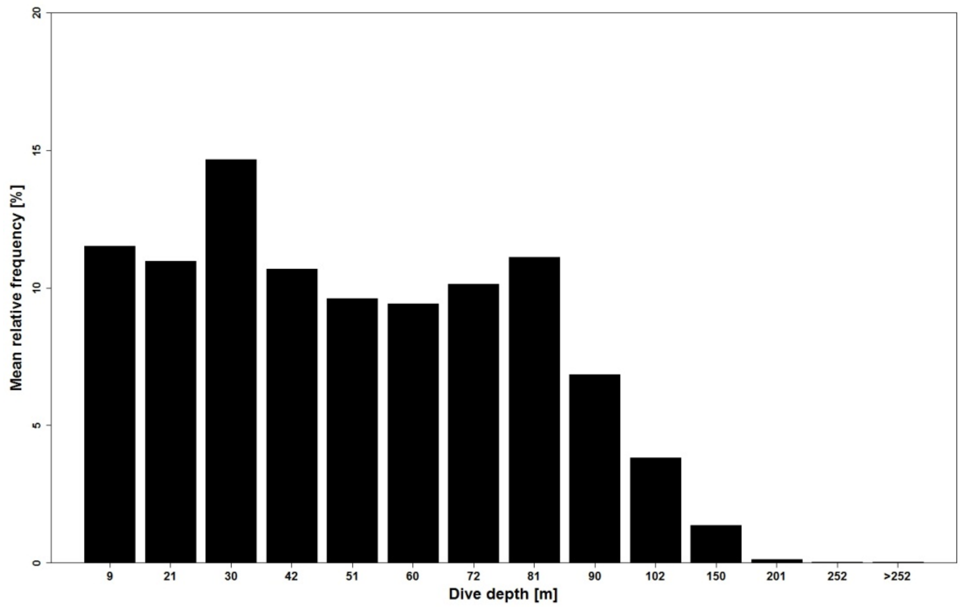


Fig. A.6: Dive depth distribution of seal 14 during an area restricted movement. Each bar represents the relative amount of dives spent in a certain depth interval e.g. 0-9 m, 10-21 m etc.

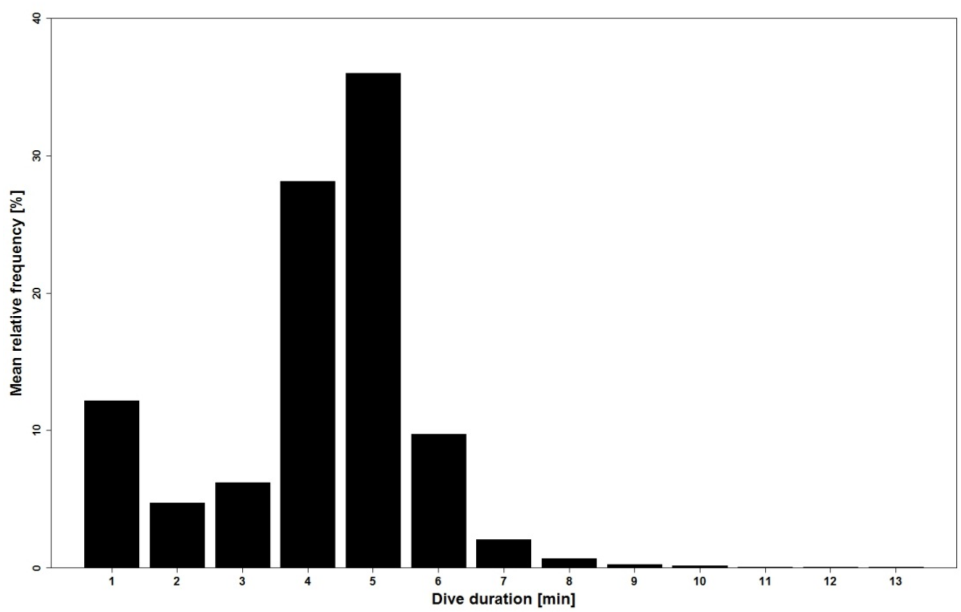


Fig. A.7: Dive duration distribution of seal 14 during an area restricted movement. Each bar represents the relative amount of dives classified in certain time intervals e.g. 0-1 min, 1-2 min etc.

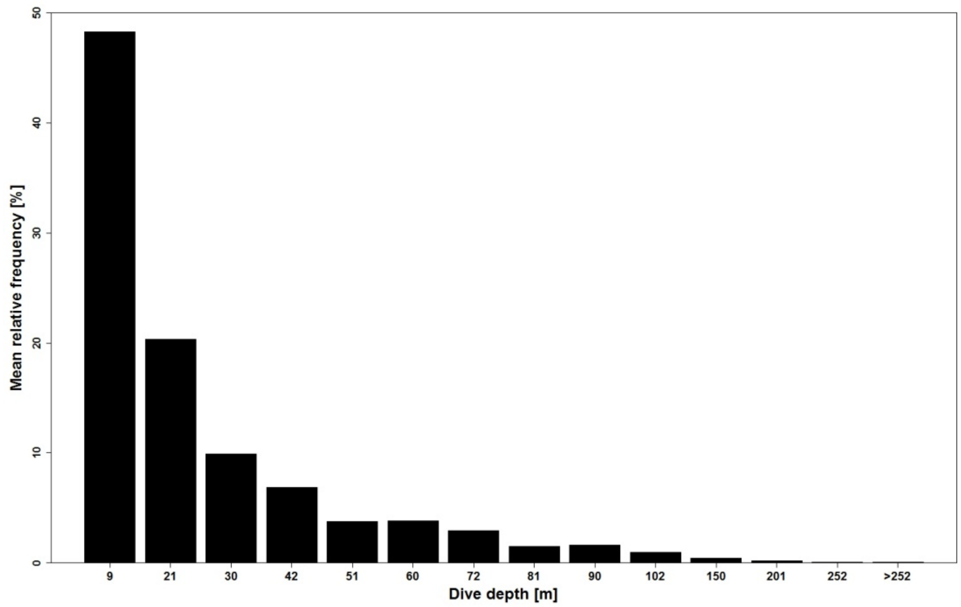


Fig. A.8: Dive depth distribution of seal 8 during an area restricted movement. Each bar represents the relative amount of dives spent in a certain depth interval e.g. 0-9 m, 10-21 m etc.

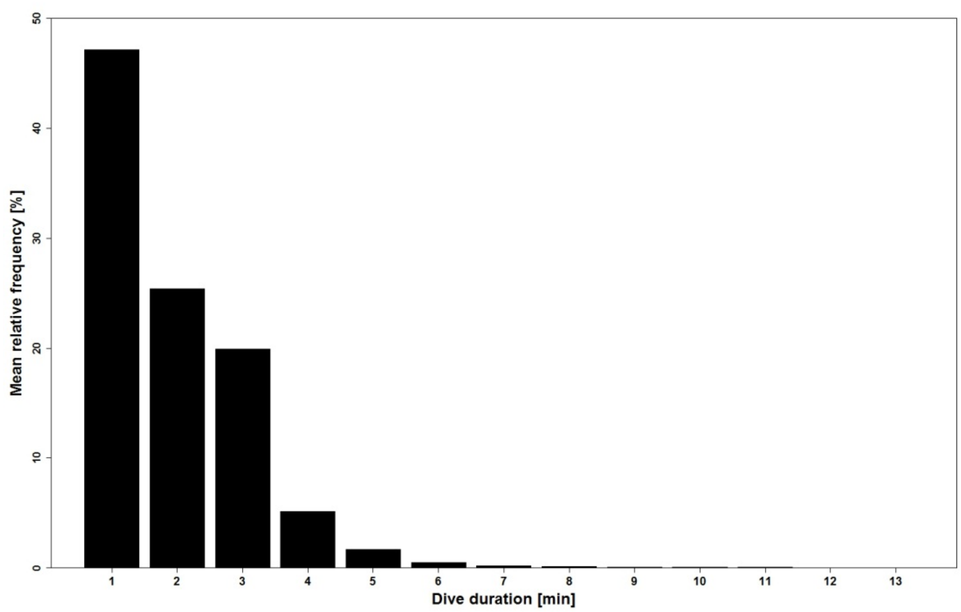


Fig. A.9: Dive duration distribution of seal 8 during an area restricted movement. Each bar represents the relative amount of dives classified in certain time intervals e.g. 0-1 min, 1-2 min etc.

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7. Declaration of Independence

I hereby confirm that I have independently composed this Bachelor Thesis and that no other than the indicated aid and sources have been used. This work has not been presented to any other examination board.

Dominik Andre Nachtsheim

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