



Foraging behaviour of Weddell seals (*Leptonychotes weddellii*) in connection to oceanographic conditions in the southern Weddell Sea

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ABSTRACT

The region of the Filchner Outflow System (FOS) in the southeastern Weddell Sea is characterized by intensive and complex interactions of different water masses. Dense Ice Shelf Water (ISW) emerging from beneath the ice shelf cavities on the continental shelf, meets Modified Warm Deep Water (MWDW) originating from the Antarctic Circumpolar Current at the sill of the Filchner Trough. These hydrographic features convert the FOS into an oceanographic key region, which may also show enhanced biological productivity and corresponding aggregations of marine top predators. In this context, six adult Weddell seals (*Leptonychotes weddellii*) were instrumented with CTD-combined satellite relay data loggers in austral summer 2014. By means of these long-term data loggers we aimed at investigating the influence of environmental conditions on the seals' foraging behaviour throughout seasons, focussing on the local oceanographic features. Weddell seals performed pelagic and demersal dives, mainly on the continental shelf, where they presumably exploited the abundant benthopelagic fish fauna. Diurnal and seasonal variations in light availability affected foraging activities. MWDW was associated with increased foraging effort. However, we observed differences in movements and habitat use between two different groups of Weddell seals. Seals tagged in the pack ice of the FOS focussed their foraging activities to the western and, partly, eastern flank of the Filchner Trough, which coincides with inflow pathways of MWDW. In contrast, Weddell seals tagged on the coastal fast ice exhibited typical central-place foraging and utilized resources close to their colony. High foraging effort in MWDW and high utilization of areas associated with an inflow of MWDW raise questions on the underlying biological features. This emphasizes the importance of further interdisciplinary ecological investigations in the near future, as the FOS may soon be impacted by predicted climatic changes.

1. Introduction

The formation and export of cold, dense and oxygenated Antarctic Bottom Water (AABW) is one of the key processes that drives the global thermohaline circulation. The southern Weddell Sea in particular is one of the key areas of dense and bottom water formation and possibly the major global source of AABW (Orsi et al., 1999; Foldvik et al., 2004). The Filchner Outflow System (FOS) around the Filchner Trough in the southeastern Weddell Sea plays a substantial role in this context, as it is characterized by the constant outflow of Ice Shelf Water (ISW) formed below the Filchner Ronne Ice Shelf. The ISW, defined as water with potential temperatures below the surface freezing point (-1.9°C),

interacts with Warm Deep Water (WDW), a modified derivative of Circumpolar Deep Water (CDW), at the shelf break off the Filchner Trough, ultimately contributing to the AABW formation (Foldvik et al., 2004; Nicholls et al., 2009). Modified Warm Deep Water (MWDW), a slightly cooler and fresher version of WDW formed via mixing with ambient water masses at the shelf break, seasonally enters the continental shelf east and west of the Filchner Trough and may even reach the Filchner Ronne Ice Shelf cavity (Nicholls et al., 2008; Darelius et al., 2016; Ryan et al., 2017). This prominent oceanographic setting (see Fig. 1) due to intensive mixing of water masses led to the conception that the FOS could also be considered a biological “hotspot” with enhanced productivity and potentially high abundances of marine top

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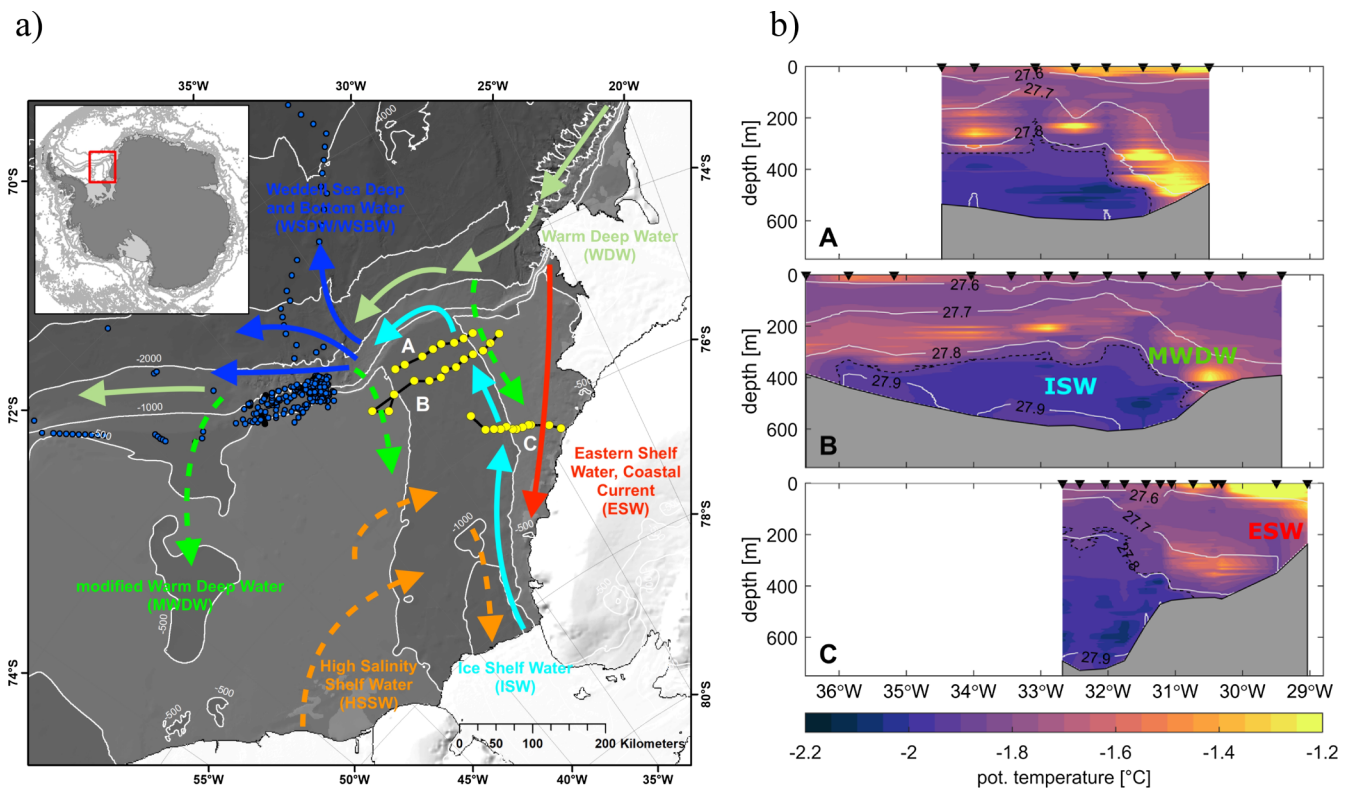


Fig. 1. (a) Location of the Filchner Outflow System (FOS) in the southeastern Weddell Sea, Antarctica (red box). White contour lines indicate the bathymetry (500–4000 m water depth). Coloured arrows illustrate the simplified oceanographic setting in the FOS, including the most important water masses and currents, modified after Bornemann et al. (2010) and Darelius et al. (2014). Dashed arrows highlight water masses whose flow strength varies seasonally, whereas solid arrows represent water masses with no known seasonality. Connected yellow dots represent three ship-borne CTD sections (A–C) across the Filchner Trough sampled during *Polarstern* expedition PS96 (Schröder et al., 2016). Blue dots exemplify winter (May–September) foraging locations of adult male southern elephant seals in 2000 (Tosh et al., 2009; Bornemann et al., 2010). (b) Potential temperature sections at CTD locations shown in (a), illustrating the far-reaching MWDW inflow on the eastern flank of the Filchner Trough. The black dotted line in the sections is the -1.9°C isotherm (surface freezing point temperature), and represents the border between ISW and overlaying water masses. Note that ISW occasionally penetrates from the Filchner Trough onto the eastern shelf (C). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

predators (Knust and Schröder, 2014).

Earlier tagging studies of adult male southern elephant seals (*Mirounga leonina*) revealed that some seals travelled more than 2000 nautical miles from their breeding/moulting sites at the Antarctic Peninsula to the FOS during both winter and summer (Tosh et al., 2009; Bornemann et al., 2010). The animals foraged in a well-defined shelf-slope area close to the outflow of the Filchner Trough for several months, as indicated by area-restricted movements (Tosh et al., 2009). However, the factors contributing to this presumed foraging hotspot of enhanced prey availability are not yet clear. Recent research efforts aimed at exploring abiotic and biotic interactions in the FOS over multiple trophic levels (Knust and Schröder, 2014; Schröder, 2016). Understanding the role and impact of the various elements in the FOS food web is crucial, in particular in the light of climate change. Climate models predict an increased melting rate of the Filchner Ronne Ice Shelf due to the redirection of warm waters (i.e., WDW) onto the continental shelf (Hellmer et al., 2012). Within the 21st century this may lead to an extensive ice-mass loss and a sharp increase in bottom water temperatures on the shelf (Hellmer et al., 2012, 2017). These profound projected changes to the physical environment call for comprehensive ecological investigations in the rarely studied FOS.

The Weddell seal (*Leptonychotes weddellii*) usually occurs in high-Antarctic regions and is the most southerly breeding mammal species (Smith, 1965; Stirling, 1969; Siniff, 1991). In these regions, including the FOS, Weddell seals aggregate in fast-ice habitats close to the Antarctic coast year-round, but they are also found in the pack ice (Smith, 1965; Testa, 1994; Árrthun et al., 2012). As top predators in the high-Antarctic food web they feed on benthic-pelagic fish species, primarily

Pleuragramma antarctica followed by *Trematomus* spp. and other notothenioid species such as Antarctic toothfish (*Dissostichus mawsoni*), but occasionally they also prey upon cephalopods and crustaceans (Plötz, 1986; Green and Burton, 1987; Burns et al., 1998; Goetz et al., 2017).

Weddell seal populations are relatively well studied in the western Ross Sea and East Antarctica (e.g., Stirling, 1969; Castellini et al., 1992; Testa, 1994; Burns et al., 1999; Lake et al., 2003; Lake et al., 2005; Goetz et al., 2017; Heerah et al., 2016) compared to populations within the Weddell Sea. Although systematic research effort on Antarctic seals in the Weddell Sea was initiated in the early 1980s (Drescher, 1982; Drescher and Plötz, 1983), existing investigations on movements of Weddell seals, especially during winter, are fragmentary (cf. Boehme et al., 2016; Langley et al., 2018). This emphasizes the need for studies on winter diving and foraging behaviour as a major part of their seasonal life cycle, particularly in the presumably attractive FOS.

For this purpose, Weddell seals were instrumented with satellite-linked dive loggers, which record data on geographic position, dive behaviour and hydrography concurrently. These *in situ* measurements provide direct insight into the oceanographic conditions experienced by the seals. Several studies previously used seal-derived hydrographic data to investigate the flow of warm water onto the continental shelf. Nicholls et al. (2008) found an inflow of Modified Warm Deep Water (MWDW) onto the shelf west of the FOS, towards the Filchner Ronne Ice Shelf front, while Árrthun et al. (2012) reported a seasonal inflow of MWDW at the eastern flank of the Filchner Trough. On the continental shelf of the western Antarctic Peninsula, seal-derived CTD profiles revealed a shelf-wide presence of Modified Circumpolar Deep Water

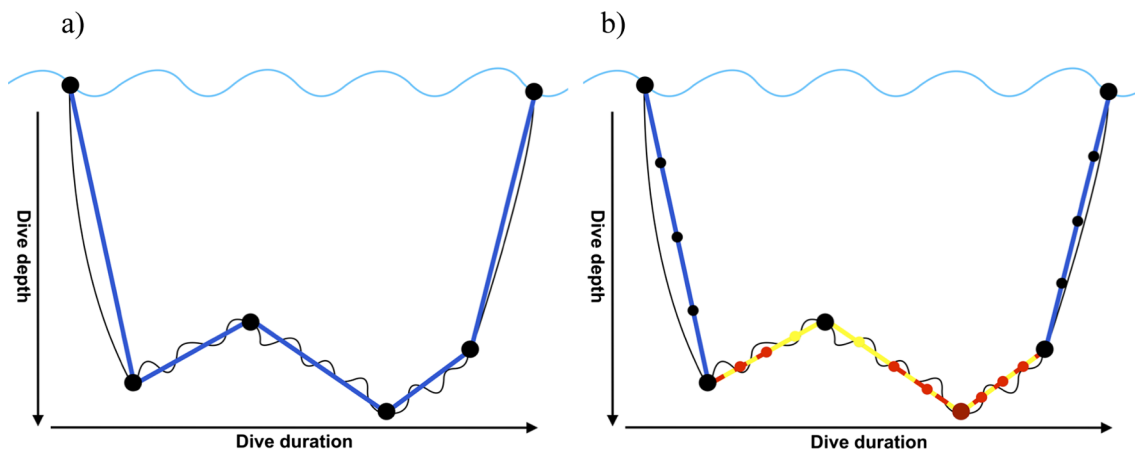


Fig. 2. (a) Schematic illustration of the compression of a dive profile. The solid black line illustrates an example high-resolution dive profile as recorded by the CTD-SRDLS. An on-board broken stick algorithm then calculates the four main inflection points, where the dive trajectory changes most significantly (Fedak et al., 2001, 2002). This results in four time-depth points as well as two points when the animal surfaced (large black dots). This simple, low-resolution dive profile is then transmitted by the CTD-SRDLS. (b) Illustration of the three foraging metrics derived from the low-resolution dive profiles. The deepest point of each dive represents the *maximum dive depth* (dark red dot). For a more reasonable calculation of bottom time, intermediate time-depth points are added via linear interpolation (small dots). All points deeper than 80% of the maximum dive depth (red dots) constitute the bottom phase of the dive, connected by the red dashed line. The time spent in these segments represents the *bottom time*. Hunting segments are characterized by low vertical velocities (≤ 0.4 m/s) (solid yellow line plus yellow-red dashed line). The time spent in these segments adds up to the *hunting time*. Blue segments represent transit phases and are not included in any foraging metric. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Costa et al., 2008). Several Antarctic seal species frequently target these warm water masses, suggesting high prey abundance (Costa et al., 2008; Heerah et al., 2013; Labrousse et al., 2015; Hindell et al., 2016; Zhang et al., 2016). In this study, we combine *in situ* hydrographic data with dive behavioural data of Weddell seals to relate their movements with the encountered oceanographic conditions in the FOS. The aim of this study is hence to elucidate the influence of oceanographic and other environmental variables on the foraging behaviour of Weddell seals in the FOS by means of specific foraging metrics throughout different seasons.

2. Materials and methods

2.1. Sampling rationale and tag deployment

Six adult Weddell seals were equipped with Conductivity-Temperature-Depth Satellite Relay Data Loggers (CTD-SRDLS) in the FOS, southeastern Weddell Sea, during research expedition PS82 of RV *Polarstern* in austral summer 2014 (Knust and Schröder, 2014). Preferred locations for the instrumentation of Weddell seals were proposed to orient along the eastern and western slope of the sill of the Filchner Trough, coinciding with winter and summer foraging locations of southern elephant seals known from earlier studies (Tosh et al., 2009; Fig. 1). However, due to unfavourable weather and ice conditions, opportunities for deployments were limited to two locations: (1) on consolidated ice floes on the western flank of the Filchner Trough and (2) on a coastal, fast ice-covered inlet east of the trough at the Brunt Ice Shelf. Seals were spotted on the ice directly from aboard the vessel or via helicopter at more distant locations relative to the ship's track. Seals were then approached on the ice by foot and selected opportunistically for deployment.

The seals were immobilised with a combination of xylazine (Rompun®, 500 mg; Bayer) and ketamine (Ketavet®, 100 mg/ml; Pfizer). Doses were injected intramuscularly by using blowpipe darts. Depending on the course of the immobilisation, additional xylazine and/or ketamine doses were administered manually to maintain or extend the narcosis. Diazepam (5 mg/ml; Ratiopharm) was reserved to reduce potential adverse effects, such as muscle tremors, which can be caused by ketamine. The antidote atipamezole (Antisedan®, 5 mg/ml; Orion Pharma) was given to reverse the xylazine component of the

immobilisation mixture (see Bornemann et al., 1998, 2014 for a detailed description of the immobilisation procedure and all dose rates, respectively).

While the seals were immobilised, body length and girth measurements were taken with the animal lying on its venter and CTD-SRDLS were glued to the hair on the animal's head using a two-component, quick setting Araldit® epoxy resin. Seals selected for instrumentation had already completed moulting their hair on the head and upper neck. Thus, the devices were expected to remain in place until the seals' next annual moult the following year.

The immobilisation of Weddell seals and deployment of CTD-SRDLS were carried out pursuant to the (SCAR) Code of Conduct for Animal Experiments. Furthermore, all procedures were approved by the German Federal Environmental Agency ("Umweltbundesamt") and the ("Bundesamt für Naturschutz") under the German acts implementing the Protocol of Environmental Protection to the Antarctic Treaty and the Convention for the Conservation of Antarctic Seals.

2.2. Tag settings and data collection

The Weddell seals were equipped with CTD-SRDLS (545 g in air; $12 \times 7.2 \times 6$ cm (L \times W \times H)) manufactured by the Sea Mammal Research Unit, University of St. Andrews, UK (Boehme et al., 2009). These devices record data on a seal's dive behaviour as well as *in situ* hydrographic conditions and transmit data through communication with polar-orbiting Argos satellites, when the seal surfaces (CLS/Service Argos, Toulouse, France). The uplinks to the Argos satellite system are used to estimate the location of a seal via the Doppler shift, so that movements of individuals can be tracked over time. Location estimates are qualified according to spatial error estimates, ranging from 0.5 km to 10 km on average (Vincent et al., 2002; Costa et al., 2010).

Dive depth and duration were recorded every 4 s during a dive, which was considered to start below a water depth of 6 m. However, due to bandwidth limitations of the Argos satellites, only a compressed dive profile, and not the full high-resolution profile, could be transmitted. This dive profile consisted of the four main inflection points, where the dive trajectory changed most rapidly (see Fedak et al., 2001, 2002). Thus, each dive profile contained four dive depth points at a given dive duration plus two surface points at the beginning and end of each dive (Fig. 2a). All times were recorded in Coordinated Universal

Time (UTC).

The CTD-SRDLs sampled pressure, temperature and salinity (*post hoc* calculated from conductivity measurements) every 1–2 s during the ascent phase of a dive. For each 6-h period, the CTD profile of the deepest dive within this period was transmitted (*i.e.*, four CTD profiles per day). Up to 16 representative, pre-defined sampling depths with corresponding temperature and salinity values were relayed, depending on the satellite connection (see Boehme et al., 2009 for more information on the sampling and transmission protocol). Water temperature and salinity were post-processed using a delayed-mode calibration, in particular to correct deviations in salinity recordings (Roquet et al., 2011). The post-processed data had an estimated accuracy of ± 0.01 °C and ± 0.03 , respectively (Roquet et al., 2011).

All behavioural and hydrographic primary data of the six Weddell seals as well as the corresponding meta-data information are accessible via the data library PANGAEA (<https://doi.pangaea.de/10.1594/PANGAEA.871104>).

2.3. Filtering of seal tracks

Weddell seal tracking data were filtered in two steps to account for spatial errors in the estimated locations. First, tracks were screened by a simple speed-distance-angle filter algorithm (R package *argosfilter*; Freitas et al., 2008). Highly inaccurate locations were removed, which required unrealistic swimming speeds greater than 5.1 m/s corresponding to the recorded maximum speed and approximately twice the mean dive speed of Weddell seals (Davis et al., 2003). Improbable spikes in the animal's track were eliminated, which were characterized by turning angles smaller than 15° and extensions greater than 2500 m or by turning angles smaller than 25° and extensions greater than 5000 m between consecutive data points (Freitas et al., 2008).

In a second step, a joint estimation or hierarchical state-space model (hSSM) was fitted to the pre-filtered Argos satellite telemetry dataset, using the R package *bsam* (Jonsen et al., 2013; Jonsen, 2016). Two Markov chains of 60,000 samples were run, from which the first 40,000 were disregarded as burn-in. From the remaining 20,000 only every 20th sample was retained leading to 1000 samples per chain. These 2000 samples were generated for each seal location and were used to obtain a position estimate as well as the associated uncertainty. A time-step of 6 h was chosen between consecutive locations, which added up to a constant number of four positions per day and animal. The hSSM also allows improved inference about hidden behavioural states along the seal tracks, *i.e.*, if an animal was either in a transient or in a resident state at a given location, and it was specifically designed for Weddell seal movement data (Jonsen, 2016). Filtered seal tracks were then plotted in ArcGIS for Desktop 10.2 (© ESRI, Inc., USA) for visualization.

Dive locations are usually not associated with a 'true' Argos location but are rather based on a simple linear interpolation method along the raw track as provided by the tag manufacturer. As the hSSM takes the spatial errors of each Argos location class into account, it provides improved location estimation compared to 'true' Argos locations (Jonsen et al., 2013; Jonsen, 2016). Therefore, dive locations were linearly interpolated along a seal's hSSM track on the basis of the start time of the dive. All dive analyses are thus based on the hSSM filtered dive locations.

2.4. Behavioural data (response variables)

As a first step, the quality of the dive profiles was examined and incomplete as well as erroneous profiles were removed from the dataset (7%). Then, vertical velocities were calculated for each segment between two time-depth points within a profile. Dive profiles, which exceeded vertical swimming speeds of 5.1 m/s in one or more segments (corresponding to the recorded maximum speed of Weddell seals; Davis et al., 2003), were also omitted. Furthermore, shallow dives (< 25 m) of Weddell seals are usually associated with activities other than

foraging (*e.g.*, social interactions, vocalizations, travel) and were therefore removed for the purpose of this study (*c.f.* Plötz et al., 2001; Davis et al., 2003; Liebsch et al., 2007; Naito et al., 2010). Moreover, only those dives to the continental shelf break (defined as 1000 m isobath) were considered for further analysis, because too few dives were made off the shelf break and mostly by only one seal. From the remaining dive data, the following three foraging metrics were derived.

First, the maximum dive depth of each dive profile was extracted as a common measure of foraging behaviour (Fig. 2b). A histogram of dive depths revealed a bi-modal distribution, indicating pelagic and demersal foraging, which is also exhibited by Weddell seals in other areas (Plötz et al., 2001; McIntyre et al., 2013). To characterize demersal dives we calculated the difference between the maximum dive depth and the sea floor depth at each dive location (Labrousse et al., 2015). A prominent mode occurred at a depth difference between -50 and +50 m, which clearly represents demersal diving (Appendix A, Fig. A.1). Ideally, the difference between bathymetry and maximum dive depth should be 0 for a demersal dive. However, errors in the seal's position and the spatial resolution of the bathymetric grid cause deviations. Thus, all dives with a distance of -50 to +50 m to the sea floor were classified as demersal dives, while all dives with a distance greater than 50 m to the sea floor were defined as pelagic dives. A few dives, which were more than 50 m deeper than the bathymetry, were excluded from further analyses.

As a second foraging proxy, the hunting time of each dive was calculated. Heerah et al. (2014) defined hunting phases using high-resolution dive data of southern elephant and Weddell seals on the basis of high vertical sinuosity ("wiggles") and prey capture attempts. This measure is also adaptable to low-resolution dive profiles, as recorded by CTD-SRDLs. Hunting phases in low-resolution dive data are characterized by reduced vertical velocities (Fig. 2b), an indication of area-restricted search for prey (Heerah et al., 2015). In the present dataset hunting phases were determined based on vertical velocities lower than or equal to 0.4 m/s, following Heerah et al. (2015). Only dives with hunting times > 0 min were selected for subsequent analyses.

The bottom phase of a dive is defined as the time spent at depths deeper than 80% of the maximum dive depth and generally considered to be related to foraging activities (Plötz et al., 2001; Watanabe et al., 2003; Liebsch et al., 2007). Time spent at the bottom phase of a dive was calculated by creating linearly interpolated time-depth points between the six transmitted points (Fig. 2b). By this means the number of time-depth points per dive profile was increased to 21 points leading to a more reasonable estimate of bottom time (McIntyre et al., 2010, 2013). As bottom time was highly correlated to hunting time, another foraging metric - standardized bottom time residuals - was derived from bottom time: Standardized bottom time residuals were obtained from a simple linear regression with bottom time as the response variable and dive duration and maximum dive depth as predictors (all log-transformed; $R^2 = 0.77$) (Bailleul et al., 2008; McIntyre et al., 2013). Bottom time residuals represent the difference between the expected and observed values in the linear regression. Positive residuals imply a longer bottom time as would be expected from the given dive depth and duration, thus indicating higher foraging effort during the bottom phase. The linear regression model was fitted using the basic R function *lm*. All assumptions of a linear regression (normality, independence, homogeneity) were verified.

2.5. Environmental data (explanatory variables)

A set of environmental parameters was matched with the seals' hSSM-corrected dive locations to investigate the influence of physical variables on the foraging behaviour of Weddell seals. These were bathymetry, sea ice concentration, distance to the closest polynya, hydrography (*i.e.*, water masses), solar elevation (*i.e.*, light intensity), season and dive type.

Bathymetric data were available from the International Bathymetric

Chart of the Southern Ocean (IBCSO) with a resolution of 500×500 m (Arndt et al., 2013). Furthermore, high-resolution bathymetric data (100×100 m) of the FOS were acquired based on multibeam echo soundings, which were measured onboard RV *Polarstern* during numerous research expeditions to the Weddell Sea over several decades. Where possible, high-resolution bathymetric data were assigned to the seal dive locations; the IBCSO data were matched with the remaining locations.

Daily satellite images of sea ice concentration recorded by AMSR2 were provided by the University of Bremen (<http://iup.physik.uni-bremen.de:8084/amr2/>) (Appendix B, Fig. B.1). Sea ice concentrations ranged from 0% (open water) to 100% (closed ice cover) with a spatial resolution of 6×4 km (Spren et al., 2008). Each dive location was assigned the closest sea ice concentration value in space and time. To investigate the utilization of persistent winter polynyas in the southern Weddell Sea (Paul et al., 2015), the distance of each dive location to the closest polynya was computed on the basis of AMSR2 sea ice concentration data. A polynya was defined as the nearest pixel with a sea ice concentration of less than 35% (Raymond et al., 2014). Both bathymetry and sea ice data were available as geo-referenced raster layers in Antarctic south polar stereographic projection, and as such imported into the R environment (R Core Team, 2016). The function *over* was used to assign the raster values to the respective seal dive locations (R package *sp*; Pebesma and Bivand, 2005; Bivand et al., 2013).

Based on temperature and salinity recordings of the CTD-SRDLs, the *in situ* hydrographic conditions experienced by the animals could be investigated. Incomplete profiles (i.e., when corresponding salinity values were missing) were omitted, resulting in a total of 1635 CTD profiles collected by the six Weddell seals (Appendix B, Fig. B.2). On the basis of salinity and potential temperature θ (temperature of seawater if raised to surface pressure level; Fofonoff and Millard Jr. 1983), the key water masses of the study area were identified based on Nicholls et al. (2009): Antarctic Surface Water (AASW), Winter Water (WW), Modified Warm Deep Water (MWDW), Eastern Shelf Water (ESW), Ice Shelf Water (ISW), High Salinity Shelf Water (HSSW) and a mix (Mix) resulting from mixing at interfaces of several water masses, such as the ISW/MWDW interface above the eastern flank of the Filchner Trough (Table 1; Fig. 3). Due to these mixing processes it is generally not straightforward to define clear boundaries between water masses. One of the above mentioned water masses was allocated to each sampling depth within the CTD profiles. Ship-borne CTD-profiles obtained by *Polarstern* in the FOS during the same expedition (PS82) were acquired to illustrate the hydrographic background of the study area compared to the CTD-profiles sampled by the Weddell seals (Fig. 3a, b).

Due to the temporal mismatch between the transmission of a CTD profile (~ 4 profiles per day) and the recording of a seal's dive, the closest profile in time was assigned to each dive, separately for each individual. As mean daily travel rates were usually less than 20 km, we deemed this CTD profile and hence the identified water masses

representative for the respective dive (Table 2). For the analysis of maximum dive depths and bottom time residuals, the CTD data of the closest sampling depth to the average depth of the dive bottom phase (i.e., 90% of the maximum dive depth) were selected. For the analysis of hunting time, the CTD data of the closest sampling depth to the mean depth of each hunting phase were chosen. As there could be multiple hunting phases within a dive and possibly different water masses used in different hunting phases, the water mass in which the seal spent most of its hunting time, was selected.

To investigate the effect of variable light availability on the foraging behaviour at a diurnal and seasonal scale, all dive records were first corrected to local time based on a seal's location (Burns et al., 2008; Heerah et al., 2013). Then, the solar elevation at the local time of each dive was calculated using the function *solarpos* (R package *maptools*; Bivand and Lewin-Koh, 2016). By this means, three periods could be classified: day (sun above horizon), twilight (sun between 0° and 12° below horizon, corresponding to nautical twilight) and night (sun lower than 12° below horizon) (Burns et al., 2008; Heerah et al., 2013). Seasons were defined according to established meteorological criteria (G. König-Langlo, pers. comm.): summer (1 December 2013–28 February 2014), autumn (1 March–31 May 2014), winter (1 June–31 August 2014) and spring (1 September–30 November 2014) (Appendix B, Fig. B.3).

Each dive was classified as either being demersal or pelagic (see Section 2.4). Dive type was then chosen as explanatory variable for the analysis of hunting time and bottom time residuals. In the case of maximum dive depths, dive type was used to separate demersal and pelagic dives prior to the statistical analysis.

Collinearity between continuous explanatory variables (bathymetry [m], sea ice concentration [%], distance to polynya [km]) was examined by calculating Pearson's correlation coefficients and subsequently considered negligible (< 0.4). Water masses, light intensity, season and dive type were modelled as categorical variables.

2.6. Statistical analysis

To investigate the effect of environmental variables (bathymetry, sea ice concentration, distance to the closest polynya, water masses, light intensity, season, dive type) on foraging metrics of Weddell seals (pelagic and demersal maximum dive depth, hunting time, bottom time residuals), a series of linear mixed effect models (LMMs) was fitted. Starting models included all explanatory variables (without interactions) as fixed effects. Since the seals were the sampling units, seals' identities were included as random effects to account for individual variability among seals. As bio-telemetry observations (i.e., in this case: foraging metrics) are repeated measures from the same sampling unit (i.e., in this case: animal), there exists considerable serial and temporal autocorrelation within each sampling unit. This violates the independence assumption of LMMs. Therefore, we added an auto-regressive model of the order 1 (AR1) to the LMMs. The AR1 is an autocorrelation structure that models the residual at time s as a function of the residual of time $s-1$ along with noise (Zuur et al., 2009). This assumes that residuals further away in time are less correlated than residuals that are adjacent in time. The AR1 needs the constant model parameter ρ as input, which describes the correlation between residuals and can be approximated from the data (Zuur et al., 2009). By adding the AR1 term to the LMMs, we effectively modelled the inherent correlation, leading to near-zero values for covariance and correlation between the repeated measures (Appendix C, Fig. C.1). Moreover, certain response variables were transformed to ensure normality as required for the LMMs (log-transformation for pelagic maximum dive depth; square-root-transformation for hunting time).

Model selection followed the steps recommended by Zuur et al. (2009). First, each explanatory variable was dropped from the full model and then this reduced model was compared to the full model via likelihood ratio tests (LRTs) using the R function *anova*. By this means

Table 1

Definitions of water masses based on Nicholls et al. (2009). Water masses were discriminated on the basis of potential temperature θ and salinity, derived from *in situ* hydrography as recorded by the six Weddell seals.

Water mass	Potential temperature θ [$^\circ$ C]	Salinity
Eastern Shelf Water (ESW)	$-2 < \theta < -1.3$	< 34.38
Modified Warm Deep Water (MWDW)	$-1.6 < \theta < 1$	$34.42 < S < 34.75$
High Salinity Shelf Water (HSSW)	$-1.95 < \theta < -1.8$	> 34.65
Winter Water (WW)	$-1.9 < \theta < -1.6$	$34.38 < S < 34.45$
Antarctic Surface Water (AASW)	$-1.3 < \theta < 1$	< 34.38
Ice Shelf Water (ISW)	≤ -1.92	> 34.4

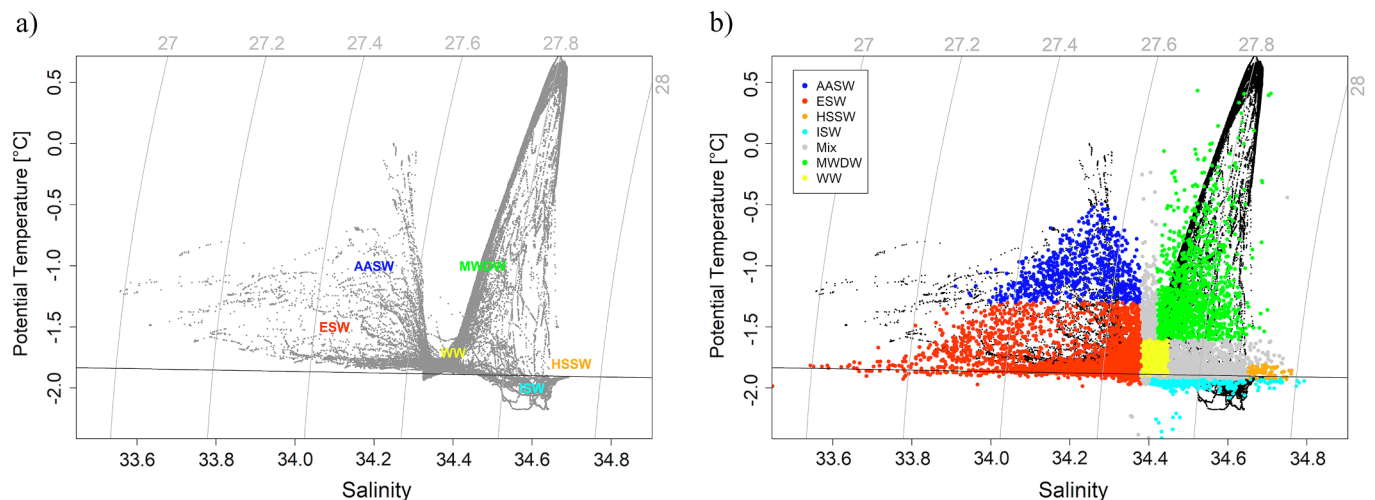


Fig. 3. (a) Diagram of salinity and potential temperature from ship-borne CTD-profiles obtained by *Polarstern* during PS82 (Schröder and Wisotzki, 2014). Isopycnals are given as solid grey lines. The solid black line illustrates the surface freezing point. Labels illustrate the typical temperature-salinity characteristics of the main water masses based on Nicholls et al. (2009). (b) Diagram of salinity and potential temperature from CTD-profiles sampled by six Weddell seals as well as the corresponding water masses in different colours. As a reference, temperature and salinity from the ship-borne CTD-profiles during PS82 are shown as black dots.

Table 2

Summary information and measurements of six Weddell seals (*Leptonychotes weddellii*) instrumented with CTD-SRDLs in the southern Weddell Sea during austral summer 2014. Track length was calculated in ArcGIS based on filtered and hSSM corrected seal locations.

Individual ID	Sex	Body length [cm]	Girth [cm]	Deployment date (dd/mm/yyyy)	Transmission duration [d]	Track length [km]	Distance per day [km]
FIL2014_wed_a_f_01	female	253	204	21/01/2014	186	1736	9.7 ± 9.1
FIL2014_wed_a_m_03	male	231	178	02/02/2014	208	3476	15.7 ± 17.6
FIL2014_wed_a_f_04	female	234	184	02/02/2014	246	4829	20.3 ± 14.3
FIL2014_wed_a_f_05	female	254	203	11/02/2014	49	822	19.0 ± 13.4
FIL2014_wed_a_f_06	female	243	171	11/02/2014	207	3154	15.1 ± 12.8
FIL2014_wed_a_f_07	female	274	197	11/02/2014	151	1997	12.5 ± 9.7

the most parsimonious model was selected, in which only significant terms were retained. Results of the LRTs (deviance, degrees of freedoms and *p*-values) of the significant model terms are reported below. In the selection process both the full and the reduced models were fitted with maximum likelihood approximation to assess the optimal fixed effect structure, while the most parsimonious model was re-fitted in the end using restricted maximum likelihood (Bolker et al., 2009; Zuur et al., 2009). We checked the assumptions of LMMs that residuals were normally distributed and homoscedastic using Q-Q plots as well as plots of fitted values vs. residuals. Independence was validated by plotting the residuals vs. the explanatory variables as well as by checking for temporal autocorrelation using the *acf* function in R. Furthermore, conditional *R*² values were calculated for all final models (package *piecewiseSEM*; Lefcheck, 2016), which give an estimate of the variance explained by both the fixed and random effects (Nakagawa and Schielzeth, 2013; Lefcheck, 2016).

All data analyses were conducted in the R statistical software package, version 3.2.5 (R Core Team, 2016). All LMMs were fitted using the function *lme* (R package *nlme*; Pinheiro et al., 2016). Statistical significance was set at *p* ≤ 0.05. All values are reported as mean ± standard deviation (SD).

3. Results

3.1. Tag performance and horizontal movements

The six CTD-SRDLs provided data for an average duration of 174.5 ± 68.9 d (range: 49–246 d), between January and October 2014 (Table 2). A total of 10,343 locations were transmitted and 4170 retained after the track filtering process. While the two Weddell seals tagged on ice floes in the western part of the FOS travelled extensively

through the pack ice, seals instrumented in a fast-ice covered inlet at the coast were more restricted to the coastline (Fig. 4). The two ‘ice floe seals’ utilized the shelf area west of the sill of the Filchner Trough intensely – they even returned to the area after longer excursions (Fig. 5a, b). In contrast, the four ‘inlet seals’ performed only short foraging trips in the vicinity of their colony on the continental shelf in the eastern FOS (Fig. 5c, d). At 88% of all locations Weddell seals were in a resident state indicating area-restricted search, while at 12% of the locations they were in transient state.

3.2. Habitat use

The Weddell seals mainly inhabited areas with high sea ice concentration (sea ice concentration greater than 80% for 82.1% of all foraging dive locations). Nevertheless, they were often found within 200 km of the closest polynya (67.7%). Furthermore, the seals were strongly confined to areas with water depths of less than 700 m (94.1%). In terms of hydrography, the Weddell seals encountered six different water masses as well as a mixture between water masses, particularly between ISW and MWDW due to mixing at the strong interfaces (Table 1, Figs. 3 and 6). The utilization of different water masses showed seasonal variations. For instance, MWDW and AASW were mainly encountered in spring and summer (Figs. 5 and 6). HSSW was only utilized in autumn and winter by seal FIL2014_wed_a_f_04 during its excursion to the south of the Filchner Trough. Apparently, seals specifically targeted MWDW when it was available, especially in spring and summer. Weddell seals utilized MWDW proportionally more during the bottom phases of their dives compared to the other water masses available (Fig. 6a vs. b).

The differences in movements between ‘ice floe seals’ and ‘inlet seals’ are also reflected in their utilization of the oceanographic

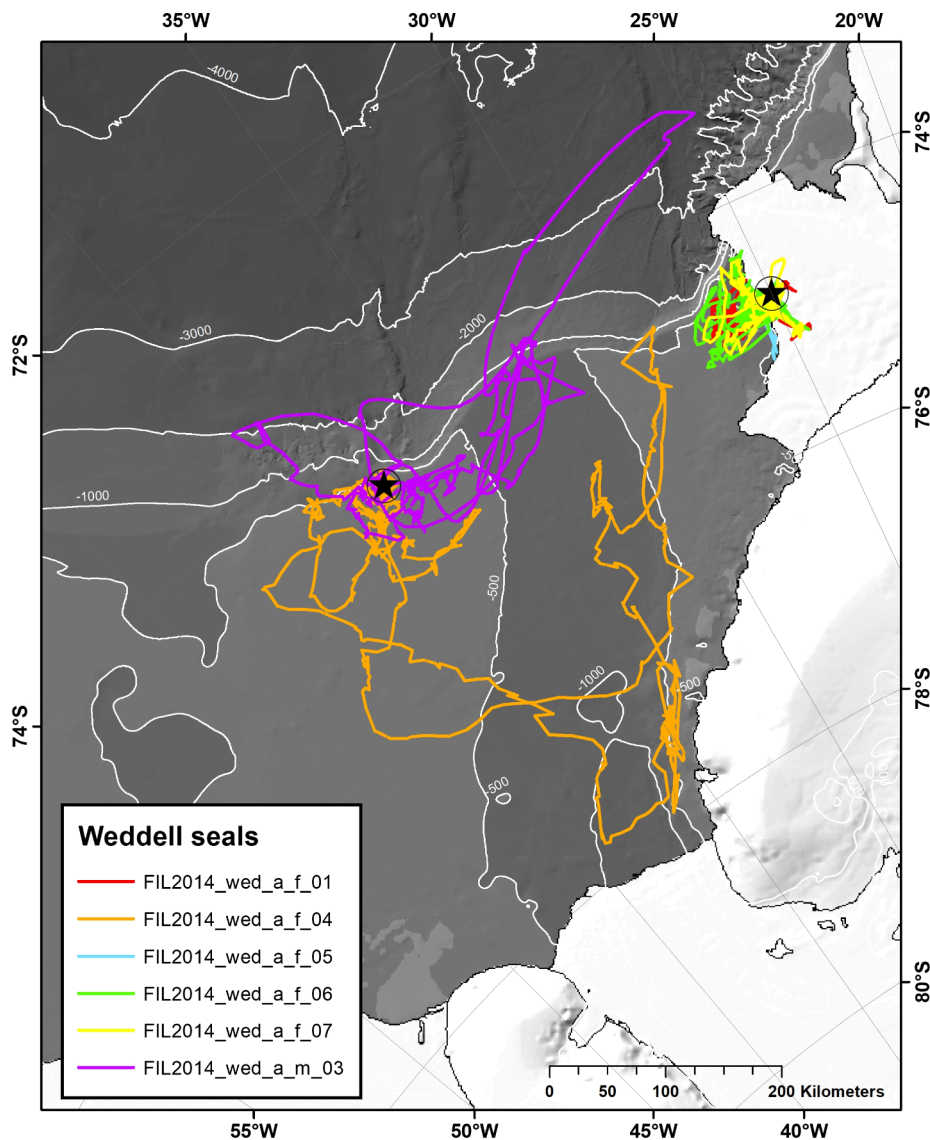


Fig. 4. Tracks of six Weddell seals (*Leptonychotes weddellii*) in the Filchner Outflow System (FOS), instrumented with CTD-SRDs in 2014. Each coloured line illustrates an individual track. Black stars show the tagging locations east and west of the FOS. Bathymetry is indicated by white contour lines.

environment (Fig. 5). While the ‘inlet seals’ hardly encountered the relatively warm and salty MWDW, ‘ice floe seals’ utilized it heavily. They mainly encountered it to the west of the Filchner Trough sill, and also partly on the eastern side (Fig. 5a, b). Interestingly, seal FIL2014_wed_a_f_04 followed the 500 m isobath of the eastern Filchner Trough quite strictly, which coincides with the interface between MWDW and ISW (Fig. 5a, b). In winter they also regularly encountered WW. ESW was encountered on the eastern flank of the trough. The ‘inlet seals’ were mainly utilizing the less saline ESW and AASW along the coast in summer and autumn. During the winter months, they mostly encountered WW, ISW, ESW and ultimately mixtures between these (Fig. 5c, d). It should be mentioned here that the ISW encountered by the ‘inlet seals’ does not originate from the Filchner Ronne Ice Shelf, but from the Brunt Ice Shelf, which is characterized by lower salinities (see Fig. 5d).

3.3. Diving behaviour

In total, 24,067 dives were transmitted, with an average of 28.8 ± 21.5 dives per day and individual (range: 1–106) (Table 3). As a result of the selection process, 12,096 dive profiles were used for

further statistical analyses. All Weddell seals exhibited both pelagic (8718 dives; 72.1%) and demersal foraging (3378 dives; 27.9%) (Fig. 7). Demersal foraging dives mainly occurred during daytime (62%) and to a lesser extent at twilight (29%). Few demersal foraging dives were made at night (9% of all demersal dives). In contrast, most pelagic foraging dives (38%) were performed at night, although pelagic foraging dives also occurred during the day (30%) and twilight (32%).

The overall mean pelagic maximum dive depth was 149.4 ± 124.5 m (range: 27.5–650 m) and the mean demersal maximum dive depth was 458.2 ± 113.4 m (range: 230–700 m). Mean hunting time of each dive was 7.6 ± 5.6 min (range: 0.1–41.7 min) and mean bottom time was 4.8 ± 4.4 min (range: 0.1–31.0 min). This illustrates that hunting activities also occurred outside the bottom phase.

3.4. Pelagic and demersal maximum dive depth

The optimal model explaining maximum dive depth for pelagic dives included the explanatory variables light intensity, water masses, sea ice concentration and distance to polynya, whereas the most parsimonious model for demersal dives included those for water masses and sea ice concentration (Table 4).

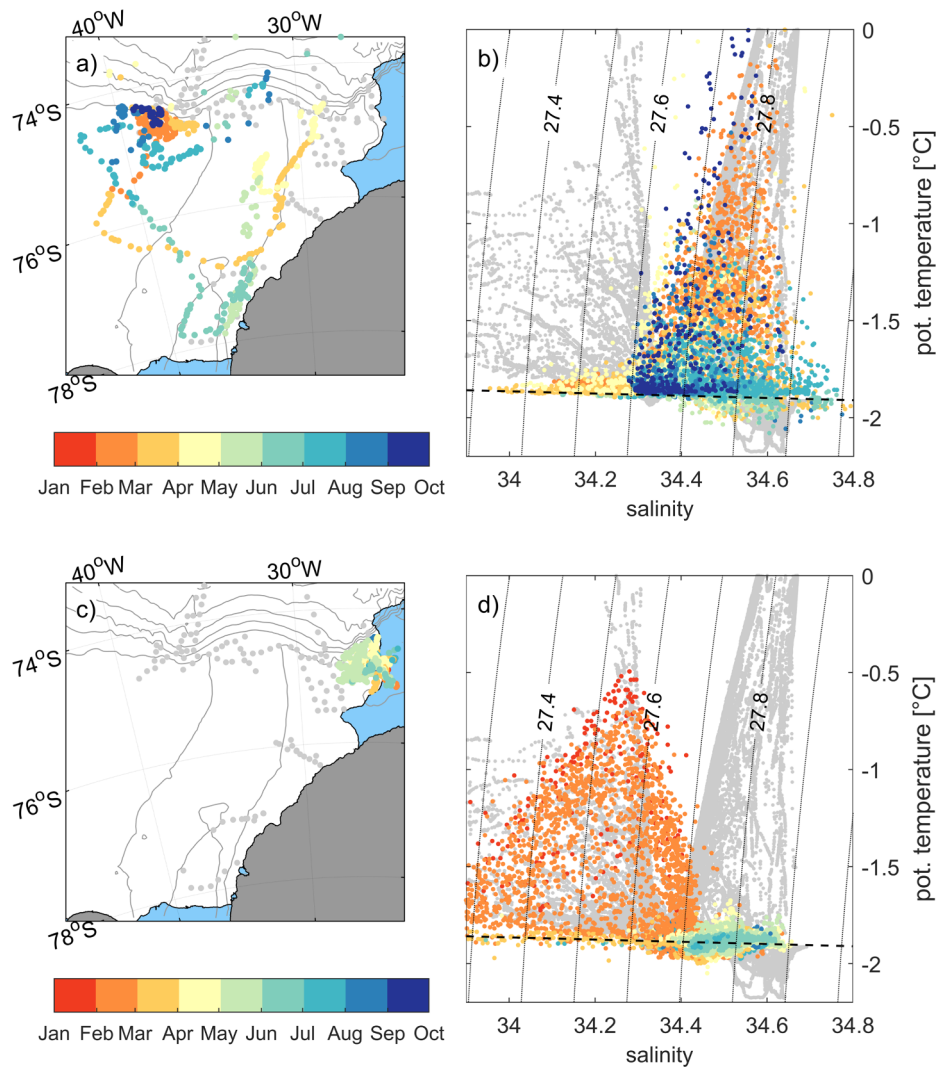


Fig. 5. Tracks and temperature-salinity diagram of (a, b) seals tagged on ice floes in the western part of the FOS and (c, d) seals tagged in an inlet in the eastern part of the FOS. The color code illustrates the progression of time, indicating the month specific areas were visited and which oceanographic conditions were encountered. Grey dots in (a, c) illustrate the locations of ship-borne CTD-stations by *Polarstern* during PS82, while grey dots in (b, d) indicate temperature and salinity measurements from the respective ship-borne CTD profiles.

Pelagic dive depths were influenced by variations in light intensity ($LRT_{\text{light intensity}}$: deviance = 141.09, $df = 2$, $p < 0.0001$). Weddell seals dived significantly deeper in the water column during day (171.2 ± 152.5 m) compared to twilight (154.9 ± 120.7 m) and nighttime (127.1 ± 97.1 m) (Table 5). However, no effect of season was observed on pelagic and demersal maximum dive depths (Table 5). Both pelagic and demersal dive depths also differed between water masses (pelagic: $LRT_{\text{water mass}}$: deviance = 1463.48, $df = 6$, $p < 0.0001$; demersal: $LRT_{\text{water mass}}$: deviance = 61.27, $df = 6$, $p < 0.0001$). Pelagic maximum dive depths increased with decreasing sea ice concentration, while demersal maximum dive depths became shallower with decreasing sea ice concentration (Table 5). Pelagic dive depths marginally increased with increasing distance to the closest polynya.

3.5. Hunting time

The most parsimonious model of hunting time included light intensity, season, and dive type. The amount of variance explained was low, however, as indicated by the conditional R^2 values of the final model (Table 4).

Hunting time showed clear differences between different light

intensity levels ($LRT_{\text{light intensity}}$: deviance = 33.67, $df = 2$, $p < 0.0001$). Hunting was longest during twilight hours (8.43 ± 5.53 min), followed by night (8.10 ± 6.21 min) and day (7.14 ± 4.93 min) (Table 5). Seasonal variations in hunting time were found as well (LRT_{season} : deviance = 52.58, $df = 3$, $p < 0.0001$). Weddell seals significantly increased their hunting time within a dive during austral winter (8.75 ± 6.51 min) compared to summer (6.95 ± 5.19 min). Hunting time was also significantly longer in demersal dives than in pelagic dives (Table 5).

3.6. Bottom time residuals

The optimal model for bottom time residuals comprised the variables water mass, sea ice concentration, season and dive type. Again, conditional R^2 values of the final model for bottom time residuals indicated that the amount of variance explained was considerably low (Table 4).

Bottom time residuals were different between seasons (LRT_{season} : deviance = 43.08, $df = 3$, $p < 0.0001$). They were higher (i.e., bottom times were longer than expected) in summer than in winter (Table 5), which contrasts with the results of hunting time (i.e., hunting time were longer in winter than in summer). Bottom time residuals differed

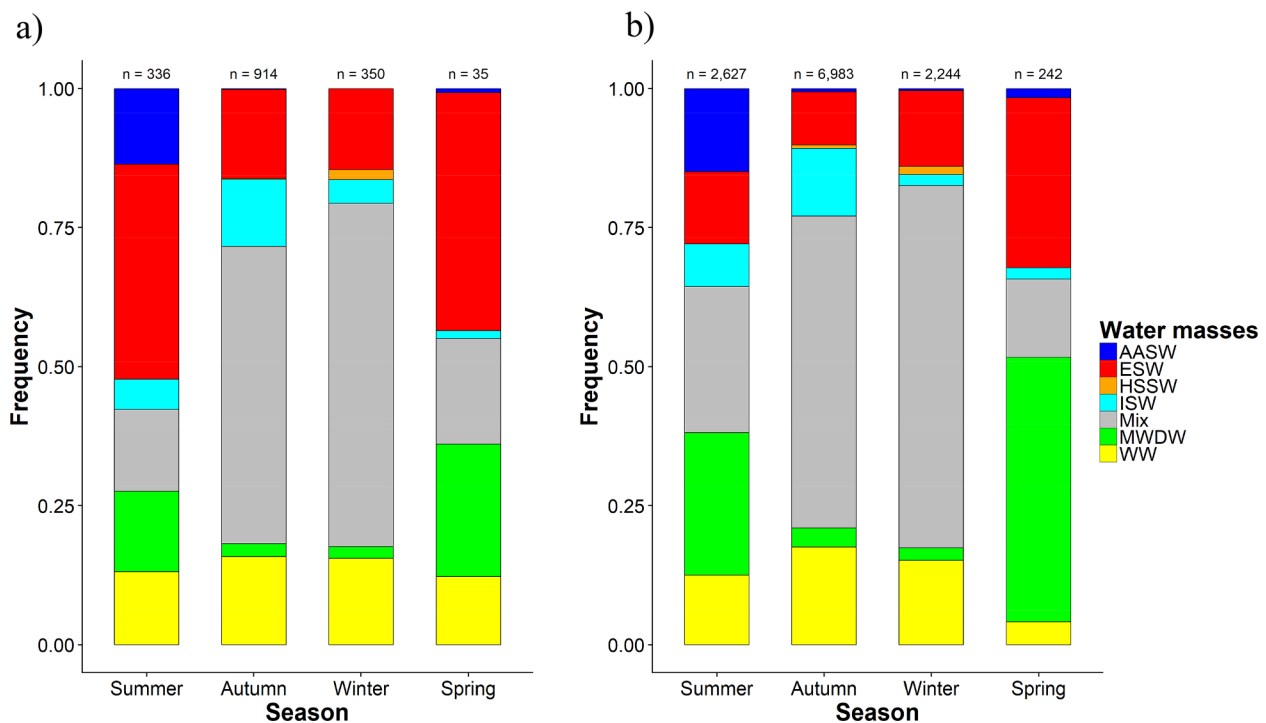


Fig. 6. Frequency of different water masses sampled by the six Weddell seals over the course of all seasons. (a) Frequency of water masses as determined from the CTD-profiles collected by the seals. n denotes the number of CTD-profiles for the specific season (b) Frequency of water masses targeted by the seals in the bottom phase of their dives. n represents the number of dives performed in the season.

between the water masses ($LRT_{\text{water mass}}$: deviance = 18.15, $df = 6$, $p = 0.0059$). Foraging effort in the bottom phase of a dive was highest in MWDW and HSSW compared to other water masses (Table 5). Bottom time residuals were also influenced by dive type ($LRT_{\text{dive type}}$: deviance = 4.93, $df = 1$, $p = 0.0264$) and higher in demersal dives than in pelagic dives (Table 5). The expected time spent in the bottom phase decreased marginally with increasing sea ice concentrations (Table 5).

4. Discussion

This study aimed at describing and quantifying the foraging behaviour of Weddell seals in the Filchner Outflow System (FOS) by combining behavioural data derived from animal-borne instruments, with both *in situ* and *ex situ* environmental data. The chosen approach allows to adequately reconcile the foraging behaviour of Weddell seals in response to their environment, which represents an improvement to earlier studies relying merely on spatially and temporally low-resolution remote-sensing data.

4.1. Horizontal movements

By tracking the movements of six Weddell seals in the FOS, distinct

differences in horizontal movements were found. The two Weddell seals tagged in the pack ice areas dispersed extensively over the course of several months, while the four seals instrumented in the coastal fast ice habitats in Halley Bay were restricted close to the tagging site. The two ‘ice floe seals’ utilized the shelf areas west and east of the sill of the Filchner Trough – however, they mostly avoided the area above the sill. Hydrographic differences between the sill itself and its eastern and western flanks are that the bottom layer at the sill is governed by outflowing ISW, whereas at the flanks MWDW intrusions occur along the bottom. In contrast, the four ‘inlet seals’ performed only short foraging trips in the vicinity of their colony on the continental shelf in the eastern FOS. This obvious behavioural difference between the two groups may be explained by the life history of this seal species. Weddell seals give birth to their young on the fast ice close to the Antarctic coastline during austral spring (Stirling, 1969; Siniff, 1991). Pups generally leave the breeding colonies shortly after being weaned and move into the pack ice zone, where they are assumed to remain for several years until reaching sexual maturity (Burns et al., 1999; Stewart et al., 2003). In contrast, the dominant adult males and females usually stay close to the fast ice (< 50 km) over winter to assert their territories (Smith, 1965; Testa, 1994; Heerah et al., 2016), and site fidelity is known to increase with age in both sexes (Cameron et al., 2007). Although all seals in this study were physically mature, it is possible that

Table 3

Hydrographic and behavioural data of six Weddell seals instrumented with CTD-SRDs in the southern Weddell Sea during austral summer 2014. The number of CTD profiles corresponds to the quality-controlled CTD data. The number of dives and foraging parameter statistics are based on the quality-controlled foraging dives (≥ 25 m) as used in the linear mixed effect modelling.

Individual ID	CTD profiles (n)	Dive (n)	Max. dive depth _{PELAGIC} [m]	Max. dive depth _{DEMERSAL} [m]	Hunting time [min]	Bottom time [min]
FIL2014_wed_a_f_01	215	1557	144.8 \pm 125.6	564.0 \pm 119.3	8.6 \pm 6.0	4.0 \pm 3.3
FIL2014_wed_a_m_03	144	968	177.0 \pm 123.8	373.1 \pm 21.6	5.7 \pm 3.7	5.7 \pm 2.9
FIL2014_wed_a_f_04	529	3582	160.0 \pm 111.1	417.0 \pm 57.3	7.7 \pm 5.6	4.8 \pm 4.2
FIL2014_wed_a_f_05	105	695	119.9 \pm 109.9	593.1 \pm 64.6	9.4 \pm 5.2	5.4 \pm 4.5
FIL2014_wed_a_f_06	389	2854	147.0 \pm 121.5	481.6 \pm 107.8	8.4 \pm 6.3	5.0 \pm 4.9
FIL2014_wed_a_f_07	330	2440	117.6 \pm 118.4	526.1 \pm 139.4	7.2 \pm 4.6	5.3 \pm 4.8

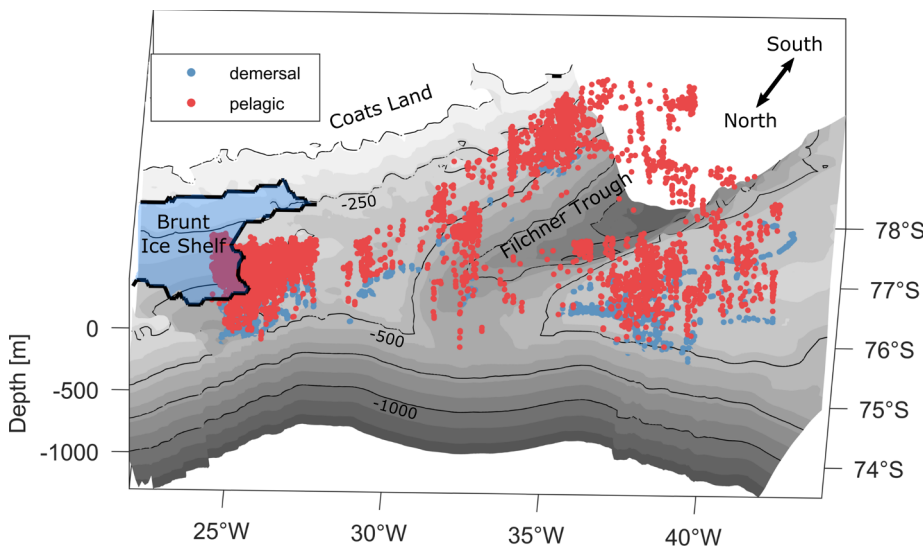


Fig. 7. Spatial distribution of demersal (blue dots) and pelagic (red dots) foraging dives ($n = 12,096$) in the FOS. The bathymetry (RTopo2, Schaffer et al., 2016) is illustrated three-dimensionally in grey shading and thin black lines illustrate isobaths in 250 m intervals. Please note the map orientation towards the South to enable a better view onto the outflow of the Filchner Trough. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4

Most parsimonious linear mixed effect model structures and corresponding summary statistics to investigate the influence of different environmental parameters on foraging metrics of six Weddell seals.

Model (fixed effects only)	n	$R^2_{\text{conditional}}$
Max.Depth _{PELAGIC} ~ Light + Hydro + Ice + Dist.Polynya	8718	0.274
Max.Depth _{DEMERSAL} ~ Hydro + Ice	3378	0.377
Hunt.Time ~ Light + Season + Dive	12,096	0.082
Bott.Time.Resid ~ Hydro + Ice + Season + Dive	12,096	0.030

Max.Depth_{DEMERSAL} = Demersal maximum dive depth; Hunt.Time = Hunting time; Max.Depth_{PELAGIC} = Pelagic maximum dive depth; Light = Light intensity; Bott.Time.Resid = Bottom time residuals; Light = Light intensity; Hydro = Water masses; Ice = Sea ice concentration; Dist.Polynya = Distance to closest polynya; Bathy = Bathymetry; Season = Season; Dive = Dive type; n = number of observations; $R^2_{\text{conditional}}$ = Conditional R^2 as described by Nakagawa and Schielzeth (2013).

seals tagged in the pack ice were younger, non-reproductive adults, whereas seals encountered on fast ice were older, territorial individuals. Our results are not conclusive given the sample sizes we compare, but this notion is supported by previous studies in the FOS, where adult

Weddell seals tagged on the pack ice also dispersed extensively throughout the study area over winter and hardly ever occupied coastal fast ice (Boehme et al., 2016; Langley et al., 2018). Similarly, Weddell seals tagged on coastal fast ice in the Drescher Inlet in the eastern Weddell Sea (~400 km northeast of the FOS) remained close to their colony over winter, supporting the idea of spatial segregation by age and/or breeding status (H. Bornemann, unpublished data). The utilized area close to the coast of Halley Bay may therefore represent the range of central-place-foraging Weddell seals from their breeding colony, even through winter. In this concept, the colony represents the central location, which they are bound to by various constraints, e.g. maintaining their territories (Orlans and Pearson, 1979). Further evidence comes from acoustic studies conducted near Antarctic research stations, which recorded year-round vocal presence of Weddell seals close to their colonies. (Rouget et al., 2007; Van Opzeeland et al., 2010) Considering the available tracking data and known locations of Weddell seal colonies in the eastern and southern Weddell Sea (Hempel and Stonehouse, 1987), we argue that Weddell seals will very likely act as central-place foragers from their colonies along the whole coastline. In general, the coastal ecosystem in the eastern and southeastern Weddell Sea is particularly productive, as indicated by a relatively high

Table 5

Results of the most parsimonious linear mixed effect models. For categorical variables (Light, Season, Hydro and Dive), coefficients are given in reference to day, summer, AASW and demersal, respectively. Significant terms are indicated in bold. For explanation of the abbreviations, see Table 4.

Environmental variables	Max.Depth _{PELAGIC}		Max.Depth _{DEMERSAL}		Hunt.Time		Bott.Time.Resid	
	Coefficient \pm SE	p -value	Coefficient \pm SE	p -value	Coefficient \pm SE	p -value	Coefficient \pm SE	p -value
Intercept	4.0914 \pm 0.1239	< 0.0001	462.730 \pm 34.527	< 0.0001	2.5697 \pm 0.1056	< 0.0001	0.1769 \pm 0.0821	0.0314
Ice	-0.0036 \pm 0.0007	< 0.0001	0.2017 \pm 0.055	0.0003	–	–	-0.0017 \pm 0.0006	0.0047
Dist.Polynya	0.00014 \pm 0.00005	0.0076	–	–	–	–	–	–
Bathy	–	–	–	–	–	–	–	–
Light (twilight)	-0.1819 \pm 0.0274	< 0.0001	–	–	0.1559 \pm 0.0295	< 0.0001	–	–
Light (night)	-0.4508 \pm 0.0316	< 0.0001	–	–	0.0412 \pm 0.0359	0.2511	–	–
Season (autumn)	–	–	–	–	0.1807 \pm 0.0373	< 0.0001	0.0100 \pm 0.0326	0.7593
Season (winter)	–	–	–	–	0.3453 \pm 0.0515	< 0.0001	-0.2007 \pm 0.0420	< 0.0001
Season (spring)	–	–	–	–	0.0117 \pm 0.1013	0.9085	0.2703 \pm 0.0830	0.0011
Hydro (ESW)	0.4899 \pm 0.0507	< 0.0001	-9.370 \pm 6.234	0.1329	–	–	0.0657 \pm 0.0629	0.2961
Hydro (HSSW)	1.5364 \pm 0.1612	< 0.0001	12.253 \pm 8.898	0.1686	–	–	-0.0005 \pm 0.1413	0.9969
Hydro (ISW)	0.9616 \pm 0.0537	< 0.0001	11.093 \pm 8.077	0.1697	–	–	0.0700 \pm 0.0660	0.2897
Hydro (Mix)	1.3975 \pm 0.0477	< 0.0001	7.307 \pm 6.812	0.2835	–	–	0.0500 \pm 0.0586	0.3929
Hydro (MWDW)	1.5867 \pm 0.0916	< 0.0001	6.049 \pm 6.973	0.3858	–	–	0.2408 \pm 0.0713	0.0007
Hydro (WW)	1.0925 \pm 0.0496	< 0.0001	-14.059 \pm 7.247	0.0525	–	–	0.0491 \pm 0.0613	0.4225
Dive (pelagic)	–	–	–	–	-0.2142 \pm 0.0247	< 0.0001	-0.0716 \pm 0.0261	0.0062

* Bathy was not considered a useful variable for the Max.Depth_{DEMERSAL} model, since demersal dive depths were initially defined over bathymetry and a strong relationship is inherent.

abundance of zooplankton (Boysen-Ennen and Piatkowski, 1988; Boysen-Ennen et al., 1991) and benthic-pelagic fishes (Schwarzbach, 1988; Gutt et al., 1994). This ecosystem does not only sustain large numbers of Weddell seals but also numerous breeding colonies of emperor penguins (*Aptenodytes forsteri*) (Hempel and Stonehouse, 1987; Fretwell et al., 2012) emphasizing the high productivity of this coastal Antarctic ecosystem.

4.2. Influence of seasonal and diurnal variations in light availability

The foraging behaviour of Weddell seals was influenced by variations in light availability on both diurnal and seasonal scales. The seals in this study dived deeper during the day compared to twilight and night, but only with regard to pelagic dives. This diurnal pattern in pelagic dives is consistent with earlier findings on Weddell seals, but also on other pinnipeds such as crabeater seals (*Lobodon carcinophaga*) (Plötz et al., 2001; Burns et al., 2008; Heerah et al., 2013). The diurnal variation in seal dive depths is typically related to the vertical migrations of their principal prey, mainly benthic-pelagic fish species such as *Pleuragramma antarctica* in case of the Weddell seal (Plötz, 1986; Burns et al., 1998). At night-time *P. antarctica* migrates into upper water layers, where it can be exploited by Weddell seals during relatively shallow dives (Plötz et al., 2001; Fuiman et al., 2002). This is also reflected by mostly pelagic dives at night and predominantly demersal dives during daytime, when *P. antarctica* occurs close to the sea floor (Plötz et al., 2001; Heerah et al., 2016; this study). The synchronization of a predator's diving pattern with the vertical migration of its prey results in an energetically efficient foraging strategy. Furthermore, Weddell seals are visual predators and often silhouette their prey against the under-ice surface while foraging (Davis et al., 1999). Therefore, they would adapt their diving behaviour to the available light intensity at depth, which also agrees with the observed diurnal differences in dive depths.

The hunting time within a dive was longest during twilight hours, followed by night. This may be the most efficient foraging strategy representing a compromise between diving deep and hunting during daytime, which is energetically costly, and searching in the dark at night, which may be inefficient due to higher effort in prey search. Since Weddell seal eyes are characterized by an extreme light sensitivity (Welsch et al., 2001), they could utilize the available light during twilight hours for the majority of foraging activities, when their primary prey ascends towards the surface (Plötz et al., 2001; Fuiman et al., 2002). Crepuscular foraging has also been emphasized in other Antarctic predators, such as crabeater seals (Bengtson and Stewart, 1992).

Hunting time also varied seasonally and was longer during dives in winter compared to those performed in summer. Adult Weddell seals, especially reproductive females and males, invest a high amount of energy into breeding and mating activities during spring, leading to a substantial weight loss (Reijnders et al., 1990; Wheatley et al., 2008a, 2008b). Thus, they need to optimize food acquisition during wintertime to build up their fat reserves, which is indicated by increased hunting activities in this time period (Boehme et al., 2016; Heerah et al., 2016; this study).

The time spent in the bottom phase of a dive is usually devoted to hunting and prey capture, which suggests that bottom time is a good indicator for foraging effort and success (Watanabe et al., 2003; Liebsch et al., 2007; Bailleul et al., 2008). Surprisingly, average foraging effort in the bottom phase (represented by the bottom time residuals) was negative during winter, which is in apparent contrast with the other results in this study. However, similar results were obtained in a comparable study on Weddell seal foraging behaviour close to Dumont D'Urville (Heerah et al., 2013). This indicates that Weddell seals probably shift their foraging strategy over winter and do not exclusively feed during the bottom phase of a dive but rather at other depth strata within a dive profile. This may reflect changes in the distribution of *P. antarctica* during winter. Daylight is limited during winter and in the

absence of light as a trigger *P. antarctica* may occur more dispersed throughout the water column, instead of performing diurnal vertical migrations. Alternatively, parts of the *P. antarctica* population may migrate to their spawning areas over winter, which makes *P. antarctica* a less predictable food source for Weddell seals (Hubold, 1992). Hence, the theoretical and simplistic metric 'bottom time residuals' may not be a useful index to describe and quantify foraging behaviour in low-resolution dive profiles (Heerah et al., 2015).

4.3. Influence of bathymetry and dive type

Hunting times were longer in demersal dives than in pelagic dives. This can partly be related to the fact that demersal dives were generally deeper and also longer than pelagic dives. However, demersal dives are presumably very important and efficient in terms of foraging, although they only comprised ~30% of all dives. Optimal foraging theory predicts that if a seal increases its dive duration and dive depth, the benefit of giving up and cancelling a dive decreases (Thompson and Fedak, 2001). For deep-diving seals it appears favourable to stay at depth as long as possible, particularly in areas with high prey density. The demersal fish fauna in the southeastern Weddell Sea is indeed rich in biomass and abundance, especially in the shelf areas east and west of the sill of the Filchner Trough (Schwarzbach, 1988; Gutt et al., 1994; Wetjen et al., 2014). Furthermore, *P. antarctica* is particularly abundant in shallow shelf areas, where it inhabits water layers below 200 m and concentrates at the sea floor during parts of its diurnal vertical migrations (Hubold, 1984; Plötz et al., 2001; O'Driscoll et al., 2011; Wetjen et al., 2014). These were the locations, where Weddell seals performed most demersal dives in this study, and they represent an attractive foraging ground since prey detection and encounter rates are likely to be high in the essentially two-dimensional benthic environment.

4.4. Influence of sea ice conditions

Both sea ice concentration and distance to polynya showed only marginal trends in relation to the foraging metrics and hence did not strongly influence foraging activities. The habitat that the Weddell seals utilized over winter showed only little variation in sea ice conditions. Usually, the seals inhabited areas with high sea ice concentrations (> 80%). Seals were often located relatively close (< 200 km) to winter polynyas, which are usually in the vicinity of the fast ice, the preferred haul-out substrate of Weddell seals. Coastal polynyas are typically characterized by enhanced productivity compared to surrounding ice-covered waters, and often support a greater abundance of marine predators (Stirling, 1997; Arrigo and van Dijken, 2003; Labrousse et al., 2018). The existence of relatively persistent, coastal polynyas in the eastern and southern Weddell Sea during winter is well known (Paul et al., 2015), and may provide important marine predator habitat. For example, a Weddell seal satellite-tracked during an earlier study (Árthun et al., 2013) stayed in close proximity to a polynya in the vicinity of the Filchner Ice Shelf front during the whole winter. Our results, however, do not suggest that seals were reliant on polynyas for foraging activities, as they often foraged in areas of high sea ice concentrations (> 80%).

4.5. Influence of in situ hydrographic conditions

The CTD-SRDL data enabled an insight into the oceanographic conditions the six Weddell seals encountered during the study period. A seasonal variability in the utilization of different water masses was observed, which agrees with the observed seasonal hydrography on the continental shelf. For instance, MWDW was mainly encountered between February and April, which is consistent with the known seasonality of the MWDW inflow onto the continental shelf (Árthun et al., 2012; Ryan et al., 2017). During wintertime the inflow usually weakens or ceases and does not penetrate far onto the shelf. This is suggested to

be controlled by a seasonal suppression of the thermocline below the shelf break depth, driven by an increase of the along-coast wind component during winter (Årthun et al., 2012; Darelius et al., 2016; Ryan et al., 2017). The shallow banks west and east of the sill of the Filchner Trough are associated with the inflow of MWDW along the sea bottom (Fig. 1b) and were used extensively by the ‘ice floe’ seals (Foster and Carmack, 1976; Årthun et al., 2012). This area is almost congruent with the region utilized by adult male southern elephant seals in winter (Fig. 1; Tosh et al., 2009; Bornemann et al., 2010) and was furthermore frequented by Weddell seals during another tracking study (Årthun et al., 2012; Langley et al., 2018). Generally, the shelf break region is subject to high turbulence due to e.g. tidal interaction with topography (Fer et al., 2016). In the present study, foraging effort in the dive bottom phase was high in MWDW. It seemed that seals focussed their foraging activities on the relatively warm and nutrient-rich MWDW. Modified Circumpolar Deep Water (MCDW), similar to MWDW, flows onto the continental shelf in other parts of Antarctica and is known to be frequently targeted by marine top predators (Costa et al., 2008; Heerah et al., 2013; Labrousse et al., 2015; Hindell et al., 2016; Zhang et al., 2016). The intense utilization of MWDW may indicate high biological productivity and enhanced prey availability. In fact, the Antarctic Slope Front/Coastal current transports juvenile stages and post-larvae of *P. antarctica* into the FOS and the inflows of MWDW may transport them further onto the continental shelf, where they settle and can be exploited by Weddell seals (Hubold, 1992; Caccavo et al., 2018). In contrast, the sill of the Filchner Trough itself, which is not characterized by an inflow of MWDW, was rarely visited by the tagged Weddell seals suggesting low prey availability or attractivity.

The ISW observed in the FOS is formed underneath the Filchner Ronne Ice Shelf and is characterized by potential temperatures below the surface freezing point (-1.9°C). It fills the Filchner Trough up to 200–300 m water depth (Nicholls et al., 2009; Darelius et al., 2014; see Fig. 1b). Ryan et al. (2017) suggest a seasonal lateral movement of the ISW layer, which extends onto the shallower eastern shelf during spring/summer and retreats or erodes in later summer/autumn, where it is replaced by the MWDW along the bottom over the eastern shelf. The ISW encountered by the ‘inlet seals’ may not originate from the Filchner Ronne Ice Shelf but from the nearby Brunt Ice Shelf. However, formation of Brunt Ice Shelf Water and possible outflow pathways are not well understood. Although ISW was not associated with enhanced foraging activities as shown by the statistical analysis, it is noteworthy that the occurrence of adult *P. antarctica* has been repeatedly linked with ISW (DeWitt, 1970; Hubold, 1984). The length frequency distribution of fish caught in ISW also matches the preferred prey size spectrum of Weddell seals (Hubold, 1984, 1985; Plötz, 1986). In fact, the interface between ISW and MWDW may be particularly important for *P. antarctica* and consequently for Weddell seals. This may explain the high amount of mixed water masses encountered by the seals and is illustrated by seal FIL2014_wed_a_f_04, which closely followed the interface between ISW and MWDW.

4.6. Limitations and perspectives

Inference on foraging behaviour from dive data is inevitably based on specific assumptions and simplifications (Carter et al., 2016). In this study, foraging behaviour could only be characterized by metrics derived from low-resolution dive profiles, and direct observations of foraging and prey capture attempts were not possible. Further technological advances are required to relate the movement behaviour of marine top predators to the distribution of their prey on a more adequate temporal and spatial scale, as addressed by Hays et al. (2016). This starts with the further development of bio-telemetry devices that can record even more data in greater detail. For instance, accelerometers and magnetometers coupled with satellite tags are extremely powerful tools to provide concurrent measurements on predators’ distribution and foraging behaviour (Heylen and Nachtsheim, 2018).

Our LMMs explained $\sim 3\text{--}38\%$ of the variance in the data. Such low to moderate R^2 values are comparable to other ecological and behavioural studies on marine top predators, including Weddell seals (e.g. McIntyre et al., 2013; Meade et al., 2015; McMahon et al., 2017). With the available data, we are not yet able to fully grasp all underlying factors that drive their behaviour. Hence, we need more comprehensive datasets with the regard to quality and quantity of the physical environment as well as the biomass and distribution of lower and intermediate trophic level components. The integration of such physical and biological data will lead to a better understanding of top predators’ foraging behaviour, movement ecology and, ultimately, the functioning of the Antarctic ecosystem.

5. Conclusions

This study emphasizes the benefits of concurrent measurements of hydrographic data and the behaviour of a marine top predator, the Weddell seal. Despite the limited sample size in our study, it became evident that Weddell seals specifically focussed on MWDW for foraging and highest foraging effort in the bottom phase was detected in this water mass. However, it remains unclear, which biological features lead to the intense utilization of MWDW. Interestingly, MWDW was mostly utilized by ‘ice floe seals’ during their extensive movements through the FOS, whereas ‘inlet seals’ remained in the vicinity of their colony. This habitat-dependent intraspecific segregation is notable and should be considered in future studies. Generally, a better understanding of the structure and trophic interactions of the FOS food web is essential, particularly in view of a proposed Marine Protected Area in the Weddell Sea (see Teschke et al., 2016). Moreover, the FOS may soon undergo rapid environmental transformations. Climate models predict an increased melting rate of the Filchner Ronne Ice Shelf during the 21st century, induced by a redirection of the coastal current and an intensified inflow of relatively warm MWDW reaching the ice shelf cavity (Hellmer et al., 2012, 2017; Darelius et al., 2016). This study demonstrates that distribution of MWDW inflows over the shelf may strongly influence Weddell seal foraging. However, the implications of changing oceanographic conditions and increases in shelf bottom temperatures are not well understood. Both the lack of comprehensive investigations and the predicted dramatic climatic changes emphasize the importance of further studies in the rarely studied FOS.

6. Declarations of interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2019.02.013>.

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