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Weddell seal behaviour during an exceptional oceanographic event in the Filchner-Ronne Ice Shelf in 2017

SARA LABROUSSE [1], SVENJA RYAN [2], FABIEN ROQUET [3], BAPTISTE PICARD [4], CLIVE R MCMAHON [5,6,7], ROBERT HARCOURT [6], MARK HINDELL [7], HERVÉ LE GOFF [1], ANTONIO LOURENCO [1], YVES DAVID [8], JEAN-BAPTISTE SALLÉE [1] and JEAN-BENOIT CHARRASSIN [1]

[1] *Sorbonne Universités, UPMC University, Paris 06, UMR 7159, LOCEAN-IPSL F-75005, Paris, France*
[2] *Department of Physical Oceanography, Woods Hole Oceanographic Institution, Woods Hole, MA, USA*
[3] *Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden*
[4] *Centre d'Études Biologiques de Chizé (CEBC), UMR 7372 Université de la Rochelle-CNRS, 79360 Villiers en Bois, France*
[5] *IMOS Animal Tagging, Sydney Institute of Marine Science, 19 Chowder Bay Road, 2088, Mosman, New South Wales, Australia*
[6] *Department of Biological Sciences, Macquarie University, Sydney, New South Wales, 2109, Australia*
[7] *Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart, 7001, Tasmania, Australia*
[8] *TBM Environnement, 2 rue de Suède, 56400 Auray, France*
sara.labrousse@gmail.com

Abstract: Rapid and regionally contrasting climate changes have been observed around Antarctica. However, our understanding of the impact of these changes on ecosystems remains limited, and there is an urgent need to better identify habitats of Antarctic species. The Weddell seal (*Leptonychotes weddellii*) is a circumpolar mesopredator and an indicative species of Antarctic marine communities. It has been extensively studied in the western Ross Sea and East Antarctica, and an understanding of its ecology in the Weddell Sea in the wintertime is emerging. We documented the behavioural response(s) of four Weddell seals from February to June in 2017 in the Filchner-Ronne Ice Shelf region and related these to unusual oceanographic conditions in 2017. Unexpectedly, we found that Weddell seals had the longest foraging effort within the outflow of Ice Shelf Water or at its turbulent boundary. They also foraged on the eastern side of the trough from April to June within the Modified Warm Deep Water and seem to take advantage of the unusual conditions of persistent inflow of warm waters through the winter. Linking animal behavioural responses to oceanographic conditions is informative for quantifying rarely recorded events and provides great insight into how predators may respond to changing conditions.

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Introduction

The Antarctic climate has changed rapidly over the past decades, but there is still a paucity of information on many of the effects of these changes on Antarctic marine communities. Thus, there is an urgent need to measure and then forecast how Antarctic marine communities, including Antarctic predators and mesopredators, will respond to these large changes in their habitats (https://www.ipcc.ch/srocc/chapter/chapter-3-2/).

Weddell seals (*Leptonychotes weddellii*) are a sentinel of the Antarctic marine ecosystem. These circumpolar mesopredators are the only mammal species breeding and living year-round in the high Antarctic (Smith 1965). Weddell seals have been intensively studied in the western Ross Sea and East Antarctica (e.g. Stirling 1969, Harcourt *et al.* 2000, Burns & Kooyman 2001, Hindell *et al.* 2002, Lake *et al.* 2005, Wheatley *et al.* 2006, Heerah *et al.* 2013); however, our understanding of their ecology in the Weddell Sea in the wintertime is still sparse (Langley *et al.* 2018, Nachtsheim *et al.* 2019, Photopoulou *et al.* 2020). Here, we document the behaviour and habitat utilization of four Weddell seals in the Filchner-Ronne Ice Shelf region in 2017.

The southern Weddell Sea continental shelf and Filchner Outflow System (FOS) (Fig. 1) play particularly important roles in the formation of ventilated dense water, which serves as a precursor of the Antarctic Bottom Water that lies at the bottom of the world's oceans (Nicholls *et al.* 2009). On the continental shelf, sea-ice formation produces High-Salinity Shelf Water (HSSW), which then enters the cavity of the

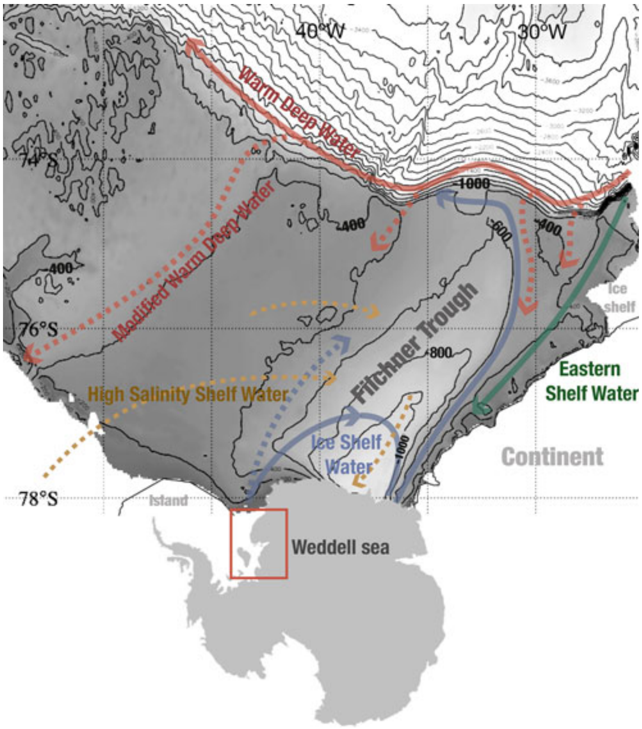

Fig. 1. Map of the study region with bathymetry and schematic ocean circulation modified from Ryan *et al.* (2020) and Nachtsheim *et al.* (2019). Arrows represent the flow of Warm Deep Water (solid red), intrusions of Modified Warm Deep Water (dashed red), Ice Shelf Water (blue), Eastern Shelf Water (green) and High-Salinity Shelf Water (orange), with dashed blue and orange arrows indicating potential pathways. The bathymetry data are from GEBCO Bathymetric Compilation Group (2020).

Filchner-Ronne Ice Shelf, by volume the largest ice shelf in Antarctica. Through interaction with the ice shelf base, a water mass with temperatures below the surface freezing point (-1.9°C), called Ice Shelf Water (ISW), is formed (Nicholls *et al.* 2009). The only pathway for it to exit the cavity is through the Filchner trough (Darelius *et al.* 2014), which gradually becomes shallower towards the shelf break, where the sill has a depth of ~600 m. Furthermore, the Filchner trough also serves as an inflow pathway of Modified Warm Deep Water (MWDW). MWDW is produced along the shelf break as an admixture of Warm Deep Water (WDW), a derivative of Circumpolar Deep Water entering the Weddell Gyre at its eastern boundary (Ryan *et al.* 2016), and the overlying Winter Water (WW). MWDW enters the continental shelf along the eastern flank of the Filchner trough in the summer/autumn (Ryan *et al.* 2017), but also to the west of the trough, where little is known about the seasonality due to heavy year-round sea-ice cover and limited observations. The Filchner sill is characterized by intense mixing of ISW and WDW/MWDW.

In 2017, an inflow of MWDW with warmer than mean (2013–16) temperatures was observed on the eastern continental shelf (~31°W) (Ryan *et al.* 2020). The 2017 MWDW inflow persisted for longer, through the whole winter, compared to conditions observed in 2013–16 (Ryan *et al.* 2020). Several studies documented important foraging efforts in the MWDW or Modified Circumpolar Deep Water (MCDW) by southern elephant seals (Biuw *et al.* 2007, Labrousse *et al.* 2015, Hindell *et al.* 2016) and by Weddell seals (Heerah *et al.* 2013, Nachtsheim *et al.* 2019, Photopoulou *et al.* 2020). Photopoulou *et al.* (2020) and Nachtsheim *et al.* (2019) reported seal diving behaviour in 2011 and 2014, respectively, on the western side of the Filchner trough in MWDW. Here, we report the behavioural response(s) of four Weddell seals to the specific oceanographic conditions of the region in 2017, which had longer and warmer MWDW inflow than usual. Identifying the distribution and habitat use of a species in different Antarctic regions and understanding its responses to changes in environmental conditions provide a baseline for the future assessment of the vulnerability and/or resilience of some communities to climate change and variability.

Methods

Tag deployment

We captured Weddell seals opportunistically on sea-ice floes from the RRS *James Clark Ross* within the Filchner-Ronne Ice Shelf region (Fig. 1). Four conductivity-temperature-depth satellite relay data loggers (CTD-SRDLs; Sea Mammal Research Unit, University of St Andrews) were deployed on Weddell seals between 17 February and 3 March 2017: two adult males, one sub-adult male and one adult female. These deployments were part of the oceanographic cruise JR16004. All animals in this study were handled in accordance with the British Antarctic Survey (BAS) animal welfare and ethical review process (AWERB). The experimental protocols were approved by BAS AWERB committee (#1029) on 23 June 2016.

Seals were captured at the end of their annual moult haul-out. The animals to be tagged were a combination of male and female adults and sub-adults, the precise mix of which was determined by the on-ice availability of animals. The tags were deployed on the most suitable animals available at those times (i.e. those that had finished moulting and were in good condition). We equipped four individual seals during the cruise; all of these deployments were post-moult, so there was no risk of pup desertion or disturbance to breeding groups. The CTD-SRDLs did not need to be recovered given that all of the data were received via satellite. Once the candidate seal had been sighted, the ship manoeuvred up to the floe and the team were deposited on the ice using a Wor Geordie. Once located and in a safe position, the seal had a canvas bag placed over its head and then was restrained to allow intravenous (IV) administration of midazolam (pre-medication) at a rate of 0.1–0.2 mg/kg (IV); those rates were lower than the recommended dose of 0.2–0.5 mg/kg (Bodley *et al.* 2005). These lower doses were sufficient to place the sedation mask on the seal but with it still being able to move its head. Once the seal was immobilized (sedation level 4 and above; Woods *et al.* 1994), the canvas bag was then removed and the sevoflurane administrated (3–5%) plus oxygen at a flow rate 10–15 l/min by mask. Immobilization was maintained with 1.5–3.0% isoflurane (or sevoflurane) plus oxygen (~6–7 l/min). The seal's body was covered with a blanket and the animal placed on an insulated mat to reduce heat loss. Respiratory rate, capillary refill, gum colour and level of immobilization were monitored. The CTD-SRDL tag was glued directly onto the fur on the seal's head to maximize communication between the tags and the Argos satellites and data transmission. We used a two-part epoxy (Araldite AW 2101 and Hardener HW 2951). The combined mass of the tags and glue was 580 g (dimensions: 105 × 70 × 40 mm). The seal was then measured. Finally, the seal was monitored during recovery to ensure the animals were fit before release.

The CTD-SRDL devices record data on a seal's diving behaviour as well as *in situ* hydrographic conditions and transmit data when the seal surfaces to breathe through communication with polar-orbiting Argos satellites (Harcourt *et al.* 2019). The seal location and then the seal movement over time is estimated via the Doppler shift from the uplinks to the Argos satellite system. For each location, spatial error estimates are given ranging from 0.5 to 10 km on average (Jonsen *et al.* 2020). Dive depth and time are recorded every 4 s, from which dive start time, dive end time, dive duration and post-dive surface interval are determined. Only the four main inflection points of the time-depth time series, indicating a rapid change of the dive shape, are transmitted for each dive. Errors were present in dive data recorded by CTD-SRDLs, such as outliers, missing or incorrect data for dive depth and duration. These errors were removed and accounted for 11.4% of the total dataset (i.e. 624 on 5452 dives). Conductivity, temperature and pressure are also recorded, and the tags transmitted ~2.0 ± 0.9 profiles per day corresponding with the ascent phase of the dives. The data points transmitted for each CTD profile are a combination of temperature and salinity at a set of pre-selected standard depths and at another set of depths chosen by a broken-stick algorithm that selects the important inflection points in temperature and salinity data (recorded every second during the ascent phase of the dives). All times were recorded in Coordinated Universal Time (UTC).

Trajectory filtration process

Tracks were fitted with a continuous-time random walk state-space model via the *foieGras R* package (Jonsen *et al.* 2019) to filter Argos location data. We chose a time step of 4 h as the non-filtered tracks had ~10 ± 7 locations per day (Table I). Each dive was then associated with a filtered Argos location using a time-based linear interpolation between the two Argos locations immediately preceding and following the dive.

Foraging effort and dive type

The proxy for foraging activity for each seal was developed at the dive scale using the method developed by Heerah *et al.* (2015), which estimates the time spent hunting during a dive. For each dive, the time spent in segments with a vertical velocity of ≤ 0.5 m s^{-1} was calculated. This time was the estimated hunting time per dive and was used as a proxy for foraging activity.

Benthic and pelagic dives were defined based on the bathymetry data from GEBCO Bathymetric Compilation Group (2020). In order to separate pelagic dives from demersal dives, for each dive the difference between the bathymetry (HGEBCO) and the maximum dive depth at the filtered dive and CTD position (HDIVE) was computed. The depth difference histogram (i.e. HGEBCO - HDIVE) showed several modes at a number of depths. Arguably, the demersal dives are all dives close to the bottom (i.e. within the first mode, close to HGEBCO - HDIVE = 0). We therefore chose the separation of the two first modes (~0 m and ~50 m) as the separation for demersal and pelagic dives. Consequently, we defined the demersal dives with a depth difference HGEBCO - HDIVE ≤ 50 m. We note that in an ideal case, demersal dives should all be associated with HGEBCO - HDIVE close to 0; however, we consider that the spread of the mode associated with demersal dives (i.e. the mode corresponding to HGEBCO - HDIVE ≤ 50 m) results from errors in bathymetry and/or errors in location. Among those, we found that 3.9% of dives had an average dive depth greater than bathymetry at the same position. Those dives were kept and also included within demersal dives.

Oceanographic conditions

In order to improve the quality of hydrographic data from the four CTD-SRDLs deployed on the Weddell seals, comparisons of CTD-SRDLs with a ship-based CTD system were performed. These comparisons were then used to correct pressure-induced linear biases on both temperature and salinity measurements using delayed-mode methods following Siegelman *et al.* (2019). The

Table I. General information regarding the four Weddell seals tagged in the Filchner-Ronne Ice Shelf region in 2017 from the RRS *James Clark Ross* icebreaker. This includes information relative to the seals' horizontal movement, sex, snout-to-tail length upon deployment, deployment start and end dates, tag duration, total number of Argos positions and the number of positions transmitted daily, the cumulated distance travelled, the average distance travelled per day between the first and last locations of each day and the average horizontal speed. Averages are expressed ± SD.

ID	Sex	Body length (cm)	Deployment date	End date	Tag duration (days)	Total locations (before filtering)	Number of locations per day (before filtering)	Cumulative distance (km)	Distance travelled per day (km)	Average speed (km/h)
wd09-408-16	Male	231	18 Feb 2017 3:55	8 Apr 2017 9:29	49	628	13 ± 6	1136	14 ± 11	0.96 ± 0.75
wd09-414-16	Male	240	19 Feb 2017 18:23	10 Jul 2017 18:37	141	887	9 ± 7	2555	12 ± 14	0.83 ± 0.81
wd09-412-16	Male	185	2 Mar 2017 16:08	1 Jul 2017 7:12	120	1424	13 ± 8	1824	9 ± 8	0.63 ± 0.46
ct128-246BAT-12	Female	250	3 Mar 2017 18:08	30 Jul 2017 1:47	148	1072	9 ± 7	2046	8 ± 9	0.57 ± 0.59
						Sum: 4011	Average: 10 ± 7		Average: 10 ± 11	Average: 0.70 ± 0.66

minimum accuracies of post-processed data were estimated to be at ±0.03°C in temperature and ±0.05 psu, increasing to ±0.01°C and ±0.02 psu in the best cases (Roquet *et al.* 2014).

We distinguished between seven water masses following the criteria described in Nachtsheim *et al.* (2019): Eastern Shelf Water (ESW), MWDW, HSSW, WW, Antarctic Surface Water (AASW) and ISW. In between ISW and MWDW properties, non-identified observations were classified as Mixed Waters (MWs). Indeed, it is impossible to draw sharp boundaries between water masses as mixing always occurs at the boundary between them.

To identify the water mass used when the seals were foraging, we used the water mass encountered during the hunting segments of each dive. Each dive was first associated with the closest CTD profile in time with an equal or deeper depth compared with the dive collected by the same individual. A maximum time interval of 12 h between the CTD and the dive was set, leading to an average distance difference between the CTD and the dive of 8.0 ± 10.8 km. Following this procedure, 81.4% of dives were associated with a CTD profile. For the analysis of hunting time, as there could be multiple hunting phases in a dive with possibly different water masses used in different hunting phases, we selected for each dive associated with a CTD profile the CTD data corresponding of the depths of the longest hunting phase segment in a dive. We then selected the most frequent water mass encountered within the longest hunting segment for each dive. This water mass was then associated with the total hunting time observed in the given associated dive.

Finally, based on the mooring data from 2013–16, Ryan *et al.* (2017) described a mean seasonal cycle with four distinct phases. This shows an inflow of warm water in summer/autumn with maximum temperatures around April and a ceasing of the inflow around July. From then on, temperatures on the shelf are near the surface freezing point, indicating that no MWDW is entering the shelf during that time. The year 2017 was exceptional because warm temperatures stayed present on the shelf throughout the whole winter, and maximum temperatures in April were ~0.5°C warmer than in previous years. Ryan *et al.* (2020) proposed a new mechanism that drove this stronger and prolonged inflow, which is the strong and early sea-ice melting upstream near the Greenwich Meridian. The freshwater input from this melting propagates along the coast and influences the dynamics at the thermocline/Antarctic Slope Front in such a way that more warm water can enter the Filchner-Ronne Ice Shelf.

Results

Summary of the tracking data

Tags recorded seal movement and diving patterns from 49 to 148 days between February and July 2017 (Fig. 2a & Table I). A total of 4011 locations were transmitted, and 2547 locations were used for the analysis after the filtration process using a state-space model with a time step of 4 h. For the individual #14414, we kept original locations for the month of June and July, as the track filtering process did not work on that part of the track. Indeed, important time gaps were observed between locations, as the number of transmissions decreased gradually before the tags stopped emitting. This led to high uncertainty in the filtering process for these gaps. Individuals travelled between 1136 and 2555 km during their recorded trips; their average speed was 0.7 ± 0.6 km h^{-1} and they travelled on average 10 ± 11 (SD) km per day (ranging from 8 ± 9 (SD) km to 14 ± 11 (SD) km depending on the individuals; Table I).

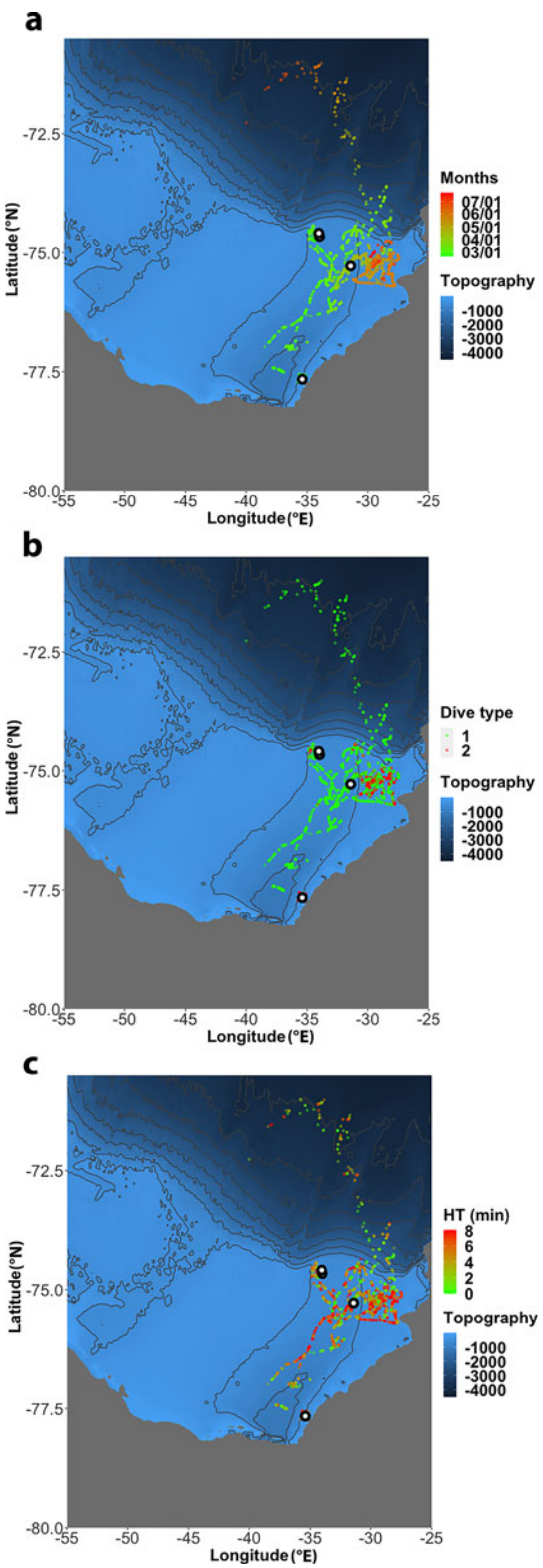

Fig. 2. Maps representing **a.** the timing in months, **b.** the diving behaviour (i.e. pelagic (1) *vs* benthic (2)) and **c.** the foraging effort (i.e. hunting time per dive in minutes) of the recorded tracking data for the four seals monitored in 2017 in the Filchner-Ronne Ice Shelf region. Black circles filled by white correspond to site deployments.

General diving patterns

A total of 4828 dives were recorded by the seals (ranging from 525 to 2475 dives depending on the individuals; Table II). Dives > 25 m were used for this study, corresponding to ~60% (2906 dives) of all dives. On average, seals made 10 ± 11 (SD) dives per day (the accuracy of this result is dependent on whether or not all of the dives were transmitted and received by the satellites from the tags) of > 25 m (ranging from 3 ± 4 (SD) dives per day to 15 ± 14 (SD) dives per day; Table II). For dives > 25 m, the average maximum depth among individuals was 198 ± 156 (SD) m (ranging from 119 ± 109 (SD) m to 219 ± 159 (SD) m; Table II) and the dive duration was 11 ± 7 (SD) min (ranging from 8.5 ± 5 (SD) min to 12 ± 9 (SD) min; Table II).

Seals performed mostly (82%) pelagic dives (ranging from 79% to 97%; Fig. 2b & Table II); the average maximum depth for these pelagic dives was 151 ± 126 (SD) m and for the benthic dives was 421 ± 57 (SD) m (Table II).

Behaviour in relation to oceanographic conditions and habitat utilization

Our study included two adult males, one sub-adult male and one adult female. While in the Filchner trough region all seals dived pelagically (and one benthically) in ISW, on the eastern side of the trough they dived benthically, mostly within ESW, WW, MW and MWDW (Figs 2b & c & 3). All seals hunted within the ISW, MW, WW, ESW and MWDW (Figs 4d & h & 5d & h). Only one seal travelled north, off the shelf (Fig. 2), where the ocean depth drops rapidly to several thousand metres. The number of dive transmissions for individuals #14414 and #ct128-246 decreased gradually before the tags stop emitting, limiting our interpretation of the behaviour after mid-May and early June, respectively, for these two individuals (Figs 4e & 5e). Below, we briefly describe the behaviour of individual seals and how their behaviour relates to oceanographic conditions and habitat utilization.

In the first half of March, the sub-adult male, individual #14412 (Fig. 4a–d), spent some time diving pelagically over the mouth of the Filchner trough in ISW and over the Filchner sill, where it mainly encountered ISW as well as MWDW. After mid-March, it then travelled north off the shelf. From mid-March to the end of April, the seal dived pelagically in surface waters (i.e. characterized by the warm temperatures in the upper 100 m), then dived principally within the MWDW until the tag stopped transmitting in July (Fig. 5a–d).

The adult female, individual #ct128-246 (Fig. 4e–h), dived benthically very briefly in early March on the western side of the sill within the ISW, then dived pelagically over the sill within the ISW from March until

Table II. Diving behaviour information regarding the four Weddell seals tagged in the Filchner-Ronne Ice Shelf region in 2017 from the RRS *James Clark Ross* icebreaker. This includes information on sex, number of dives (including both dives < 25 m and > 25 m), the average maximum depth, dive duration, the percentage of benthic dives and the average maximum depth for pelagic and benthic dives. Averages are expressed ± SD.

ID	Sex	Number of dives (including dives < 25 m)	Number of dives per day (dives > 25 m)	Average of maximum depth (m) (dives > 25 m)	Average of dive duration (min) (dives > 25 m)	Percentage pelagic dives	Average of maximum depth pelagic dives (m)	Average of maximum depth benthic dives (m)
wd09-408-16	Male	829	15 ± 14	212 ± 171	11 ± 5	90	184 ± 158	451 ± 66
wd09-414-16	Male	999	3 ± 4	119 ± 109	8.5 ± 5	79	164 ± 132	423 ± 30
wd09-412-16	Male	525	9 ± 8	219 ± 159	12 ± 9	97	110 ± 94	464 ± 61
ct128-246BAT-12	Female	2475	14 ± 12	198 ± 152	12 ± 7.5	79	140 ± 111	414 ± 61
		Sum: 4828	Average: 10 ± 11	Average: 198 ± 156	Average: 11 ± 7	Percentage: 82	Average: 151 ± 126	Average: 421 ± 57

mid-April. This region of the sill is generally very turbulent and intermittent warm intrusions are observed above the outflowing ISW layer (Fig. 3d). From mid-April to June, the female spent most of her time diving benthically on the eastern side of the trough within the inflow pathway of MWDW (Fig. 4e–h). As part of the seasonal cycle, the temperatures on the continental shelf usually drop towards June and the warm inflow ceases (Ryan *et al.* 2017). However, in 2017, the temperature increased again slightly after June and stayed at ~-1.5°C through the winter, indicating a prolonged warm inflow, instead of being close to the surface freezing point temperature of -1.9°C. Temperature and salinity characteristics sampled from the female clearly show warm water in June-July at the bottom of the water column, as it dived into this water mass (Fig. 4h; see the part of the plot indicated by the black arrow).

One of the adult males, individual #14414 (Fig. 5e–h), showed similar behaviour to the female. It briefly dived benthically on the western side of the sill in the second half of February and then spent the first half of March diving pelagically in the deeper part of the trough to the south, where it repeatedly dived down to the upper boundary of the ISW layer, located at ~300–400 m depth. In the second half of March, it returned northward along the eastern side of the trough and onto the shallower eastern shelf in the MWDW inflow region. There it dived benthically from April to May, mainly within the MWDW (Fig. 4e–h), during the period of strongest inflow and warmest temperatures along the bottom.

Finally, diving records only lasted until early April for the fourth individual, adult male #14408 (Fig. 5a–d), and this was the only seal tagged in the southern part of the Filchner trough. This adult male showed similar behaviour to seals #ct128-246 and #14414, as it very briefly dived benthically over the shallower eastern slope of the trough and then dived pelagically within the central trough from late February to early March in the ISW while slowly moving northward. Interestingly, this seal dived at a consistent depth into the ISW layer during this time, which contrasts with the diving behaviour of #14414. After shortly moving northward off-shelf, this seal dived benthically on the eastern side of the trough from mid-March to mid-April in the MWDW (Fig. 5a–d), which is the time of the strongest and warmest inflow in that region, similarly to seals #14414 and #ct128-246.

Hydrographic properties

A total of 734 CTD profiles were recorded by the four seals (from 114 to 228 depending on the individuals; see Table III) with an average of 2.0 ± 0.9 profiles per day. However, 108 profiles did not have salinity data and so could not be associated with the dive data. Based on

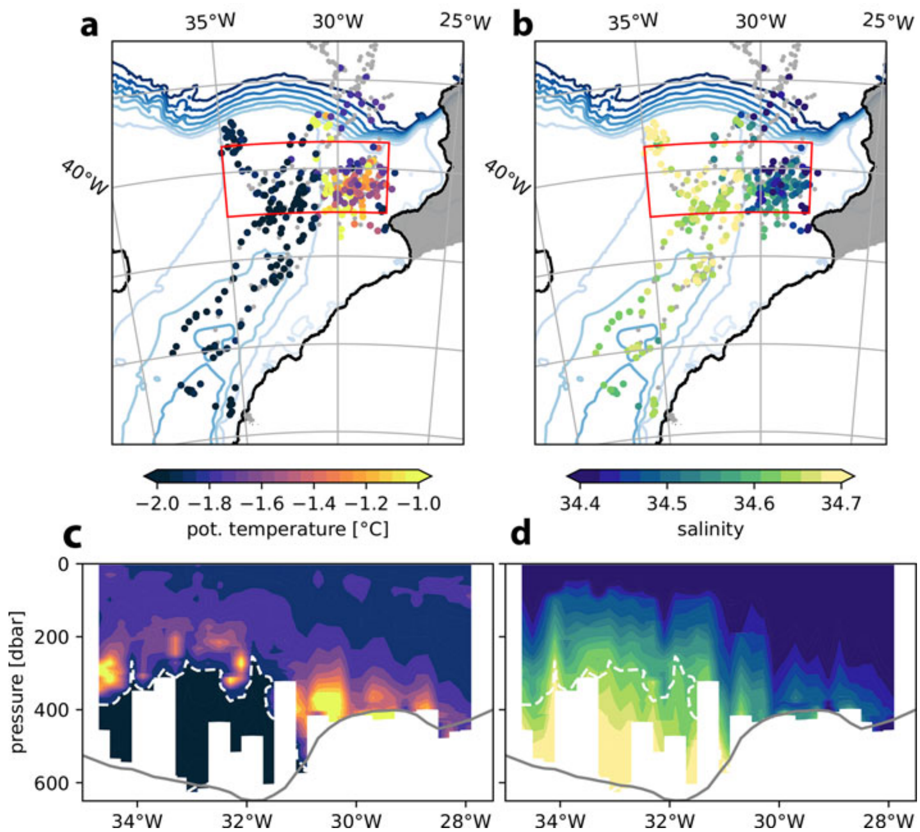

Fig. 3. Oceanographic properties encountered by the seals in the Filchner-Ronne Ice Shelf region in 2017. Panels **a.** and **b.** represent temperature and salinity, respectively, from conductivity-temperature-depth (CTD) profiles where the maximum depth is within 50 m of the bottom for bathymetry < 500 m and CTD profiles where the maximum depth is at least 300 m for bathymetry > 500 m (i.e. the trough). This selection excludes those profiles within the surface layer. Panels **c.** and **d.** represent temperature and salinity, respectively, for all seal CTD profiles binned between 74.7°S and 75.5°S (red rectangles in panels **a.** and **b.**) along longitude (0.2° intervals). The grey lines show the mean bathymetry between 74.7°S and 75.5°S (based on *RTopo-2.0.1*). The white dashed lines mark the -1.9°C isotherm (i.e. the Ice Shelf Water boundary).

depth and time conditions, a total of 81.4% of dives were associated with a CTD profile.

Interestingly, the average hunting time per dive was the longest in ISW (7.4 ± 3.7 min; pelagic dives: 7.4 ± 3.3 min; benthic dives: 7.0 ± 5.4 min; Table III) compared with the MWDW (6.8 ± 3.2 min; pelagic dives: 4.8 ± 2.6 min; benthic dives: 7.7 ± 3 min; Table III), the MW (5.3 ± 3.3 min; pelagic dives: 5.3 ± 3.3 min; benthic dives: 5.1 ± 2.2 min; Table III) and the rest of the water masses (see Table III).

Finally, the seals spent 37% of their total hunting time (over the recorded track) in ESW, 20% in WW, 16% in ISW, then 13% in MWDW and 13% in MWs, and 0.7% in HSSW and 0.3% in AASW (Table III).

Discussion

All seals dived pelagically and one benthically over the Filchner trough in ISW, the water mass where their average foraging effort (i.e. hunting time per dive) was the greatest. This is a novel observation and in contrast to the earlier findings from the Weddell Sea (Nachtsheim *et al.* 2019, Photopoulou *et al.* 2020). Seals were found within the outflow, at the mouth of the trough, over the sill or travelling N-S over the central part or over the eastern side at the boundary of ISW or within it. All seals dived benthically on the eastern side of the trough from April to June within MWDW or an admixture of water masses. Seals also seemed to benefit from the strong and persistent inflow of warm waters onto the continental shelf. Only one seal travelled northward off the shelf.

Despite important foraging effort in ISW and MWDW, counterintuitively seals spent a greater proportion of their total hunting time in ESW and WW (followed by ISW, MWDW and MWs; Table III). Ryan *et al.* (2020) reported that MWDW properties on the eastern shelf during winter in 2017 indicated mixing with a slightly fresher water mass than in previous years. This mixing

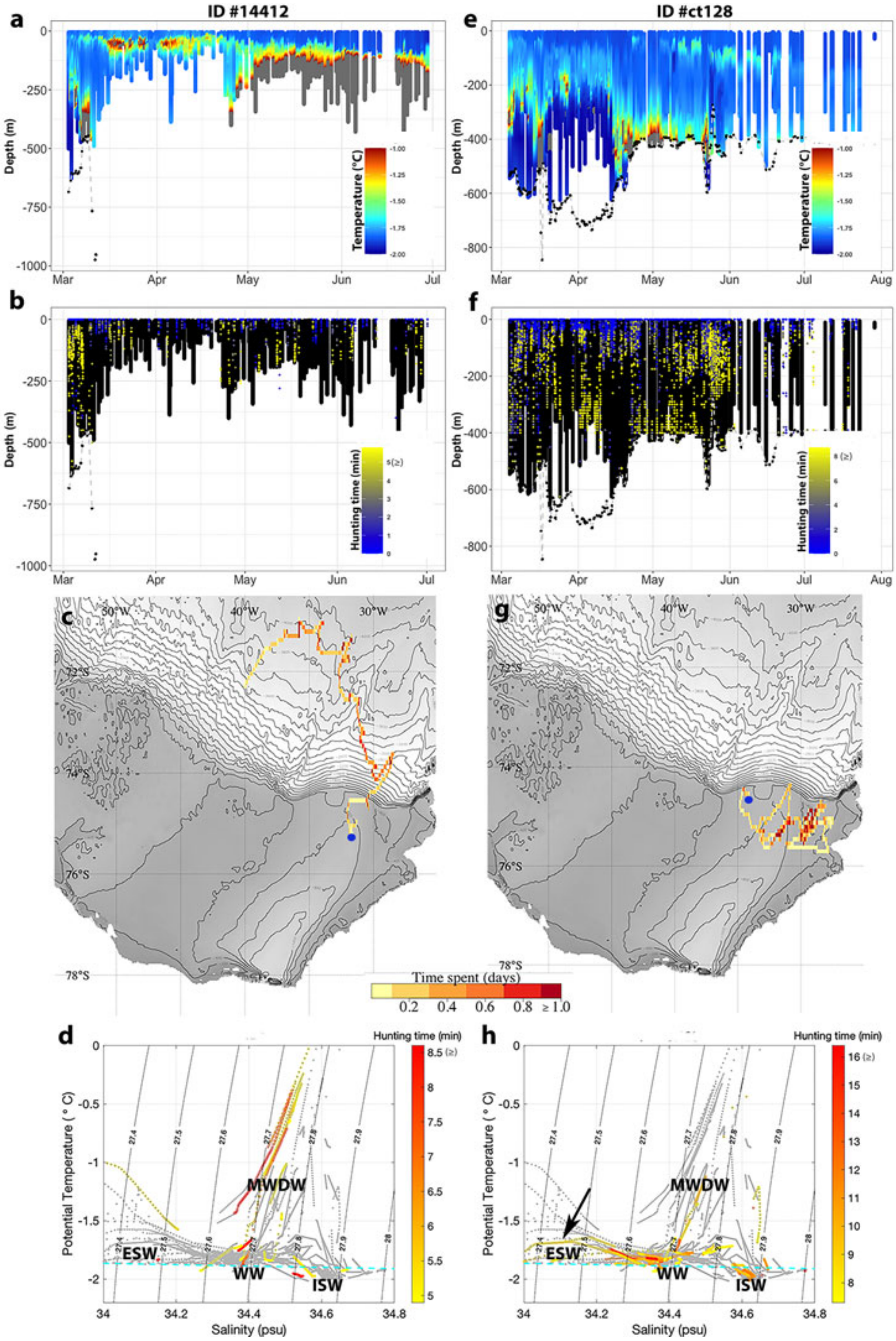

Fig. 4. Movement and diving behaviour associated with the oceanographic properties sampled by seals #14412 and #ct128-246 in 2017. Panels **a.**, **b.**, **e.** and **f.** represent a time series combining temperature profiles (panels **a.** and **e.**) and dive information (panels **b.** and **f.**; the hunting time per dive is coloured at each time/depth inflexion point of the dive on top of the profiles coloured in black). For illustrative purposes, all hunting values above the 75% quantile were set to the 75% percentile values. Black dots linked by grey lines represent the bathymetry < 1000 m. Panels **c.** and **g.** represent maps of the average time spent (days) for each individual seal per grid cell (~0.08° × 0.08°; expressed in days) computed using the dive data. Blue dots correspond to deployment sites. Panels **d.** and **h.** represent temperature-salinity diagrams of hydrologic properties sampled during the longest hunting time segments of each dive from 2017 seal conductivity-temperature-depth casts. The colour corresponds to only the greatest hunting time values (i.e. above the median) for the given seal. Water masses are labelled on the temperature-salinity diagrams. For illustrative purposes, all values > 1 day were set to 1 day. ESW = Eastern Shelf Water; ISW = Ice Shelf Water; MWDE = Modified Warm Deep Water; WW = Winter Water.

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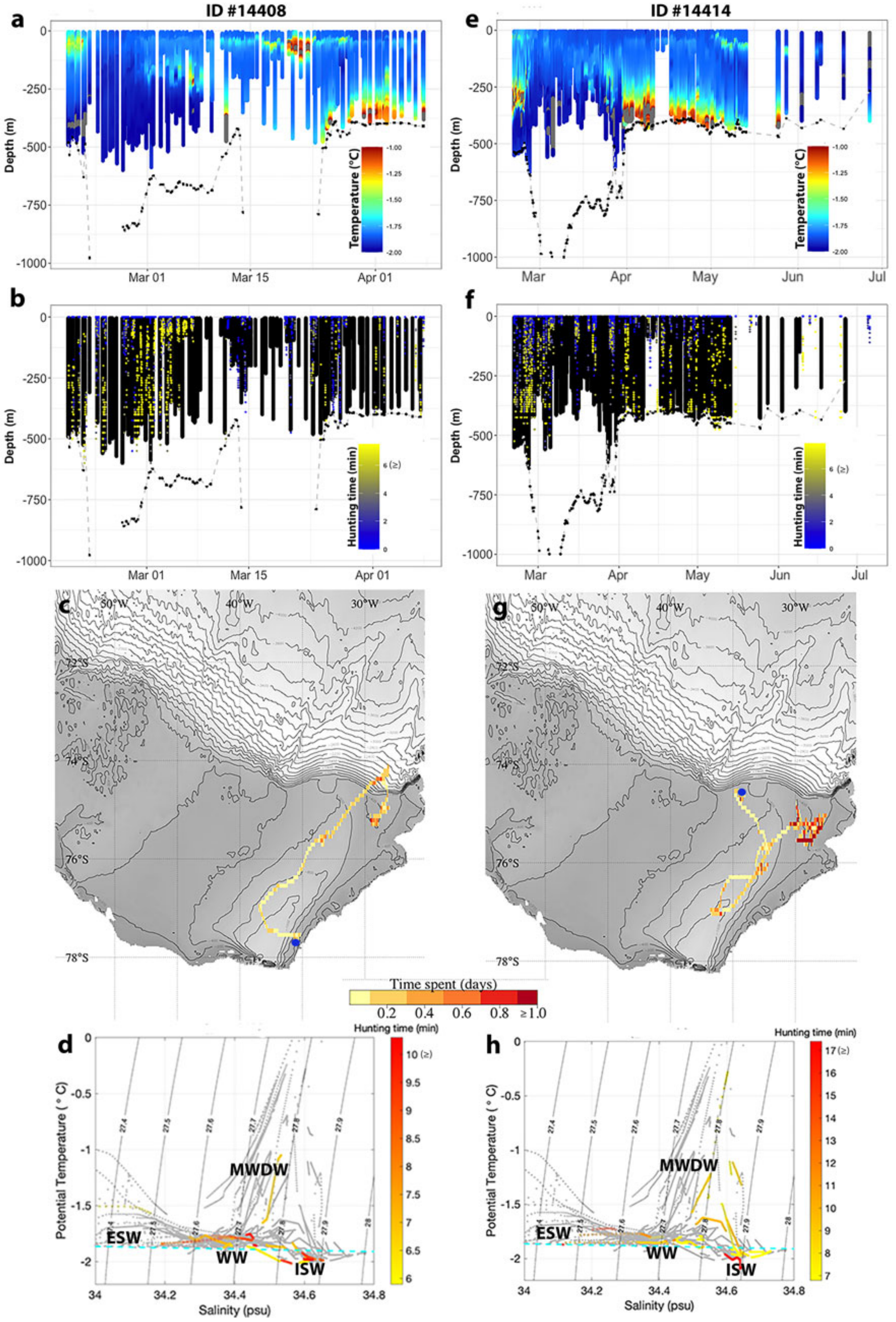

Fig. 5. Movement and diving behaviour associated with the oceanographic properties sampled by seals #14408 and #14414. Refer to Fig. 4 for the legend description.

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Table III. Oceanographic and foraging information regarding the four Weddell seals tagged in the Filchner-Ronne Ice Shelf region in 2017 from the RRS *James Clark Ross* icebreaker. This includes information on sex, the number of conductivity-temperature-depth (CTD) profiles transmitted daily, the total number of CTD profiles, the average hunting time per dive in Eastern Shelf Water (ESW), Modified Warm Deep Water (MWDW), High-Salinity Shelf Water (HSSW), Winter Water (WW), Antarctic Surface Water (AASW), Ice Shelf Water (ISW) and Mixed Waters (MWs) and the percentage of total dive duration and hunting duration across all seals in each of these water masses. Averages are expressed ± SD.

ID	Sex	Number of CTD profiles per day	Number of CTD profiles	Average hunting time per dive in ESW (min)	Average hunting time per dive in MWDW (min)	Average hunting time per dive in HSSW (min)	Average hunting time per dive in WW (min)	Average hunting time per dive in AASW (min)	Average hunting time per dive in ISW (min)	Average hunting time per dive in MW (min)
wd09-408-16	Male	2.4 ± 0.9	114	4.2 ± 3.4	4.9 ± 1.8	0	6.2 ± 3.1	1.5 ± 2.1	6.9 ± 2.6	5.8 ± 3.4
wd09-414-16	Male	2.2 ± 1.0	196	4.1 ± 9.6	6.6 ± 2.7	0	4.0 ± 3.8	0	6.2 ± 2.6	4.8 ± 2.5
wd09-412-16	Male	1.8 ± 0.7	196	3.9 ± 2.8	5.4 ± 2.1	0	5.6 ± 4.1	4.5 ± 1.2	6.6 ± 2.4	4.2 ± 2.4
ct128-246BAT-12	Female	2.1 ± 1.0	228	4.7 ± 4.0	7.5 ± 3.2	4.7 ± 2.2	4.5 ± 4.3	0	9.1 ± 4.5	6.0 ± 3.5
		Average: 2.0 ± 0.9	Sum: 734	Average: 4.4 ± 4.4	Average: 6.8 ± 3.2	Average: 4.7 ± 2.2	Average: 4.7 ± 4.0	Average: 3.7 ± 1.9	Average: 7.4 ± 3.7	Average: 5.3 ± 3.3
Percentage of total dive duration in each water mass across all seals				33%	15%	Negligible (1.0%)	19%	Negligible (0.3%)	18%	13%
Percentage of total hunting duration in each water mass across all seals				37%	13%	Negligible (0.7%)	20%	Negligible (0.3%)	16%	13%

probably occurred with ESW, which is generally found upstream of the Filchner trough on the narrow continental shelf. As ESW and WW lie relatively shallow in the water column, seals encountered these water masses more frequently during their vertical diving movements (i.e. proportion of total dive duration is 33% in ESW and 19% in WW compared with 18% in ISW, 15% in MWDW and 13% in MWs; Table III). This may explain why the proportion of the total hunting time was higher in ESW and WW, while on average on the dive scale, the hunting time was higher in ISW and in MWDW. Due to our limited sample size, we are purposely presenting only a qualitative description of the behaviour of seals instead of quantifying the behaviour.

Both the female and the three males in our study displayed a mixture of pelagic and benthic dives; however, pelagic dives were more common that benthic dives for both sexes. This is in contrast to what Photopoulou *et al.* (2020) found, where males performed only benthic dives on the shelf and females left the shelf and moved northward. We found no obvious sex-specific differences nor any seasonal shifts in behaviour, but given that our sample size was small, this conclusion is not definitive.

Generally, the end of the summer has been characterized by the beginning of a reduction in the inflow of warm water onto the continental shelf in the southern Weddell Sea (Ryan *et al.* 2017). Warm water enters the shelf as MWDW in the region of the Filchner trough, especially at the eastern and western parts of the Filchner sill (Ryan *et al.* 2017). In 2017, an exceptional inflow of MWDW with warmer temperatures was present on the eastern shelf, and these warmer temperatures persisted through the whole winter in 2017, in contrast to conditions observed in 2013–16 (Ryan *et al.* 2020). This may explain why we did not observe any change in the behaviour of the seals once they reached the eastern side of the shelf. The three seals that did not move off the shelf remained on the eastern shelf diving benthically within the MWDW between approximately mid-March to mid-April until the tags stopped transmitting (April, May and July). This period corresponds with the strongest inflow of MWDW and warmest temperatures along the bottom (Ryan *et al.* 2017, 2020). Photopoulou *et al.* (2020) and Nachtsheim *et al.* (2019) reported seal diving behaviour in 2011 and 2014, respectively, on the western side of the Filchner trough in MWDW. Although two seals were tagged in the western part and one in the southern part in the present study, they all converged and remained in the eastern part later in the season. We hypothesized that this behaviour could be explained by the longer inflow of MWDW on the eastern flank throughout the winter in 2017 (Ryan *et al.* 2020).

Several studies have observed important foraging efforts in MWDW or MCDW by southern elephant seals (Biuw *et al.* 2007, Labrousse *et al.* 2015, Hindell *et al.* 2016) and by Weddell seals (Heerah *et al.* 2013, Nachtsheim *et al.* 2019, Photopoulou *et al.* 2020). We also observed Weddell seals diving benthically in MWDW, suggesting that this water mass is probably important to a suite of Antarctic predators. It is now known that intrusions of nutrient-rich water masses onto the shelf (e.g. Circumpolar Deep Waters) stimulate primary productivity (Nicol *et al.* 2005) and the population growth of mid (Prézelin *et al.* 2000) and upper trophic levels (La Mesa *et al.* 2010) and the top predators that feed on these lower trophic preys. The shelf areas west and east of the Filchner trough may be particularly biologically rich. Indeed, these areas seem to

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be dynamic and may enhance nutrient mixing and trophic flows. For example, the Antarctic silverfish (*Pleuragramma antarcticum*), one of the main prey items of Weddell seals (Smith *et al.* 2007), is abundant in shallow shelf areas, inhabiting depths from 400 to 700 m (La Mesa & Eastman 2012) and exhibiting diurnal vertical migration (Lancraft *et al.* 2004).

Surprisingly, the hunting time per dive was longest in ISW during pelagic dives, and this was not observed in comparable studies by Photopoulou *et al.* (2020) and Nachtsheim *et al.* (2019). The ISW observed in the Filchner region is formed underneath the Filchner-Ronne Ice Shelf and is characterized by potential temperatures below the surface freezing point (-1.9°C). Weddell seals feed predominantly on Antarctic silverfish, which have a life history that is hypothesized to be structured by circulation associated with glacial trough systems (Ashford *et al.* 2017). Adult Antarctic silverfish spawn in the vicinity of the ice shelf during late winter and early summer, exposing them to the outflow of ISW (Caccavo *et al.* 2019). Caccavo *et al.* (2019) sampled exclusively large-length fish in ISW at 77°S just east of the trough flank at 700 m compared to sharply decreasing numbers at shallower depths over the adjoining shelf. Adults are then entrained northward in the ISW trough outflow. Plötz *et al.* (2001) also performed some trawling during the daytime and confirmed that Antarctic silverfish were by far the most abundant fish both in the pelagic region and close to the bottom within the Filchner trough. This may explain the pelagic dives over the Filchner trough in ISW observed for individuals #14414 and #14408: one individual dived down to the upper boundary of ISW, located at ~300–400 m depths in March, while the other briefly dived benthically over the shallower eastern slope of the trough at 77°S and then dived consistently relatively deep and into the ISW layer. Both individuals may have been feeding on adult Antarctic silverfish. The two individuals then moved northward, diving pelagically within the central or the eastern side of the trough between late February and March, where their movements may also coincide with the presence of their main prey. Moreover, Caccavo *et al.* (2019) reported large-length fish at the trough mouth, which were also associated with incursions of MWDW east of the Filchner sill, exactly matching with the behaviour of the four seals. Some researchers spotted Antarctic toothfish (*Dissostichus mawsoni*) with a remotely operated vehicle at a great distance under the Ross Ice Shelf in very cold waters (D. Ainley, personal communication 2020). The Antarctic toothfish, another important prey species for Weddell seals (Ainley *et al.* 2020), is also likely to associate with very cold ISW; for example, Weddell seals that live near White Island have been seen feeding within the crack of the Ronne Ice Shelf on toothfish (D. Ainley, personal communication 2020). Further evidence of Weddell seals feeding on toothfish comes from commercial fisheries (summarized in Ainley *et al.* 2013). Typically, toothfish are reported to occur regularly on or near the sea floor, and larger, neutrally buoyant individuals also occur within the water column, especially under heavy ice cover, and are therefore accessible to the seals throughout the water column. For example, fish were regularly found within ~100 m of the bottom, which is coincident with the Weddell seal pelagic dives in ISW. Finally, several seals in our study dived over the deep part of the trough or over the sill at the interface between the upper boundary of ISW and warm intrusions, where the turbulence and mixing (Fer *et al.* 2016) may lead to the advection of different prey (e.g. small Antarctic silverfish sampled in Caccavo *et al.* 2019), as is expected at the mouth of the trough in the sill regions. McIntyre *et al.* (2013) also reported increased foraging efforts for Weddell seals at specific water depth layers, where increased water temperature stratification probably concentrates prey.

Oceanographic observations during the autumn/winter are rare in this region, with a strong bias existing for observations from the summer months. This is primarily due to the heavy sea-ice conditions almost year-round limiting access for research vessels and sampling floats. Consequently, animal-borne oceanographic observations in autumn/winter are valuable for ecological studies and for physical oceanography. Temperature-salinity profiles collected by seals have made valuable contributions to the analysis of oceanographic conditions on the southern Weddell Sea continental shelf (Darelius *et al.* 2016). Similarly, in this study, the seal data confirmed temperatures > 1°C in May 2017, in agreement with mooring observations reported in Ryan *et al.* (2020). Unfortunately, no data were available from July onward, and consequently there are no concurrent data with which to compare the hydrographic conditions observed from the fixed moorings during the 2017 winter.

This communique based on four individual seals highlights that: 1) Weddell seals seemed to take advantage of the unusual conditions of the persistent inflow of warm waters through the winter in 2017 and 2) Weddell seals were unexpectedly associated with the outflow of ISW on the Filchner trough or at the turbulent interface between ISW and MWDW, where their main prey species of Antarctic silverfish is expected to be, as well as potentially another dominant prey species, the Antarctic toothfish. This study reveals the importance of documenting seal behavioural responses to anomalous oceanographic conditions, as even a small sample provides important insights into potential variability in Antarctic predators' responses to change and/or variability in Antarctic oceanographic conditions.

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Author contributions

SL developed the concept, directed the data analysis and shared responsibility for writing the manuscript. SL and SR performed the data analysis and made the figures. BP and FR performed the calibration procedure of the animal-borne oceanographic data. J-BC, CRM, RH and MH provided the instruments deployed on Weddell seals. AL, HLG, YD, J-BS and SL deployed the tags on Weddell seals in the field. SL, SR, J-BS and J-BC helped with the interpretation of the results. J-BS led the oceanographic cruise. All authors shared responsibility for contributing to the final version of the manuscript prior to submission.

Details of data deposit

Data and data products related to the paper will be available upon publication on the following repository: http://dx.doi.org/10.17632/kwy3gwrwbd.1.

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