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# The nightlife of a Ross seal: diving and haul-out behaviour from the eastern Weddell Sea

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**Abstract:** Ross seals (*Ommatophoca rossii*) travel away from the pack ice and spend most of their year foraging pelagically. Here, we augment the few existing records of Ross seal diving and haul-out behaviour, providing novel insights into how these are influenced diurnally and seasonally. We used biologging devices that recorded the dive behaviour (n = 5) and/or haul-out behaviour (n = 9) of Ross seals in the eastern Weddell Sea (2016–2019). Ross seals mostly dived between 100 and 200 m deep, often > 300 m, and for 5–12 min in duration, often > 20 min. During March–July, when Ross seals forage pelagically, diving metrics varied diurnally. The seals dived deeper during twilight and shallowest at night, while the number of dives and diving duration did not follow a clear diurnal pattern. Consequently, diving effort was highest during the night. Ross seals preferentially hauled out in the middle of the day during September, October, February and December, but not during the rest of the year. Three females that entered the pack ice during breeding season were hauled out continuously for 5–7 days, punctuated by water entries for 1–3 h during and/or after such continuous haul-outs over the breeding season. This behaviour might suggest that Ross seals alternate between capital and facultative income breeding.

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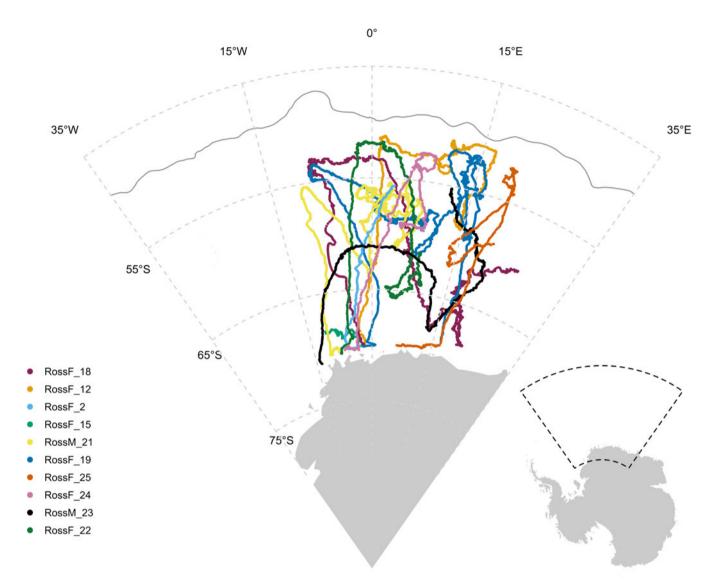
**Keywords:** Antarctica, biologging, breeding season, diurnal behaviour, Queen Maud Land, Southern Ocean

## Introduction

The diving behaviour of marine predators forms a critical component in our understanding of how they interact with prey in their oceanic environment (Bestley *et al.* 2015). These diving marine predators contend with finding prey distributed vertically in the water column and at various population densities over their geographical range. Seals are air-breathing marine predators that breed and rest on land or ice. Their hunting and foraging behaviour can be affected by the seal's age, sex, breeding stage and various external factors, such as season, time of day, etc. (Boehme *et al.* 2016). How individuals balance their time between active hunting/foraging and passive haul-out phases all while acquiring enough prey resources to breed and reproduce could determine their fitness, survival and reproductive success (Costa & Gales 2003).

This behavioural balance has probably developed over time to overlap with the three-dimensional movements and behaviour of their prey species, which in turn are influenced by a range of environmental and oceanographic factors. For example, several prey species such as mesopelagic fish from the family Myctophidae (lantern fish) and Antarctic krill (*Euphausia superba*) make a diurnal vertical migration, which their diving predators follow closely (Croxall *et al.* 1985). The seasonal cycle also influences the distribution of resources through, for example, the mixed-layer depth or positioning of fronts. Even the moon is known to influence the vertical movements of prey and their predators, resulting in individuals diving deeper during full moon (Sterling *et al.* 2014), while tides are also implicated in the underwater activity and body temperature of Weddell seals (Bornemann *et al.* 1998).

Ross seals (Ommatophoca rossii), unlike other Antarctic counterparts such as the crabeater seal Weddell (Lobodon carcinophaga) and seal (Leptonychotes weddellii) that remain in the ice year round, travel away from the Antarctic continent and spend most of their life cycle in the open ocean to forage pelagically (Arcalís-Planas et al. 2015, Blix & Nordøy 2007, Wege et al. 2021). Furthermore, unlike crabeater and Weddell seals that prey on Antarctic species, such as Antarctic krill, ice fish (Nototheniidae spp., Channichthyidae spp.) and



**Fig. 1.** At-sea movement data of Ross seals carrying dive (n = 5) and temperature and haul-out behaviour (n = 5) recorders. The position of the Polar Front is shown by the grey line (Orsi *et al.* 1995). Inset: Location of the study area in relation to Antarctica. Dive recorders were deployed on RossF\_12, RossF\_18, RossF\_22 and RossM\_23; haul-out only recorders were deployed on RossF\_15, RossF\_19, RossM\_21, RossF\_24 and RossF\_25.

toothfish (*Dissostichus* spp.), Ross seals predominantly forage at a different trophic level than crabeater and Weddell seals (Brault *et al.* 2019). They prey on squid, fish and occasionally crustaceans and benthic invertebrates (Øritsland 1977) taken from a wider geographical range. Myctophid fish and cephalopods are taken while foraging in the open ocean, and Antarctic silverfish (*Pleuragramma antarctica*) are taken when the seals forage over the continental shelf during their annual moult (Skinner & Klages 1994, Blix & Nordøy 2007). Ross seals travel northwards from the Antarctic continent and forage in the open ocean just like several sub-Antarctic predator species that travel southwards from their sub-Antarctic islands to also forage in the open ocean.

Unlike sub-Antarctic predators that haul out on land and are relatively easily accessible, Ross seals prefer to haul out in dense, consolidated pack ice (Condy 1977, Skinner & Klages 1994), which makes gaining access to them difficult. They are rarely encountered in the pack ice and, combined with their unique oceanic movements and preference to haul out in difficult-to-access areas, this has resulted in them being poorly studied. Despite the advances made in the field of biologging and the range of data loggers available to observe these previously unobservable phases of marine predators, currently only four studies exist that report on Ross seal diving and haul-out behaviour recorded by biologging devices (Bengtson & Stewart 1997,

Southwell 2003, Blix & Nordøy 2007, Arcalís-Planas et al. 2015).

The limited knowledge of Ross seal diving and haul-out behaviour suggests that Ross seals' diving behaviour follows a diel pattern when they forage pelagically, but this changes based on time of the year and location (Blix & Nordøy 2007). Diving effort is at its lowest during the annual moult (late January-early February) and at its highest late during February-April when Ross seals travel north from the Antarctic pack ice towards the Polar Front and forage pelagically (Blix & Nordøy 2007). Ross seals remain pelagic and do not haul out post-moult onward until October-November, when breeding individuals return southwards to the pack ice (Blix & Nordøy 2007, Arcalís-Planas et al. 2015). Despite these understandings of Ross seal diving and haul-out behaviour, several aspects remain uncertain. For example, their lactation period was first estimated to last 4 weeks (Riedman 1990) or even up to 6 weeks (Skinner & Klages 1994). However, observational data questioned these estimates (Southwell et al. 2003), and haul-out data from satellite-linked recorders showed that three breeding individuals presumably hauled out continuously for ~13 days to pup and care for their offspring (Blix & Nordøy 2007).

In this study, we provide novel insights into how the diving and haul-out behaviour of Ross seals is influenced by diurnal, seasonal and environmental variation using advances made in biologging technologies and tag capabilities. We also present some of the first results of the diurnal haul-out behaviour of Ross seals during the breeding season.

#### Methods

Study area and animal instrumentation

Ross seals were captured in the King Haakon VII Sea and Lazarev Sea along the coast of Dronning Maud Land (between 69°53.90'–72°19.22'S and 2°0.00'–17°45.96'W, hereafter collectively referred to as the 'eastern Weddell Sea'; Fig. 1) during the South African National Antarctic Expedition S55 (December 2015–February 2016), the German Antarctic Expedition PS111 (January–March 2018) and in two cases in the southern Indian Ocean around ~59°S and 5°–21°E in spring 2019 during the South African Southern Ocean Seasonal Experiment (a.k.a. SCALE; Table S1). Ross seals were captured and

physically restrained on pack-ice floes as the animals were encountered along the cruise track of the SA Agulhas II (2016, 2019) and RV Polarstern (2018). An A-frame net was used to capture the seals; a small hole was cut into the net where the top of the seal's head was located for placement of the satellite transmitter (Wege et al. 2021). Quick-setting Araldite epoxy (AW2101/HW2951) was used to glue the transmitter to the seal's head. Animals from the S55 and PS111 expeditions were in the late or final stages of their annual moult, and loose moulted hair was removed from the animal prior to device attachment. The tagging procedure followed similar methods to those used by Arcalís-Planas et al. (2015). Animals were restrained for a maximum of 1 h (Wege et al. 2021). We determined the sex of the animals while they were physically restrained. We deployed seven (S55: n = 5; PS111: n = 2) SPLASH 10-309A (n = 6) or SPLASH 9 (n = 1); Wildlife Computers, Redmond, WA, USA) dive recorders and eight (S55: n = 6; SCALE: n = 2) ARGOS-linked (CLS, Toulouse, France) satellite-linked tracking devices that also recorded the haul-out behaviour of animals (deployments were either a SPOT 5 or SPOT 6 tag; Wildlife Computers, Redmond, WA, USA; Table S1).

#### Filtering of satellite tracking data

Location data collected through the ARGOS satellite system contain intrinsic errors. To account for this, we fitted a two-state, behaviourally switching, state-space model to individual tracks (Jonsen et al. 2005, Jonsen 2016). This filtered erroneous location estimates and provided interpolated tracks with estimated locations at 3 h time intervals. Bayesian state-space models were fitted using Markov chain Monte Carlo in 'rjags' (https://CRAN.R-project.org/package=rjags) via the 'bsam' library (Jonsen et al. 2005, Jonsen 2016) implemented in R (R Core Team 2021). Two Markov chains were run in parallel, each of 55 000 iterations, only using every 50th value, while the first 10 000 values (i.e. burn-in) were excluded. Diagnostic plots were used to assess converging and appropriate mixing of the two Markov chains (Jonsen et al. 2013). Further details on this procedure can be read in Wege et al. (2021).

## Dive and haul-out data analyses

Satellite-transmitted dive data were collected in 4 h blocks and stored in 14 bins of histogram distributions; time

**Table I.** Cut-off values for each of the dive parameters and their respective 14 bins.

Parameter	Bin1	Bin2	Bin3	Bin4	Bin5	Bin6	Bin7	Bin8	Bin9	Bin10	Bin11	Bin12	Bin13	Bin14
Dive depth (m)	5	10	50	100	150	200	250	300	350	400	450	500	600	> 600
Dive duration (min)	0.5	2	4	6	8	10	12	14	16	18	20	25	30	> 30
Time at depth (m)	5	10	50	100	150	200	250	300	350	400	450	500	600	> 600

blocks started at 00h00, 04h00, 08h00, 12h00, 16h00 and 20h00 GMT, respectively. Within each time block the number of dives within the 14 bins were recorded for maximum dive depth (m), dive duration (min) and time at depth (min at m). The tags' programmed upper limits for each bin of the four variables are given in Table I. Haul-out behaviour was measured as the duration that the conductivity sensor recorded as being dry at 90 s intervals and again measured as being wet for consecutive transmission intervals to 50 s. This interval of time was then transformed into the percentage per hour during which the tag was wet, resulting in 24 bins (1 per hour in the day). The hourly percentages sent via satellite were not always consecutive, and not all dives

binned per day were received. Therefore, to avoid any bias in the data favouring hours that received the most transmissions, we removed all observations where not all 24 h bins were received for a particular day per tag.

Data were extracted using Wildlife Computers' software WC-DAP (V.3.0.363). To calculate the mean depth and duration per 4 h bin period, the range midpoint of each bin and the lower limit of the largest bin were used (Thomton et al. 2008, Lea et al. 2010, Sterling et al. 2014). To exclude surface and resting behaviour, only dives deeper than 5 m and longer than 30 s were included in the analyses, which involved discarded data from Bin 1 (Womble et al. 2013). Within each 4 h block, we calculated the mean depth and duration for each bin

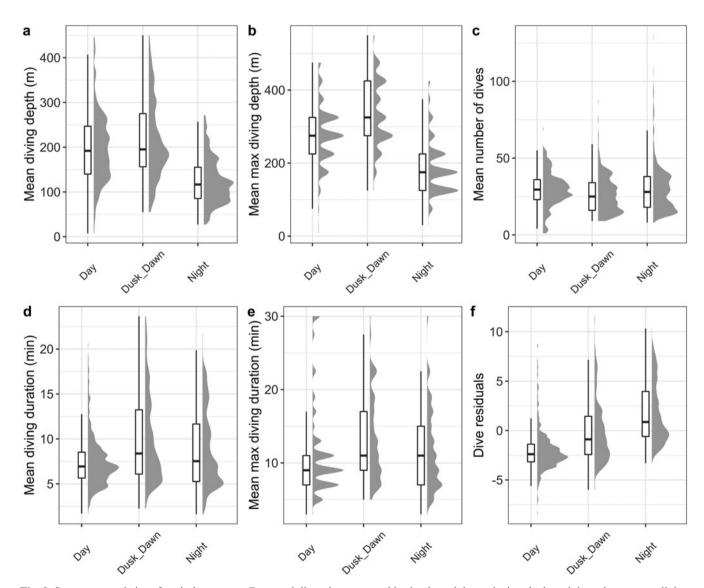


Fig. 2. Summary statistics of variation among Ross seal dives that occurred in the day, night or during dusk and dawn in a. mean diving depth (m), b. mean maximum diving depth (m), c. mean number of dives, d. mean diving duration (min), e. mean maximum diving duration (min) and f. dive residuals.

following Lea et al. (2010):

$$\{[Freq(b_2) \times midpoint(b_2)] + \ldots + [Freq(b_{14}) \times midpoint(b_{14})\} \Sigma [Freq(b_2;b_{14})]$$

where  $b_2$  to  $b_{14}$  represent the dive depth, dive duration or time at depth bin values.

Maximum dive depth and duration were calculated as the midpoint of the largest bin for each of the 4 h blocks (Lea *et al.* 2010); number of dives was calculated as the sum of dives of each bin. The 4 h binned data were recorded according to GMT time. Local apparent time, sunset time and sunrise time for each of the bins were subsequently calculated using the 'maptools' library in *R* (https://CRAN.R-project.org/package=maptools). All other analyses were conducted in *R* (R Core Team 2021).

As a proxy for diving effort, we calculated a 'dive residual' following Bestley *et al.* (2015). The ascent and descent phases of a dive will increase in duration with depth; the dive residual will indicate whether, for that

given depth, the dive was longer or shorter than expected. Relatively longer dives potentially indicate a higher relative effort while foraging (Bestley *et al.* 2015). Dive residuals were the Pearson residuals from a linear mixed-effect model of the relationship between dive duration and dive depth. Individual seal identification was included as the model's random effect and fixed effect and was fitted via restricted maximum-likelihood estimation in *R* (R Core Team 2021) using package 'nlme' (https://cran.r-project.org/package=nlme).

#### Results

Of the seven dive recorders deployed, two failed within 5 days and the individuals made no dives. We present diving and time-at-depth data from the remaining five animals, the tracks of which lasted 35–253 days. Haul-out behaviour is presented for nine animals, which lasted 35–348 days. With the various combinations of dive and haul-out recorders, we have data for ten Ross seals (eight females, two males). Exploratory data

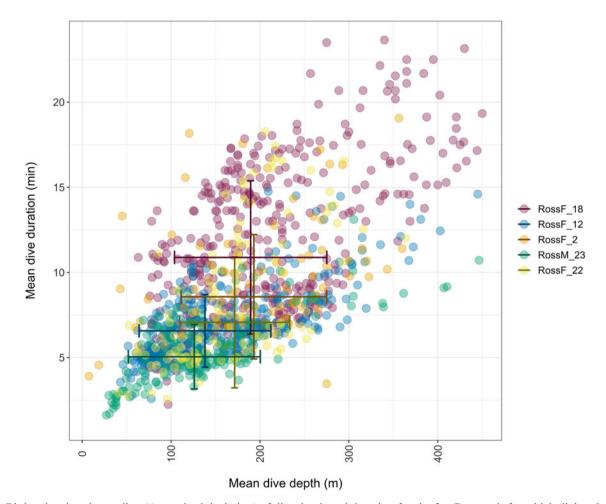


Fig. 3. Biplot showing the median (± standard deviation) of dive depth and duration for the five Ross seals for which diving data were recorded. Raw diving depths and durations are plotted in the background. Different colours represent different individuals.

analysis and non-linear mixed-effects modelling, using diving and haul-out variables as response variables and environmental cues as predictor variables, showed that individual variation overshadowed most of the other model effects. Models fitted poorly and did not meet model assumptions. The large individual variation is most probably a by-product of the small sample size of animals and precluded any feasible analyses. We therefore opted to present exploratory plots and summary results of Ross seal diving and haul-out behaviour.

The deepest dive was 752 m by RossF\_18 in the 08h00-12h00 bin. There were 46 dives of  $\geq 30 \text{ min}$  duration, of which 42 were made by RossF\_18 and 4 by RossF\_2, spread out across the entire day. Mean and maximum diving depth followed a diurnal pattern, where dives were deeper during dusk and dawn, followed closely by day dives, but all were deeper than night dives

(Fig. 2a & b). Mean and maximum dive duration, however, was longer at dusk and dawn, but only slightly longer than night dives, with day dives being the shortest (Fig. 2d & e). The mean number of dives were similar across the daily cycle (Fig. 2c), but interestingly the diving residuals were highest at night, followed by at dusk and dawn and lastly by day dives (Fig. 2f). The variation of diving means, maximum depth and duration, dive residuals and number of dives across the months showed that the diurnal patterns persisted mostly in the months when Ross seals were foraging pelagically but not during the entire year (Fig. S1). Individual variation in diving depth and duration (Fig. 3) and a small sample size obscured any potential variation in diving variables among months and/or latitude. Visually, there are no clear patterns as to whether any of the dive metrics changed spatially (Fig. S2). Despite the variation

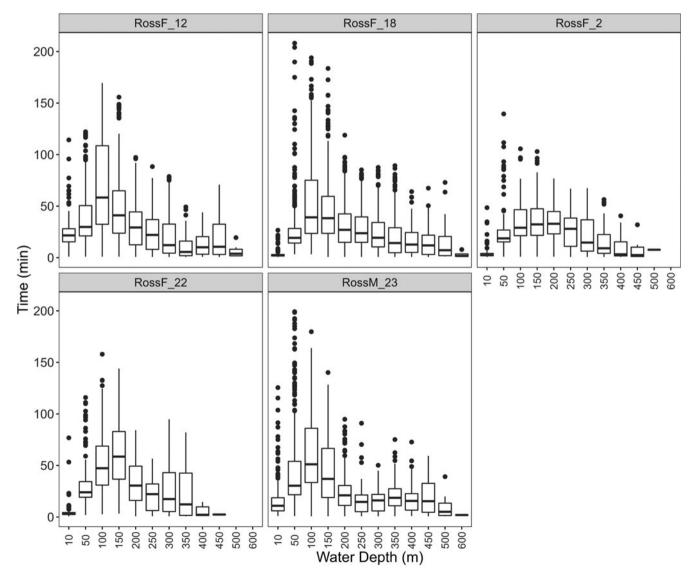


Fig. 4. Time (min) spent at depth (m) for each of the Ross seals for which diving data were recorded.

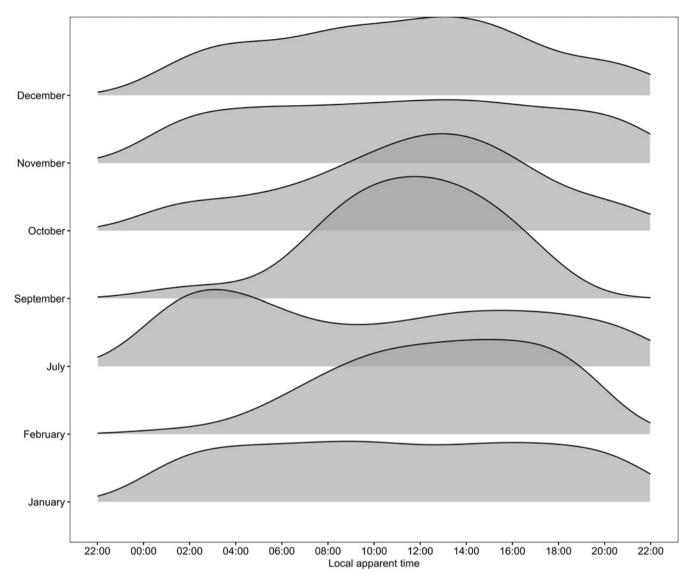


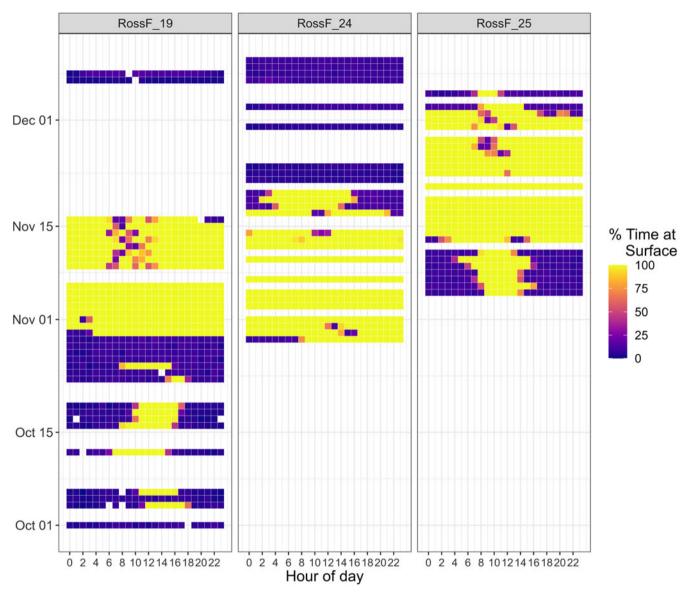
Fig. 5. Monthly frequency density ridges across the day for the relative amount of time Ross seals spent hauled out (i.e. > 75% of an hour hauled out). March and April were excluded because Ross seals were exclusively in open water and were never close to ice to haul out during these months. May, June and August were excluded because Ross seals hardly hauled out during these months and too few animals were sampled during these months.

in diving metrics among individuals, the depth at which Ross seals spent most of their time while diving was centred at  $\sim 100-200$  m depth (Fig. 4).

## Haul-out behaviour

Ross seals were preferentially hauled out in the middle of the day in September, October, February and, to a lesser extent, December (Fig. 5). There was no diurnal variation in haul-out behaviour in January, November or July (Fig. 5). March–May, June and August were excluded from these plots because Ross seals are in the open ocean and few haul-out data exit for these months. Three females returned to the ice during the breeding

season and hauled out presumably to breed. RossF\_19 hauled out on 30 October and remained at the surface until 2 November, when it spent ~2 h in the water, then remained at the surface until 9 November, after which she alternated between short ~1–2 h sojourns into the water and being hauled out between 05h00 and 12h00 (Fig. 6). After 16 November, she travelled north towards the Polar Front again and was submerged the entire time (Fig. 6). RossF\_24 hauled out on 28 October and remained at the surface until 14 November; during this time, she made six 2–3 h trips into the water. RossF\_25 hauled out on 12 November and remained hauled out until 1 December; during this time, she made seven 1–4 h trips into the water, all between 06h00 and 12h00



**Fig. 6.** Hourly haul-out percentages for three female Ross seals during the assumed breeding season haul out (October to mid-December). Gaps in the graph represent missing data that were not transmitted via satellite. Note that RossF\_24 and RossF\_25 only received their tags on 27 October and 2 November 2019, respectively.

(Fig. 6). The values presented represent the percentage of time spent at the surface, but females were not always in the water for the entire hour (i.e. the tag recorded 100% being wet for that hour). We do not have direct evidence as to whether these females produced pups or not.

## Discussion

#### Diving behaviour

This study reports on diving data (n = 5) and haul-out data (n = 9) of Ross seals in the eastern Weddell Sea. These Ross seals mostly dived between 100 and 200 m deep, but they often dived deeper than 300 m, and one seal

recorded a dive to 728 m depth (Table S2). In previous studies, Ross seals also dived to depths of 100–300 m, occasionally reaching depths of close to 800 m (Bengtson & Stewart 1997, Southwell 2003, Blix & Nordøy 2007). Our sample size was too small and individual variation too high to perform any meaningful statistical analyses, but exploratory data analyses showed that the five Ross seals dived deeper during dusk and dawn and shallowest during night (Fig. 2a & b). Diurnal variation of diving depth changed monthly (Figs S1–S3), and the Ross seals only dived deeper during the day and shallower at night from March to July. Diving depth did not vary diurnally in January and February, when the Ross seals were close to the Antarctic continent and

undergoing their annual moult. This is in contrast with Bengtson & Stewart (1997), where a single female exclusively dived at night over 2 days in January 1987, making deeper crepuscular dives. Blix & Nordøy (2007) also showed that during summer Ross seals also did not necessarily dive deeper in the day than during the night. Diurnal variation in diving behaviour happens in response to vertical migration of prey, whereby prey migrate to the sea surface at night (Banse 1964, Luo et al. 2000, Aumont et al. 2018). Between late December and February, Ross seals have been found in the consolidated pack ice close to the Antarctic ice shelf (Bester et al. 1995, Wege et al. 2021). It is probable that because there is nearly 24 h of continuous light during this period, this results in desynchronized vertical movements of prey (Cohen & Forward 2009), which in this case ultimately affected Ross seal diurnal diving patterns. From May to July, Ross seals reside in the open ocean and it is dark for long periods of the 24 h daily cycle. Ross seals then follow the diurnal diving pattern in response to the movements of their prey. Interestingly, the number of dives did not follow a clear diurnal pattern (Figs 2c-f & S1), which is in contrast to crabeater seals, their pack-ice counterparts, which demonstrate diurnal variations in diving frequency across the year (Burns et al. 2004). Why diving effort (dive residuals) was highest at night is currently unknown. We suggest that the seals are potentially reaching their aerobic dive limit and therefore their dive duration is limited (Kooyman et al. 1980). However, this would require further investigation.

The single male Ross seal for which diving behaviour was recorded, typically made the shortest dives (Fig. 3), but not the shallowest dives. Although dive depth and duration are species, gender and area specific in some cases, larger body sized pinnipeds typically dive deeper and longer than smaller pinnipeds (Mori 2002, Schreer et al. 2001). Given that male Ross seals are typically smaller than females (Skinner & Klages 1994), body size could explain the male's shorter dives. Similarly, dive depth and duration are scaled with body mass in many air-breathing marine vertebrates (Schreer et al. 2001); perhaps with a larger sample size data will show that female Ross seals dive deeper and longer than males.

## Haul-out behaviour

Contrary to Blix & Nordøy (2007), we found no diurnal haul-out behaviour in the tracked Ross seals in January (Fig. 5). In fact, during the PS111 expedition in 2018, we observed seven Ross seals hauled out in a single night (31 January–1 February 2018) between the hours of 23h00 and 05h00, and then a further six Ross seals during midday of 1 February 2018 between 12h00 and 14h00 local time. In the Amundsen Sea, only one out of

four tracked Ross seals showed a peak haul-out time at approximately midday (Arcalís-Planas *et al.* 2015) during December–January. Ross seals might exhibit a bimodal haul-out behaviour pattern similar to that of Weddell seals (Boehme *et al.* 2016). However, in September and October, when there are distinct day/night phases, the tracked Ross seals showed a diurnal haul-out pattern (Fig. 5) similar to the findings of Arcalís-Planas *et al.* (2015).

## Breeding season

Ross seals breed between late October and early December, with pups sighted as early as 2 October and as late as 22 November (Southwell et al. 2003) - with an outlier at the South Sandwich Islands on 6 December (Solyanik 1964). Blix & Nordøy (2007) showed that three potentially breeding females travelled south and entered the pack ice in early October and then hauled out continuously on the ice to most probably pup and breed. They estimated 13 days for Ross seal lactation duration. The movement and haul-out data from the three potential breeding females in our study show that they occasionally enter the water for 1-3 h during the breeding period (Fig. 6), and all females spent a maximum of 7-9 days continuously hauled out at any given time. Arcalís-Planas et al. (2015) also found that during the breeding season one seal hauled out continuously for 8 days and thereafter spent only 90% of its time on the ice over the following 10 days, while another female seal only spent 35% of its time hauled out during the breeding season, even though it was in the pack ice (Arcalís-Planas et al. 2015). Similarly to Blix & Nordøy (2007) and Arcalís-Planas et al. (2015), we have no evidence that these three females had indeed pupped. But typically, these breeding females would return northwards towards the area south of the Polar Front immediately post-breeding to forage before they travelled south towards the Antarctic continent in early January for the annual moult (Blix & Nordøy 2007, Arcalís-Planas et al. 2015, Wege et al. 2021). That the three females in this study remained hauled out on the ice for extended periods of time suggests that they may have been nursing pups. Their entering the water periodically may suggest that Ross seals could potentially use an alternating breeding strategy in which some individuals are capital breeders (and perhaps are in good condition) who remain hauled out with their pups until weaning or become facultative income breeders (perhaps those who are in poorer physical condition) that enter the water during pup rearing, similar to what is found in Weddell seals (Wheatley et al. 2008). However, Weddell seals breed on the fast ice that is more sheltered from potential predators (e.g. killer whales (Orcinus orca)) compared to Ross seals that breed on the

pack ice and might not want to enter the water during pup rearing for fear of predation of their pups. Alternatively, these females could have remained on the pack ice to mate. No observations exist on Ross seal mating behaviour, but King (1983) examined the reproductive tracts of female Ross seals and suggested that mating possibly occurred at the end of December. On the Eckström Ice Shelf near the eastern Weddell Sea coast. the Perennial Acoustic Observatory in the Antarctic Ocean (PALAOA; a stationary listening station) has recorded some Ross seal vocalizations in December (mainly from mid-December). The number of Ross seal vocalizations increased rapidly from January (Van Opzeeland et al. 2010), when tracking data show Ross seals returning for their annual moult (Blix & Nordøy 2007, Wege et al. 2021). However, tracking data show that after the breeding haul-out females almost immediately travelled northwards out of the pack ice (Blix & Nordøy 2007, Arcalís-Planas et al. 2015, Wege et al. 2021), which would then suggest that either breeding would happen pelagically out of the ice, which is improbable given the low likelihood of finding potential breeding mates, or that breeding occurred on the pack ice or nearby in the water soon after/before weaning of the pup. In this study, a male (RossM\_21) also travelled south towards the pack ice at the start of October (Fig. 1). The male was hauled out on the ice for a day before its tracker unfortunately stopped working. Although we cannot determine how long he was hauled out, this is the first evidence for a male entering the ice in the same period as females during the breeding season, which would probably suggest that mating happens at the same time as the pupping period and contradicts King (1983). This is also in line with genetic evidence from Ross seals that suggests that they are not polygynous (Curtis et al. 2011).

#### Conclusion

Here, we presented the results of only the fifth study on Ross seals' diving and haul-out behaviour (Bengtson & Stewart 1997, Southwell 2003, Blix & Nordøy 2007, Arcalís-Planas *et al.* 2015, this publication). In all of the aforementioned investigations, the available sample size of instrumented animals never exceeded ten, and as a consequence of this small sample size, the interpretation of the data is limited to observational descriptions because individual variation is too high to draw comprehensive conclusions for the species as a whole. For example, the timing and duration of the Ross seal breeding season are still not definitively known. This limitation derives from the Ross seals' commuting behaviour to and from pelagic foraging areas north of the pack ice, where they remain inaccessible in the open

ocean for most of the year (Blix & Nordøy 2007, Arcalís-Planas et al. 2015, Wege et al. 2021). Furthermore, the deployment of biologging devices is limited to the spring and summer when the seals return to the pack ice to breed and moult very briefly; here, they prefer dense concentrations of interior pack ice (Condy 1977, Bester et al. 2019), making it difficult to access them. However, advances in determining the distribution and abundances of Ross seals (Bengtson et al. 2011, Southwell et al. 2012, Gurarie et al. 2017) and the identification of areas where Ross seals can predictably be found (Blix & Nordøy 2007, Bester et al. 2020, 2021) invite further investigations. We suggest that an initiative for a coordinated, multinational, circumpolar, synchronous, comprehensive investigation into the ecology of the Ross seal is needed, especially in view of the United Nations Decade of Ocean Science and Sustainable Development (2021–2030; www.oceandecade.org).

## Data availability

All primary dive and haul-out data are publicly available and can be found at https://doi.pangaea.de/10.1594/PANGAEA.

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#### **Ethical standards**

The University of Pretoria Animal Ethics Committee cleared the procedures of this project (Number EC082-15) under South African Department of Environmental Affairs Permit 04/2015-2016, pursuant to the provisions of Article 3 of the Protocol on Environmental Protection to the Antarctic Treaty and Annex II and Annex V (Article 10(2)).

#### **Author contributions**

MNB, HB and MW contributed funding and collected the new data. MW analysed the data and wrote the first draft. All authors edited and contributed intellectual input to the final manuscript.

## Supplemental material

Four supplemental figures and two supplemental tables will be found at https://doi.org/10.1017/S0954102022000438.

#### References

- ARCALÍS-PLANAS, A., SVEEGAARD, S., KARLSSON, O., HARDING, K.C., WÂHLIN, A., HARKONEN, T., et al. 2015. Limited use of sea ice by the Ross seal (*Ommatophoca rossii*), in Amundsen Sea, Antarctica, using telemetry and remote sensing data. *Polar Biology*, 38, 10.1007/s00300-014-1602-y.
- Aumont, O., Maury, O., Lefort, S. & Bopp, L. 2018. Evaluating the potential impacts of the diurnal vertical migration by marine organisms on marine biogeochemistry. *Global Biogeochemical Cycles*, **32**, 10.1029/2018GB005886.
- Banse, K. 1964. On the vertical distribution of zooplankton in the sea. *Progress in Oceanography*, **2**, 55–125.
- Bengtson, J.L. & Stewart, B.S. 1997. Diving patterns of a Ross seal (*Ommatophoca rossii*) near the eastern coast of the Antarctic Peninsula. *Polar Biology*, **18**, 214–218.
- Bengtson, J.L., Laake, J.L., Boveng, P.L., Cameron, M.F., Bradley Hanson, M. & Stewart, B.S. 2011. Distribution, density, and abundance of pack-ice seals in the Amundsen and Ross Seas, Antarctica. *Deep-Sea Research II: Topical Studies in Oceanography*, 58, 10.1016/j.dsr2.2010.10.037.
- Bester, M.N., Erickson, A. & Ferguson, J.W.H. 1995. Seasonal change in the distribution and density of seals in the pack ice off Princess Martha Coast, Antarctica. *Antarctic Science*, 7, 357–364.
- Bester, M.N., Wege, M., Oosthuizen, W.C. & Bornemann, H. 2020. Ross seal distribution in the Weddell Sea: fact and fallacy. *Polar Biology*, **43**, 10.1007/s00300-019-02610-4.
- Bester, M.N., Lübcker, N., Haddad, W., Bornemann, H. & Wege, M. 2021. Antarctic pack ice seal observations during spring across the Lazarev Sea. *Polar Record*, **57**, 10.1017/S003224742100005X.
- Bester, M.N., Wege, M., Lübcker, N., Postma, M. & Syndercombe, G. 2019. Opportunistic ship-based census of pack ice seals in eastern Weddell Sea, Antarctica. *Polar Biology*, **42**, 10.1007/s00300-018-2401-7.

- Bestley, S., Jonsen, I.D., Hindell, M.A., Harcourt, R.G. & Gales, N.J. 2015. Taking animal tracking to new depths: synthesizing horizontal-vertical movement relationships for four marine predators. *Ecology*, **96**, 410.1890/14-0469.1.
- BLIX, A.S. & NORDØY, E.S. 2007. Ross seal (*Ommatophoca rossii*) annual distribution, diving behaviour, breeding and moulting, off Queen Maud Land, Antarctica. *Polar Biology*, **30**, 10.1007/s00300-007-0306-y.
- BOEHME, L., BAKER, A., FEDAK, M.A., MARIUS, Å., NICHOLLS, K., ROBINSON, P., *et al.* 2016. Bimodal winter haul-out patterns of adult Weddell seals (*Leptonychotes weddellii*) in the southern Weddell Sea. *PLoS ONE*, **11**, 10.1371/journal.pone.0155817.
- Bornemann, H., Mohr, E., Plötz, J. & Krause, G. 1998. The tide as zeitgeber for Weddell seals. *Polar Biology*, **20**, 10.1007/s00300050320.
- Brault, E.K., Koch, P.L., Costa, D.P., McCarthy, M.D., Hückstädt, L.A., Goetz, K.T., *et al.* 2019. Trophic position and foraging ecology of Ross, Weddell, and crabeater seals revealed by compound-specific isotope analysis. *Marine Ecology Progress Series*, **611**, 10.3354/meps12856.
- Burns, J.M., Costa, D.P., Fedak, M.A., Hindell, M.A., Bradshaw, C.J.A., Gales, N.J., et al. 2004. Winter habitat use and foraging behavior of crabeater seals along the western Antarctic Peninsula. Deep-Sea Research II: Topical Studies in Oceanography, 51, 10.1016/j.dsr2.2004.07.021.
- COHEN, J.H. & FORWARD, R.B.J. 2009. Zooplankton Diel vertical migration - a review of proximate control. *In Gibson*, R.N., ATKINSON, R.J.A. & GORDON, J.D.M., *eds. Oceanography and marine biology* (1st edition). Boca Raton, FL: CRC Press, 77–109.
- CONDY, P.R. 1977. Results of the fourth seal survey in the King Haakon VII Sea, Antarctica. South African Journal of Antactic Research, 7, 10–13.
- Costa, D.P. & Gales, N.J. 2003. Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecological Monographs*, **73**, 27–43.
- CROXALL, J.P., EVERSON, I., KOOYMAN, G.L., RICKETTS, C. & DAVIS, R.W. 1985. Fur seal diving behaviour in relation to vertical distribution of krill. *Journal of Animal Ecology*, 54, 1–8.
- Curtis, C., Stewart, B.S. & Karl, S.A. 2011. Genetically effective population sizes of Antarctic seals estimated from nuclear genes. *Conservation Genetics*, **12**, 10.1007/s10592-011-0241-x.
- Gurarie, E., Bengtson, J.L., Bester, M.N., Blix, A.S., Cameron, M., Bornemann, H., *et al.* 2017. Distribution, density and abundance of Antarctic ice seals off Queen Maud Land and the eastern Weddell Sea. *Polar Biology*, **40**, 10.1007/s00300-016-2029-4.
- JONSEN, I.D. 2016. Joint estimation over multiple individuals improves behavioural state inference from animal movement data. *Scientific Reports*, 6, 10.1038/srep20625.
- JONSEN, I.D., FLEMMING, J.M. & MYERS, R.A. 2005. Robust statespace modeling of animal movement data. *Ecology*, 86, 10.1890/ 04-1852.
- JONSEN, I.D., BASSON, M., BESTLEY, S., BRAVINGTON, M.V., PATTERSON, T.A., PEDERSEN, M.W., et al. 2013. State-space models for bio-loggers: a methodological road map. Deep-Sea Research II: Topical Studies in Oceanography, 88–89, 10.1016/j.dsr2.2012.07.008.
- King, J E. 1983. Seals of the world. Brisbane: University of Queensland Press, 240 pp.
- KOOYMAN, G.L., WAHRENBROCK, E.A., CASTELLINI, M.A., DAVIS, R.W. & SINNETT, E.E. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. *Journal of Comparative Physiology B*, **138**, 335–346.
- Lea, M.A., Johnson, D.S., Melin, S., Ream, R.R. & Gelatt, T. 2010. Diving ontogeny and lunar responses in a highly migratory mammal, the northern fur seal *Callorhimus ursinus*. *Marine Ecology Progress Series*, **419**, 10.3354/meps08758.

Luo, J., Ortner, P.B., Forcucci, D. & Cummings, S.R. 2000. Diel vertical migration of zooplankton and mesopelagic fish in the Arabian Sea. *Deep-Sea Research II: Topical Studies in Oceanography*, 47, 10.1016/S0967-0645(99)00150-2.

- MORI, Y. 2002. Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology*, **15**, 10.1046/j.1420-9101.2002.00382.x.
- ØRITSLAND, T. 1977. Food consumption of seals in the Antarctic pack ice.
   In Llano, G.A., ed. Adaptations within Antarctic ecosystems.
   Washington, DC: Smithsonian Institute, 749–768.
- Orsi, A.H., Whitworth, T. & Nowlin, W.D. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Research I: Oceanographic Research Papers*, **42**, 10.1016/0967-0637 (95)00021-W.
- R Core Team 2021. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org.
- RIEDMAN, M. 1990. *The pinnipeds: seals, sea lions, and walruses* (Issue 12). Berkeley, CA: University of California Press, 439 pp.
- SCHREER, J.F., KOVACS, K.M. & O'HARA HINES, R.J. 2001. Comparative diving patterns of pinnipeds and seabirds. *Ecological Monographs*, 71, 10.1890/0012-9615.
- SKINNER, J.D. & KLAGES, N.T.W. 1994. On some aspects of the biology of the Ross seal *Ommatophoca rossii* from King Haakon VII Sea, Antarctica. *Polar Biology*, 14, 467–472.
- SOLYANIK, G.A. 1964. Experiment in marking seals from small ships. Soviet Antarctic Expedition Bulletin, 5, 212.
- SOUTHWELL, C.J. 2003. Haul-out behaviour of two Ross seals off eastern Antarctica. *Antarctic Science*, **15**, 10.1017/S0954102003001251.

- Southwell, C.J., Kerry, K., Ensor, P., Woehler, E.J. & Rogers, T.L. 2003. The timing of pupping by pack-ice seals in East Antarctica. *Polar Biology*, **26**, 10.1007/s00300-003-0534-8.
- SOUTHWELL, C.J., BENGTSON, J.L., BESTER, M.N., BLIX, A.S., BORNEMANN, H., BOVENG, P.L., et al. 2012. A review of data on abundance, trends in abundance, habitat use and diet of ice-breeding seals in the Southern Ocean. CCAMLR Science, 19, 1–26.
- STERLING, J.T., SPRINGER, A.M., IVERSON, S.J., JOHNSON, S.P., PELLAND, N.A., JOHNSON, D.S., et al. 2014. The sun, moon, wind, and biological imperative-shaping contrasting wintertime migration and foraging strategies of adult male and female northern fur seals (*Callorhinus ursinus*). PLoS ONE, 9, 10.1371/journal.pone.0093068.
- THOMTON, J.D., MELLISH, J.A.E., HENNEN, D.R. & HORNING, M. 2008. Juvenile Steller sea lion dive behavior following temporary captivity. *Endangered Species Research*, 4, 10.3354/esr00062.
- VAN OPZEELAND, I., VAN PARIJS, S., BORNEMANN, H., FRICKENHAUS, S., KINDERMANN, L., KLINCK, H., et al. 2010. Acoustic ecology of Antarctic pinnipeds. Marine Ecology Progress Series, 414, 10.3354/meps08683.
- WEGE, M., BORNEMANN, H., BLIX, A S., NORDØY, E.S., BIDDLE, L. & BESTER, M.N. 2021. Distribution and habitat suitability of Ross seals in a warming ocean. *Frontiers in Marine Science*, 8, 10.3389/ fmars.2021.659430.
- WHEATLEY, K.E., BRADSHAW, C.J.A., HARCOURT, R.G. & HINDELL, M.A. 2008. Feast or famine: evidence for mixed capital-income breeding strategies in Weddell seals. *Oecologia*, 155, 11–20).
- Womble, J.N., Horning, M., Lea, M.A. & Rehberg, M.J. 2013. Diving into the analysis of time-depth recorder and behavioural data records: a workshop summary. *Deep-Sea Research II: Topical Studies in Oceanography*, 88–89, 10.1016/j.dsr2.2012.07.017.