



## Early diving behavior in Weddell seal (*Leptonychotes weddellii*) pups

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During the dependency period in mammals with parental care, offspring must develop the behavioral skills that allow them to forage independently and thus survive into early adulthood. Deep-diving Weddell seals (*Leptonychotes weddellii*) are a model species for research on diving physiology, yet previous studies lack a thorough investigation into the diving behavior of dependent pups when they first begin to enter the water. To capture fine-scale dive behavior during the dependency period, we deployed time-depth recorders (TDRs) on Weddell seal pups ( $n = 18$ ) from the age of 1 week through 7 weeks, during the 2017 and 2019 breeding seasons in McMurdo Sound, Antarctica. Dive parameters were correlated with time of day, age, sex, and weaning status, to characterize diving behavior, and we used raw wet/dry data to determine which times of the day pups were most likely to be in the water. Pups made their deepest and longest dives and had the longest post-dive durations in the morning hours. Pups were in the water more during the late night and morning hours than in the afternoon. Whereas dive depth significantly increased with age, dive duration significantly increased with age and after weaning. Post-dive duration significantly decreased with age and after weaning. We discuss how dependent pups may prioritize the development of swimming and navigational abilities as opposed to building and practicing foraging skills.

Key words: Antarctic, dive development, dive duration, phocid

In animals with parental care, becoming nutritionally independent is a critical life-history stage. During the dependency period, offspring must develop the physiological and behavioral capabilities required to successfully forage on their own and survive in adulthood (Kooyman et al. 1980; Bernardo 1996; Boness and Bowen 1996; Burns 1999; Burns et al. 1999; Vázquez-Medina et al. 2006). Among phocid (true seal) pups, there is interspecific variation in the timing of the first water entry as well as the amount of behavioral input pups receive from their mothers. Phocid species such as Weddell seals (*Leptonychotes weddellii*, 6-week dependency), ringed seals (*Pusa hispida*, 6 weeks), and bearded seals (*Erignathus barbatus*, 24 days) exhibit aquatic behavior while dependent, whereas hooded seals (*Cystophora cristata*, 4-day dependency), harp seals (*Pagophilus groenlandicus*, 12 days), and elephant seals (*Mirounga angustirostris*, 28 days) typically do not enter the water until after a postweaning fast (Lydersen and Kovacs 1999; McDonough 2010). These strategies result in well-documented differences in physiological development of pups at weaning (Burns et al. 2004, 2007; Noren et al. 2005; Clark et al. 2006, 2007; Richmond et al. 2006), but the impact on the behavioral development of pups is not as well

understood. In particular, the speed and timing of development of diving skills is not well known for the young of species that live in environments that are difficult to access. In polar regions, climate change is altering sea ice habitat rapidly (e.g., sea ice thickness and extent, early ice breakup, increased storm events—Turner et al. 2015; Ogawa et al. 2018). Changes in habitat suitability decrease population health, specifically because of declines in juvenile survival (Lindström 1999; Stearns 2000; Durant et al. 2007; Friedlaender et al. 2010). Thus, fine-scale data are needed to determine how early in life animals exhibit behavioral traits needed to successfully transition to independence to predict how environmental shifts may affect the timing and success of early development and ultimately survival of young seals.

Understanding the overall process of development is particularly important in a species such as the Weddell seal, as development occurs in an extremely cold environment over several weeks. Weddell seals exhibit early aquatic behaviors while dependent on their mother (Stirling 1969; Burns and Testa 1997; Burns 1999; Burns et al. 1999). This early experience likely results in a trade-off between gaining diving experience and allocating energy to growth and development.

Further, Weddell seals have one of the longest dependency periods among phocids (McDonough 2010), which may reflect the extended time needed to develop in an extreme environment and may allow pups to develop behaviors similar to those of adults during this time. It is hypothesized that Weddell seal mothers “teach” their pups to dive and forage, and pups have been observed following their mothers on dives (Sato et al. 2002, 2003). Although Weddell seal pups do not visit the same foraging grounds of adults (with respect to depth or geographic location), early practice of the skills they will need to use to successfully transition to nutritional independence likely is beneficial to their overall survival (Sato et al. 2003).

Fine-scale dive behaviors of dependent Weddell seals, particularly around the time they first enter the water, still are unknown. Burns and Testa (1997) began studying dive behavior of Weddell seal pups at 2 weeks of age and collected depth data every 10 s for a few days every 2 weeks. Sato et al. (2003) collected higher-resolution data with depth recordings every 1 s, but tags were attached to pups between the ages of 20–31 days old for 15 days. The lack of continuous, high-resolution data beginning from when pups first enter the water and throughout the dependency period leaves gaps in the understanding of the developments in diving behaviors pups undergo as they begin to dive.

In this study, we used time-depth recorders (TDRs) to collect high-resolution diving data from Weddell seal pups starting at 1 week of age, which is around the time pups first begin to enter the water (Lindsey 1937; Stirling 1969), and throughout nursing, to capture the early diving and behavioral development. We hypothesized that pups would make their deepest and longest dives in the afternoon but would spend more time in the water during the late night and morning hours, because adult, subadult, and yearling Weddell seals make their deepest, longest dives in the afternoon, but spend more time in the water during the late night to early morning hours (Kooyman 1967, 1975; Siniff et al. 1977; Kooyman et al. 1981; Thomas and DeMaster 1983; Testa et al. 1985; Castellini et al. 1992; Testa 1994; Burns and Testa 1997; Burns 1999; Burns et al. 1999). We also hypothesized that we would be able to predict when pups were more likely to be in the water based on time of day, weaning status, and age. Although previous research found no significant diel effect on diving behaviors in young pups when days were split into 6-h time bins (Burns and Testa 1997; Burns and Castellini 1998), we predicted that segmenting the day into 3-h time bins would facilitate detection of any temporal trends.

## MATERIALS AND METHODS

*Study site and animal handling.*—This study was carried out in 2017 and 2019 during the Weddell seal pupping seasons (October–December). Research took place in McMurdo Sound, Erebus Bay, Antarctica (~77°44′42″S, 166°46′26″E). We targeted pups from females that had successfully weaned at least two pups previously, because these females had the greatest likelihood of producing healthy pups (Hadley et al. 2007; Mannas et al. 2011; Chambert et al. 2013, 2014). Information

on mothers and pup date of birth was obtained from the long-term population monitoring study on this population (project B-009), in collaboration with Drs. Rotella and Garrott (Montana State University). Day of birth was determined by daily population surveys. Pups were opportunistically resighted throughout the study period. Weaning was defined as a pup observed alone on three consecutive days.

Pups were separated from their mother using wooden herding boards (~1 m × 0.75 m), then captured in a net. The pup was moved a safe distance (50–100 m) from the mother during handling, and mothers were visually monitored for the duration of the separation. Mother-pup reunions were monitored for at least 30 min to ensure the pair remained bonded. Time spent in the water and diving behavior were recorded with flipper-mounted TDRs (Lotek LAT1800XLFP, 11 g, 13 × 44 mm) attached when pups ( $n = 18$ ) were 1 week of age and retrieved when pups were 7 weeks old, which was at or near the time of weaning. Lidocaine was administered to reduce pain, and TDRs were attached to the interdigital webbing of the hind flippers. All research procedures on live animals followed ASM guidelines (Sikes et al. 2016) and were carried out under National Marine Fisheries Service Permit #21006-01, California Polytechnic State University IACUC #1904, and Antarctic Conservation Act Permit #2018-013 M#1.

*Dive data processing.*—Time-depth recorders were programmed to record pressure every 4 s when wet, at a resolution of 0.5 m. Data from tags were downloaded using Lotek TagTalk software (v. 1.10.9.9). Pressure measurements (dbars) were converted to depths (m), which then were calibrated using a custom function in R that filtered raw data for zero offset correction and extracted discrete dives. A “dive” was defined using a depth threshold of 4 m to account for sea ice thickness and surface noise; only dive depths greater than 4 m were included in analyses, to eliminate any recording taken while the pup was at the surface. Similarly, we only included dives longer than 30 s in duration to filter out short-duration swimming activity near the surface. For each dive, the maximum dive depth (m) was considered the deepest point of the dive, and maximum dive duration (s) was the amount of time between when the pup began the dive (> 4 m) to when the pup resurfaced (< 4 m). Each dive also was associated with a post-dive duration (s), or the amount of time the pup spent at the surface (< 4 m) between consecutive dives. Post-dive durations less than 10 min were included in analyses; after this, post-dive durations in our data set were multiple hours long, indicating that pups were hauled out. Further, we also noted pups did not dive in bouts, which generally is when we would see recovery from long, anaerobic dives in older animals (Kooyman et al. 1980). Thus, we analyzed discrete dives and each dive’s associated recovery (i.e., the surface interval immediately following that dive).

*Statistical analyses.*—All statistical analyses were undertaken using JMP Pro 12 (SAS Institute Inc., Cary, North Carolina) or R (RStudio Team 2018), and  $\alpha = 0.05$  was considered statistically significant. For each pup, we noted the earliest recorded entry into the water and calculated the means of maximum dive depth, maximum dive duration, and

post-dive duration every 2 weeks (i.e., ages 1, 3, 5, and 7 weeks). To do this, values were averaged from 2 days before through 2 days after the target age (1, 3, 5, and 7 weeks old) to account for daily variation in dive behavior and to capture a more comprehensive picture of diving ability. Trends in early dive behavior were analyzed using discrete dives, and the raw wet/dry data were used to determine when pups were most likely to be in the water.

To describe trends in early dive behavior, we ran a series of linear mixed models (LMMs) with a dive parameter (maximum depth of the dive [m], dive duration [s], or post-dive duration in seconds) as the response, animal ID as a random effect, and time of day (3-h bins; Table 1), whether or not the pup was weaned (yes/no), sex, and age as predictor variables, followed by Tukey's HSD test. Response variables were log-transformed to achieve homogeneity of variance in model selection. Age and weaning status were not independent, so the effects of weaning status were analyzed separately from age.

To directly compare our results with those of previous studies (Burns and Testa 1997; Burns and Castellini 1998; Burns and Kooyman 2001), we binned the discrete dives into the same four time periods (6-h bins; Table 1), then ran a LMM with a dive parameter (i.e., maximum dive depth [m], dive duration [s], or post-dive duration [s]) as the response, animal ID as a random effect, and time of day (morning, afternoon, evening, night) as the predictor, followed by Tukey's HSD test. Response variables all were log-transformed to achieve homogeneity of variance in model selection. In addition, we used a Pearson's chi-squared test to characterize differences in dive frequency by time of day (3-h bins; Table 1). For comparison purposes, we only included dives greater than 12 m in depth as this cutoff was used in previous studies (Burns and Testa 1997; Burns and Castellini 1998; Burns and Kooyman 2001).

To determine if age or weaning status affected how much time each pup spent in the water during a given time period, we ran a mixed binary logistic regression with the proportion of time in the water per time period (0–1) as the response, time of day (3-h bins; Table 1), weaned (yes/no), and age (days) included as fixed effects, and animal ID as a random effect. Age and weaning are colinear variables, so these were not included in the same model. This analysis was followed by Tukey's HSD test.

**Table 1.**—Time of day bins used in this study (3 h) and from previous studies (6 h) for comparative purposes (Burns and Testa 1997; Burns and Castellini 1998; Burns and Kooyman 2001).

Time of day (3 h)	Time of day (6 h)	Hours of day
Late night	Night	0001 – 0300
Early morning	Morning	0301 – 0600
Mid-morning	Morning	0601 – 0900
Late morning	Afternoon	0901 – 1200
Early afternoon	Afternoon	1201 – 1500
Early evening	Evening	1501 – 1800
Late evening	Evening	1801 – 2100
Early night	Night	2101 – 2400

## RESULTS

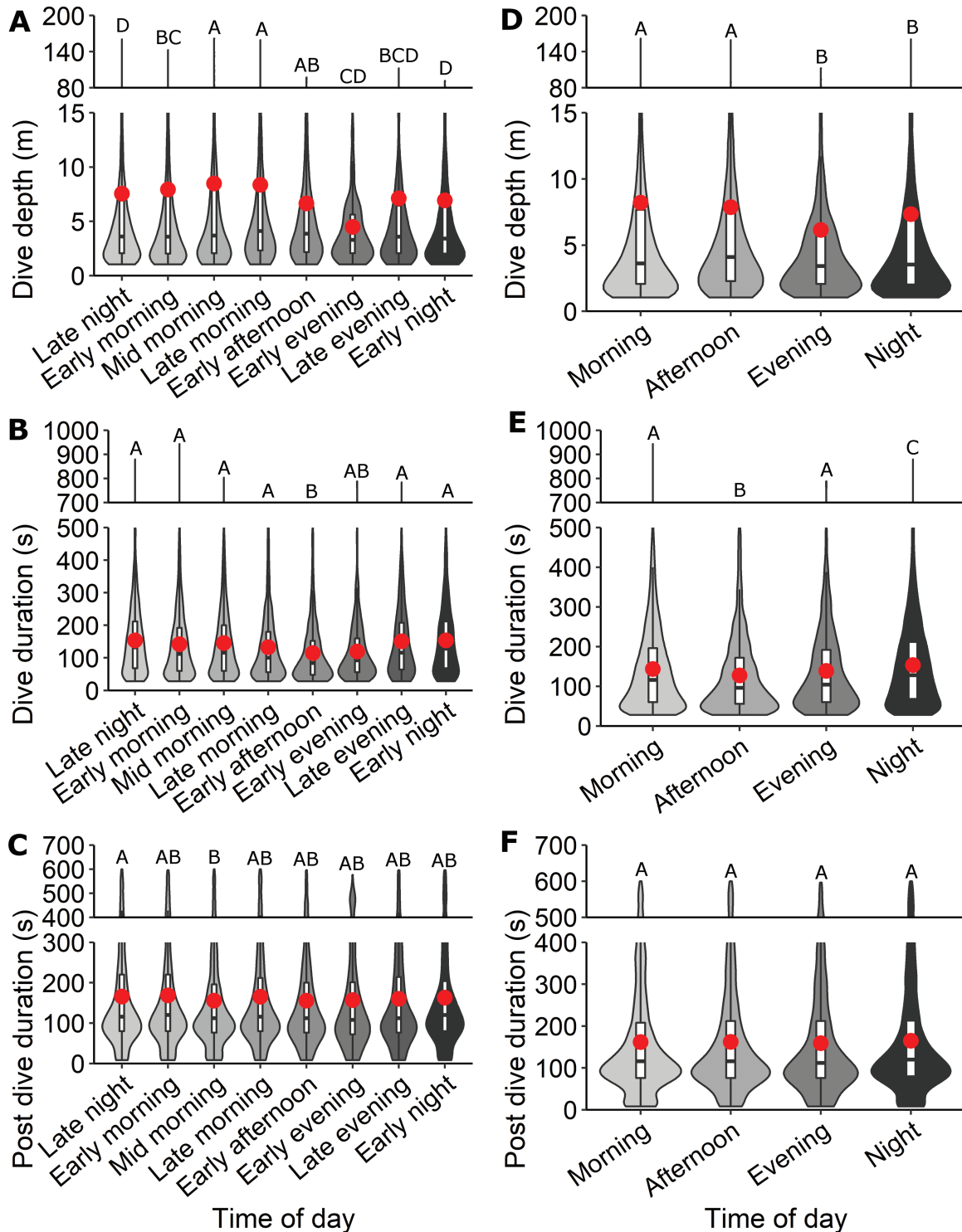
There was no significant effect of sampling year on any of the data analyzed, so both years of data were combined in statistical models. In total, six of the 18 pups were not weaned (i.e., still nursing) at the time of TDR recovery at 7 weeks of age. The range for first TDR-recorded entries into the water was 7 – 16 days old; the average age for a first recorded entry into the water was  $10.25 \pm 3$  days old in 2017 and  $7.7 \pm 0.6$  days old in 2019. Post-dive duration increased significantly with maximum dive depth ( $F_{1,30117} = 840.8, P < 0.0001$ ) and maximum dive duration ( $F_{1,30125} = 497.68, P < 0.0001$ ).

Overall, 39.3% of dives were between 4 and 5 m, 38.65% of dives were between 5 and 10 m, 12.43% were between 10 and 20 m, and 9.64% were > 20 m. Maximum dive depth varied significantly with time of day ( $F_{7,14652} = 20.54, P < 0.001$ ; Table 1; Fig. 1A); with the exception of the early afternoon period, pups dove significantly deeper in the mid- and late morning than in all other times of the day ( $P < 0.0015$ ). Maximum dive depth increased significantly with age ( $F_{1,14658} = 887.11, P < 0.0001$ ; Table 2), but was not significantly correlated with weaning status or sex. Individual variation contributed to nearly 25% of the variation in maximum dive depth, which ranged from 19.9 to 163.8 m. Dive duration also varied significantly with time of day ( $F_{7,14657} = 5.48, P < 0.0001$ ; Fig. 1B); besides the early evening, pups had significantly shorter dive durations in the early afternoon than during any other time of the day ( $P < 0.0251$ ). Dive duration increased significantly with age ( $F_{1,14498} = 752.71, P < 0.0001$ ; Table 2) and after weaning ( $F_{1,14043} = 52.58, P < 0.0001$ ; Table 2); it did not differ significantly between sexes. The maximum dive durations ranged from 30 s to approximately 15 min, although pups in our study only made 37 dives (~2% of dives) that lasted more than 10 min. The average dive duration for all pups was 2.38 min.

Post-dive duration significantly varied by time of day ( $F_{7,12036} = 2.12, P = 0.0377$ ; Fig. 1C), but this was only reflected in significantly longer post-dive durations in the late night than the mid-morning ( $P = 0.0155$ ). Post-dive duration also decreased significantly with age ( $F_{1,9214} = 55.51, P < 0.0001$ ; Table 2) and after weaning ( $F_{1,5056} = 5.59, P = 0.0181$ ; Table 2), but did not vary with sex. The average post-dive duration was 2.71 min.

Using 6-h bins, maximum dive depth still varied significantly by time of day ( $F_{3,14659} = 10.55, P < 0.0001$ ). Maximum dive depth was significantly deeper in the morning and afternoon than during the evening or night ( $P < 0.0254$ ; Fig. 1D). Dive duration also varied significantly by time of day with 6-h bins ( $F_{3,14663} = 33.15, P < 0.0001$ ), with the longest dives occurring at night ( $P < 0.0009$ ), followed by the morning and evening, and the shortest dives occurring during the afternoon ( $P < 0.0036$ ; Fig. 1E). Finally, post-dive duration did not vary significantly with 6-h time bins (Fig. 1F). Dive frequency was significantly different during different times of day ( $\chi^2_{49} = 102704, P < 0.0001$ ), with a greater proportion of dives > 12 m occurring in the morning hours (Fig. 2).

Time of day significantly predicted when pups were more likely to be in the water ( $F_{7,5196} = 132.05, P < 0.0001$ ). All pups spent significantly more time in the water during early morning



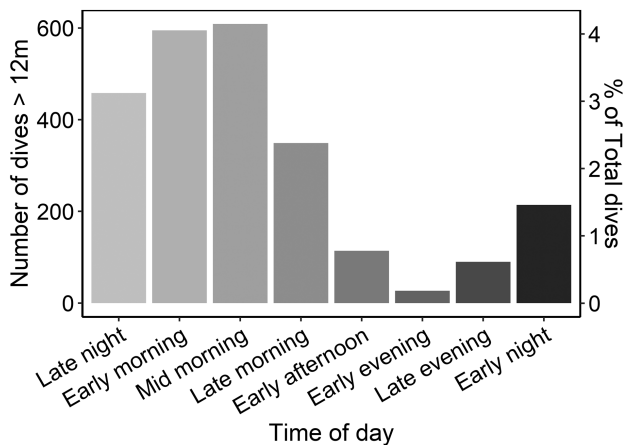
**Fig. 1.**—Dive characteristics of Weddell seal (*Leptonychotes weddellii*) pups ( $n = 18$ ) in McMurdo Sound, Antarctica, in 2017 and 2019. Behavior is divided into 3-h (A–C) and 6-h (D–F) time bins (Table 1). Dive characteristics include: (A, D) maximum dive depth (m); (B, E) maximum dive time (s); and (C, F) post-dive duration (s). All values are graphed as a distribution containing a boxplot showing the median, 25th and 75th percentiles, and the red dot represents the mean. Different letters indicate statistically significant differences based on Tukey's HSD post hoc test.

( $43.52 \pm 1.62\%$ ; Table 1) than any other time of the day ( $P < 0.0317$ ; Fig. 3). After the early morning, pups spent the most time in the water during the adjacent late night and mid-morning periods, followed by the more distant late morning and early night ( $P < 0.0001$ ). Pups spent the least amount of time in

the water during the early afternoon ( $8.54 \pm 0.83\%$ ), early evening ( $5.73 \pm 0.74\%$ ), and late evening periods ( $10.47 \pm 0.98\%$ ,  $P < 0.0001$ ; Fig. 3). Finally, individual variation (animal ID) contributed 1.33% of variation in model results and was significant ( $P = 0.0197$ ). For all pups, the probability of being

**Table 2.**—Mean  $\pm$  standard error of maximum dive depth (m), maximum dive time (s), and post-dive duration (s) at four time points during early development and pre- and postweaning in Weddell seal pups ( $n = 18$ ). Values were averaged from 2 days before through 2 days after each time point to account for daily variation.

Parameter	Age in weeks				Weaned?	
	1	3	5	7	N	Y
Max dive depth (m)	4.77 $\pm$ 3.14	5.97 $\pm$ 0.09	9.87 $\pm$ 0.24	15.00 $\pm$ 0.49	8.96 $\pm$ 0.10	13.89 $\pm$ 0.35
Max dive time (s)	56.85 $\pm$ 8.37	98.83 $\pm$ 1.73	135.98 $\pm$ 1.93	218.02 $\pm$ 3.54	129.28 $\pm$ 0.82	218.52 $\pm$ 2.94
Post-dive duration (s)	240.77 $\pm$ 26.09	178.84 $\pm$ 4.45	157.58 $\pm$ 3.08	142.46 $\pm$ 3.14	166.10 $\pm$ 1.33	144.19 $\pm$ 2.80



**Fig. 2.**—Frequency of dives greater than 12 m (left axis) conducted by Weddell seal (*Leptonychotes weddellii*) pups ( $n = 18$ ) in McMurdo Sound, Antarctica, during 2017 and 2019. Dives greater than 12 m are also expressed as a percentage of the total number of discrete dives (right axis) for a given time interval (Table 1).

in the water increased significantly with age ( $F_{1,4706} = 461.63$ ,  $P < 0.0001$ ). Proportion of time spent in water also significantly increased after weaning ( $F_{1,4932} = 177.27$ ,  $P < 0.0001$ ).

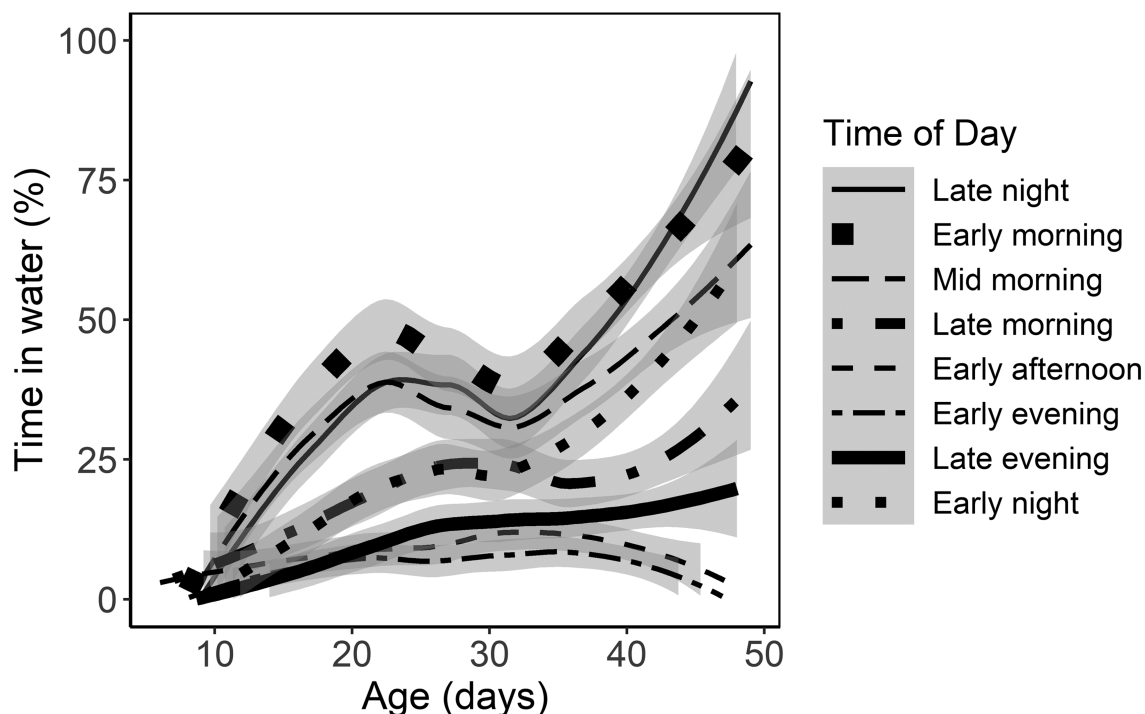
## DISCUSSION

These data represent some of the earliest dive recordings for Weddell seal pups; we recorded some pups entering the water on the day of TDR attachment (1 week old), indicating these pups may have entered the water prior to tag deployment. We found that, despite notable individual variation, all pups adhered to the same general patterns in their development of swimming and diving abilities: diving effort and performance increased as pups aged, and the daily timing of these behaviors appeared to follow the predicted diel “schedule” seen in adult and juvenile Weddell seals. Prey distribution in the water column often has been considered an important determinant of diving behavior in Weddell seals; adult, subadult, and even yearling seals have consistently demonstrated diel behaviors in diving, spending more time in the water during the night and dawn/dusk periods (Testa 1994; Schreer and Testa 1996; Burns and Testa 1997; Burns and Castellini 1998; Burns 1999; Burns et al. 1999; Burns and Kooyman 2001; Plötz et al. 2002). These are the times when the bulk of the Weddell seal diet, Antarctic silverfish (*Pleuragramma antarcticum*), are thought to be migrating vertically upwards in the water column (Dearborn

1965; Clarke and Macleod 1982; Eastman 1985; Testa et al. 1985; Kellermann 1986; Plötz 1986; Green and Burton 1987; Hubold and Ekau 1990; Castellini 1991; White and Piatkowski 1993; Goetz 2015), and it also is when adult females spend the majority of their time in the water (Testa 1994; Goetz 2015). Accordingly, we saw that, despite the significant contribution of individual variation, all pups spent the most time in the water during the morning hours (Fig. 1). These results support our hypothesis that pups would demonstrate similar temporal and diel patterns as do adult females. However, given that the average dive depth for pups is  $\sim 10$  m, it is unlikely that pups are following their mothers on foraging dives, which typically occur around 300 m (Sato et al. 2002, 2003).

We also noted pups had the greatest dive frequency and made their longest, deepest dives in the late night to late morning hours (Figs. 1A, 1B, 1D, 1E, and 2). These facts reject our hypothesis and are not what has been documented previously for older, weaned pups and yearlings, which make their longest, deepest dives during the afternoon hours (Burns 1999; Burns et al. 1999). In contrast, our pups had the lowest dive frequency and made their shortest, shallowest dives during the afternoon to early evening hours (Figs. 1A, 1B, and 2). It is likely that dependent pups are attempting deeper and longer dives during the times they are already in the water the most, which in this case is the morning (Fig. 3). It appears that at this young age, diving effort (i.e., frequency, depth, and duration of dives) may be linked more with when pups are in the water than with foraging attempts. Our results, in combination with previous research, indicate that dependent pups likely are prioritizing developing their swimming and diving capabilities over attempting to forage, and as such, would not need to be diving deeply in the afternoon hours (Sato et al. 2003). Furthermore, pups could be spending less time in the water during the afternoon because that is when the adult females are foraging most deeply and would not be able to bring their pups to such depths. Dependent pups may have greater diving efforts in the late night and early morning hours because this is when females are foraging for more shallow prey (Plötz et al. 2002); if pups are foraging at all before they are weaned, shallow prey would be the easiest to pursue based on pups’ physiological constraints and lack of ability to reach and remain at depths necessary to forage in the afternoon (Burns et al. 1997, 1999; Burns and Testa 1997; Burns and Castellini 1998; Burns 1999).

We observed that post-dive duration significantly decreased as pups got older, in contrast with dive depth and duration. Post-dive durations also were significantly shorter after pups



**Fig. 3.**—Model output from binary logistic regression, showing the percentage of time spent in the water during each 3-h time period (Table 1) with age, for Weddell seal (*Leptonychotes weddellii*) pups ( $n = 18$ ) from McMurdo Sound, Antarctica, in 2017 and 2019. The gray regions represent the 95% confidence interval.

were weaned. We noted very few significant differences among times of day in terms of post-dive duration. Post-dive duration only was significantly different when time of day was split into 3-h bins rather than 6-h bins. The post-dive duration is the time spent at the surface after a dive, when the animal replenishes oxygen stores, and in adult seals it is directly related to the length of the dive and whether or not the aerobic dive limit (ADL) was surpassed (Kooyman et al. 1980). One explanation for the differences in significance of the post-dive duration could be that it is not used in dependent pups in the traditional sense for replenishing oxygen stores because pups are not experiencing much, if any, hypoxia. The ADL reported for 6-week-old Weddell seal pups is approximately 6 min (Burns et al. 1999); the average dive duration for pups in our study was 2.38 min, and only ~4% of dives were longer than 6 min. This indicates pups generally were not diving long enough to reach, let alone surpass, their ADL, so they would not experience a rise in blood lactate levels and would not need a long post-dive duration before their next dive.

Our results show that all pups spent more time in the water as they aged and both dive depth and duration significantly increased with age. Pups also spent more time in the water and dove deeper and longer after they were weaned, which is consistent with the finding that weaned pups have more enhanced diving abilities than dependent pups (Burns et al. 1999). In previous studies, age was the most significant determinant of diving behavior in dependent pups, and time of day was not a significant factor influencing diving behaviors until pups were at least 3 months old (Burns et al. 1997, 1999; Burns and Castellini 1998; Burns 1999). In this study, however, we found

that time of day significantly influenced all diving parameters for dependent pups. Dive depth and duration were significantly different based on time of day, whether time of day was split into 3- or 6-h bins (Burns et al. 1997, 1999; Burns and Testa 1997; Burns and Castellini 1998; Burns 1999). This novel result may be a consequence of using tags that continuously recorded depth as opposed to tags that sorted data into predefined bins, as used in previous studies.

Developing diving capabilities is crucial to the survival of Weddell seal pups because it is necessary for foraging (Kooyman et al. 1980; Burns 1999). Furthermore, many preweaning mortalities in Weddell seal pups are attributed to drowning as a result of underdeveloped swimming and diving skills (Schreer and Testa 1996). The link between diving capability and pup survival has population-level implications; pup survival is an important indicator of population growth rates, as any decrease in pup survival is immediately reflected in the number of individuals entering subsequent age classes, which in turn affects the entire population (Berkson and DeMaster 1985; Cameron and Siniff 2004). Weddell seals are a long-lived, upper trophic level predator in the Antarctic, and often these types of animals are considered ecosystem indicators due to their sensitivity to environmental changes affecting their diet and habitat (Le Boeuf and Crocker 2005; Reid and Forcada 2005).

Regardless of when they were in the water and the timing of diving efforts, pups spent about 80% of their time in the water at the surface. This is seen in other polar phocids that enter the water during dependency: nursing bearded seals spend 58% of their time in the water at the surface (Lydersen et al. 1994), and nursing ringed seals spend 79.5% of their

time at the surface (Lydersen and Hammill 1993). Harp, hooded, and northern elephant seals all wean more abruptly, and usually before their first water entry; pups from these species spend less time at the surface and expedite the development of diving capabilities for foraging because they are no longer receiving food input from their mothers (Le Boeuf and Laws 1994; Folkow et al. 2010; Malde 2019). For example, hooded seals exhibit rapid development of diving ability and dive to depths > 100 m and for 15 min within 3 weeks of age (Folkow et al. 2010). Pups from these other phocid species face additional pressures from predation while hauled out, and several are born on unstable nursing terrain (Lydersen and Kovacs 1999), which also likely influence dive development. Weddell seals are unique among polar phocids in that they have no terrestrial predators and are born on stable fast ice. Results from this study support previous findings that during dependency, Weddell seal pups are attempting little if any foraging, because most prey are found at greater depths than those to which the pups were diving routinely (Sato et al. 2003). This is in contrast to bearded and ringed seals, which begin to forage while they are still nursing from their mothers. However, their main prey is found at shallower depths (< 100 m—Kingsley et al. 1985) accessible to young pups, whereas prey of Weddell seals is found at depths beyond the capabilities of nursing Weddell seal pups (> 200 m—Plötz et al. 2002). Instead, aquatic behavior during dependency may be driven by the necessity to acquire swimming and navigational skills. Weddell seals, unlike many other pinnipeds, are faced with the challenge of finding and maintaining breathing holes because they dive under fast ice (Stirling 1969). One of the main causes of pup mortality in Weddell seals is drowning, due to undeveloped swimming skills or the inability to locate breathing holes (Schreer and Testa 1996). Thus, it is critical for pups to learn how to navigate under the ice and locate breathing holes while dependent on their mothers. Mothers may even be “teaching” their pups while in the water with them, because previous research showed mothers altered their dive behavior when accompanied by their pup compared with dives without their pup (Sato et al. 2003).

For ice-associated and ice-dependent pinnipeds, climate change threatens their ice habitat, and habitat loss may reduce survival and have implications for population growth rates (Laidre et al. 2008; Friedlaender et al. 2010). Climate change may cause seasonal sea ice to recede too rapidly, in which case seal pups may be forced to enter the water before they are physiologically capable of doing so (Burns et al. 2007; Lestyk et al. 2009; Pearson et al. 2019). Further, Weddell seals pups currently are protected from predators such as killer whales (*Orcinus orca*) by extensive fast ice and thus have a high chance of surviving to weaning (Cameron and Siniff 2004). When the Antarctic warms and the fast ice begins to break apart sooner, our findings indicate dependent Weddell pups are not strong divers and may be unable to evade predation from killer whales. While changing climate may not affect Weddell seals for some time yet, future changes in ice condition could

introduce new predation pressures on dependent pups. The negative effects of climate change have been reported in Arctic pinnipeds, and these effects are predicted to worsen (Stenson and Hammill 2014). An increase in mortality and a decrease both in body condition and recruitment have been reported in recent years for bearded seals and harp seals due to decreased ice cover (Ferguson et al. 2005; Moore and Huntington 2008; Stenson and Hammill 2014). Although Weddell seal pups have a much longer period of dependence than most polar seals, knowing proportionally when dive capabilities are being developed could be useful to apply to other species. This research will help to predict potential effects of continued ice depletion on inaccessible polar seals using information gathered on this model species.

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### LITERATURE CITED

- BERKSON, J. M., AND D. P. DEMASTER. 1985. Use of pup counts in indexing population changes in pinnipeds. *Canadian Journal of Fisheries and Aquatic Sciences* 42:873–879.
- BERNARDO, J. 1996. Maternal effects in animal ecology. *Integrative and Comparative Biology* 36:83–105.
- BONESS, D. J., AND W. D. BOWEN. 1996. The evolution of maternal care in pinnipeds: new findings raise questions about the evolution of maternal feeding strategies. *Bioscience* 46:645–654.
- BURNS, J. M. 1999. The development of diving behavior in juvenile Weddell seals: pushing physiological limits in order to survive. *Canadian Journal of Zoology* 77:737–747.
- BURNS, J. M., AND M. A. CASTELLINI. 1998. Dive data from satellite tags and time-depth recorders: a comparison in Weddell seal pups. *Marine Mammal Science* 14:750–764.
- BURNS, J. M., M. A. CASTELLINI, AND J. F. SCHREER. 1997. Physiological effects on dive patterns and foraging strategies in yearling Weddell seals (*Leptonychotes weddellii*). *Canadian Journal of Zoology* 75:1796–1810.

- BURNS, J. M., M. A. CASTELLINI, AND J. W. TESTA. 1999. Movements and diving behavior of weaned Weddell seal (*Leptonychotes weddellii*) pups. *Polar Biology* 21:23–36.
- BURNS, J. M., C. A. CLARK, AND J. P. RICHMOND. 2004. The impact of lactation strategy on physiological development of juvenile marine mammals: implications for the transition to independent foraging. *International Congress Series* 1275:341–350.
- BURNS, J. M., AND G. L. KOOYMAN. 2001. Habitat use by Weddell seals and emperor penguins foraging in the Ross Sea, Antarctica. *American Zoologist* 41:90–98.
- BURNS, J. M., K. C. LESTYK, L. P. FOLKOW, M. O. HAMMILL, AND A. S. BLIX. 2007. Size and distribution of oxygen stores in harp and hooded seals from birth to maturity. *Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology* 177:687–700.
- BURNS, J. M., AND J. W. TESTA. 1997. Developmental changes and diurnal and seasonal influences on the diving behaviour of Weddell seal (*Leptonychotes weddellii*) pups. Pp. 328–334 in *Antarctic communities: species, structure and survival* (B. Battaglia, J. Valencia, and D. Walton, eds.). Cambridge University Press, Cambridge, United Kingdom.
- CAMERON, M. F., AND D. B. SINIFF. 2004. Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. *Canadian Journal of Zoology* 82:601–615.
- CASTELLINI, M. A. 1991. The biology of diving mammals: behavioral, physiological, and biochemical limits. Pp. 105–134 in *Advances in comparative and environmental physiology*. Springer, Berlin and Heidelberg, Germany.
- CASTELLINI, M. A., R. W. DAVIS, AND G. L. KOOYMAN. 1992. Annual cycles of diving behavior and ecology of the Weddell seal. *Bulletin of the Scripps Institute of Oceanography of the University of California, San Diego* 28:1–54.
- CHAMBERT, T., J. J. ROTELLA, AND R. A. GARROTT. 2014. An evolutionary perspective on reproductive individual heterogeneity in a marine vertebrate. *Journal of Animal Ecology* 83:1158–1168.
- CHAMBERT, T., J. J. ROTELLA, M. D. HIGGS, AND R. A. GARROTT. 2013. Individual heterogeneity in reproductive rates and cost of reproduction in a long-lived vertebrate. *Ecology and Evolution* 3:2047–2060.
- CLARK, C. A., J. M. BURNS, J. F. SCHREER, AND M. O. HAMMILL. 2006. Erythropoietin concentration in developing harbor seals (*Phoca vitulina*). *General and Comparative Endocrinology* 147:262–267.
- CLARK, C. A., J. M. BURNS, J. F. SCHREER, AND M. O. HAMMILL. 2007. A longitudinal and cross-sectional analysis of total body oxygen store development in nursing harbor seals (*Phoca vitulina*). *Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology* 177:217–227.
- CLARKE, M. R., AND N. MACLEOD. 1982. Cephalopod remains in the stomachs of eight Weddell seals. *BAS Bulletins* 57:33–40.
- DEARBORN, J. H. 1965. Food of Weddell seals at McMurdo Sound, Antarctica. *Journal of Mammalogy* 46:37–43.
- DURANT, J. M., D. Ø. HJERMANN, G. OTTERSEN, AND N. C. STENSETH. 2007. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research* 33:271–283.
- EASTMAN, J. T. 1985. *Pleuragramma antarcticum* (Pisces, Nototheniidae) as food for other fishes in McMurdo Sound, Antarctica. *Polar Biology* 4:155–160.
- FERGUSON, S. H., I. STIRLING, AND P. MCLOUGHLIN. 2005. Climate change and ringed seal (*Phoca hispida*) recruitment in western Hudson Bay. *Marine Mammal Science* 21:121–135.
- FOLKOW, L. P., E. S. NORDØY, AND A. S. BLIX. 2010. Remarkable development of diving performance and migrations of hooded seals (*Cystophora cristata*) during their first year of life. *Polar Biology* 33:433–441.
- FRIEDLAENDER, A. S., D. W. JOHNSTON, AND P. N. HALPIN. 2010. Effects of the north Atlantic oscillation on sea ice breeding habitats of harp seals (*Pagophilus groenlandicus*) across the north Atlantic. *Progress in Oceanography* 86:261–266.
- GOETZ, K. T. 2015. Movement, habitat, and foraging behavior of Weddell seals (*Leptonychotes weddellii*) in the western Ross Sea, Antarctica. Ph.D. dissertation, University of California Santa Cruz, Santa Cruz, California.
- GREEN, K., AND H. R. BURTON. 1987. Seasonal and geographical variation in the food of Weddell seals, *Leptonychotes weddellii*, in Antarctica. *Wildlife Research* 14:475–489.
- HADLEY, G., J. J. ROTELLA, AND R. A. GARROTT. 2007. Influence of maternal characteristics and oceanographic conditions on survival and recruitment probabilities of Weddell seals. *Oikos* 116:601–613.
- HUBOLD, G., AND W. EKAU. 1990. Feeding patterns of post-larval and juvenile notothenioids in the southern Weddell sea (Antarctica). *Polar Biology* 10:255–260.
- KELLERMANN, A. 1986. Geographical distribution and abundance of postlarval and juvenile *Pleuragramma antarcticum* (Pisces, Notothenioidei) off the Antarctic Peninsula. *Polar Biology* 6:111–119.
- KINGSLEY M., I. STIRLING, AND W. CALVERT. 1985. The distribution and abundance of seals in the Canadian high Arctic, 1980–82. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1189–1210.
- KOOYMAN, G. L. 1967. An analysis of some behavioral and physiological characteristics related to diving in the Weddell seal. *Antarctic Research Series* 11:227–261.
- KOOYMAN, G. L. 1975. A comparison between day and night diving in the Weddell seal. *Journal of Mammalogy* 56:563–574.
- KOOYMAN, G. L., M. A. CASTELLINI, AND R. W. DAVIS. 1981. Physiology of diving in marine mammals. *Annual Review of Physiology* 43:343–356.
- KOOYMAN, G. L., E. A. WAHRENBROCK, M. A. CASTELLINI, R. W. DAVIS, AND E. E. SINNETT. 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. Biochemical, Systemic, and Environmental Physiology* 138:335–346.
- LAIDRE, K. L., I. STIRLING, L. F. LOWRY, Ø. WIIG, M. P. HEIDE-JØRGENSEN, AND S. H. FERGUSON. 2008. Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecological Applications* 18:S97–S125.
- LE BOEUF, B. J., AND D. E. CROCKER. 2005. Ocean climate and seal condition. *BMC Biology* 3:9.
- LE BOEUF, B. J., AND R. M. LAWS. 1994. *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley, California.
- LESTYK, K. C., L. P. FOLKOW, A. S. BLIX, M. O. HAMMILL, AND J. M. BURNS. 2009. Development of myoglobin concentration and acid buffering capacity in harp (*Pagophilus groenlandicus*) and hooded (*Cystophora cristata*) seals from birth to maturity. *Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology* 179:985–996.
- LINDSEY, A. A. 1937. The Weddell seal in the Bay of Whales, Antarctica. *Journal of Mammalogy* 18:127–144.
- LINDSTRÖM, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution* 14:343–348.



- LYDERSEN, C., AND M. O. HAMMILL. 1993. Diving in ringed seal (*Phoca hispida*) pups during the nursing period. *Canadian Journal of Zoology* 71:991–996.
- LYDERSEN, C., M. O. HAMMILL, AND K. M. KOVACS. 1994. Diving activity in nursing bearded seal (*Erignathus barbatus*) pups. *Canadian Journal of Zoology* 72:96–103.
- LYDERSEN, C., AND K. M. KOVACS. 1999. Behaviour and energetics of ice-breeding, north Atlantic phocid seals during the lactation period. *Marine Ecology Progress Series* 187:265–281.
- MALDE, A. 2019. Development of diving capacity and behaviour in harp seal (*Pagophilus groenlandicus*) weanlings from the Greenland Sea stock. Ph.D. dissertation, UiT Norges Arktiske Universitet, Tromsø, Norway.
- MANNAS, J. M., R. A. GARROTT, J. J. ROTELLA, AND K. M. PROFFITT. 2011. Variation in Weddell seal pup mass: maternal investment in offspring. *Intermountain Journal of Sciences* 17:74.
- MCDONOUGH, K., W. F. PERRIN, B. WÜRSIG, AND J. G. M. THEWISSEN (EDS.). 2010. *Encyclopedia of marine mammals*. Elsevier, London, United Kingdom.
- MOORE, S. E., AND H. P. HUNTINGTON. 2008. Arctic marine mammals and climate change: impacts and resilience. *Ecological Applications* 18:s157–s165.
- NOREN, S. R., S. J. IVERSON, AND D. J. BONESS. 2005. Development of the blood and muscle oxygen stores in gray seals (*Halichoerus grypus*): implications for juvenile diving capacity and the necessity of a terrestrial postweaning fast. *Physiological and Biochemical Zoology* 78:482–490.
- OGAWA, F., ET AL. 2018. Evaluating impacts of recent Arctic sea ice loss on the northern hemisphere winter climate change. *Geophysical Research Letters* 45:3255–3263.
- PEARSON, L. E., E. L. WEITZNER, J. M. BURNS, M. O. HAMMILL, AND H. E. M. LIWANAG. 2019. From ice to ocean: changes in the thermal function of harp seal pelt with ontogeny. *Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology* 189:501–511.
- PLÖTZ, J. 1986. Summer diet of Weddell seals (*Leptonychotes weddelli*) in the eastern and southern Weddell sea, Antarctica. *Polar Biology* 6:97–102.
- PLÖTZ, J., H. BORNEMANN, R. KNUST, A. SCHRÖDER, AND M. BESTER. 2002. Foraging behaviour of Weddell seals, and its ecological implications. Pp. 148–156 in *Ecological studies in the Antarctic sea ice zone* (W. E. Arntz and A. Clarke, eds.). Springer, Berlin, Germany.
- REID, K., AND J. FORCADA. 2005. Causes of offspring mortality in the Antarctic fur seal, *Arctocephalus gazella*: the interaction of density dependence and ecosystem variability. *Canadian Journal of Zoology* 83:604–609.
- RICHMOND, J. P., J. M. BURNS, AND L. D. REA. 2006. Ontogeny of total body oxygen stores and aerobic dive potential in Steller sea lions (*Eumetopias jubatus*). *Journal of Comparative Physiology, B. Biochemical, Systemic, and Environmental Physiology* 176:535–545.
- RSTUDIO TEAM. 2018. RStudio: integrated development for R. RStudio, Inc. Boston, Massachusetts. [www.rstudio.com/](http://www.rstudio.com/). Accessed 1 February 2019.
- SATO, K., Y. MITANI, M. F. CAMERON, D. B. SINIFF, Y. WATANABE, AND Y. NAITO. 2002. Deep foraging dives in relation to the energy depletion of Weddell seal (*Leptonychotes weddellii*) mothers during lactation. *Polar Biology* 25:696–702.
- SATO, K., Y. MITANI, Y. NAITO, AND H. KUSAGAYA. 2003. Synchronous shallow dives by Weddell seal mother-pup pairs during lactation. *Marine Mammal Science* 19:384–395.
- SCHREER, J. F., AND J. W. TESTA. 1996. Classification of Weddell seal diving behavior. *Marine Mammal Science* 12:227–250.
- SIKES, R. S., AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- SINIFF, D. B., D. P. DEMASTER, R. J. HOFMAN, AND L. L. EBERHARDT. 1977. An analysis of the dynamics of a Weddell seal population. *Ecological Monographs* 47:319–335.
- STEARNS, S. C. 2000. Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* 87:476–486.
- STENSON, G. B., AND M. O. HAMMILL. 2014. Can ice breeding seals adapt to habitat loss in a time of climate change? *ICES Journal of Marine Science* 71:1977–1986.
- STIRLING, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. *Ecology* 50:573–586.
- TESTA, J. W. 1994. Over-winter movements and diving behavior of female Weddell seals (*Leptonychotes weddellii*) in the southwestern Ross Sea, Antarctica. *Canadian Journal of Zoology* 72:1700–1710.
- TESTA, J. W., D. B. SINIFF, M. J. ROSS, AND J. D. WINTER. 1985. Weddell seal-Antarctic cod interactions in McMurdo Sound, Antarctica. Pp. 561–565 in *Antarctic nutrient cycles and food webs* (W. R. Siegfried, P. R. Condy, and R. M. Laws, eds.). Springer, Berlin, Germany.
- THOMAS, J. A., AND D. P. DEMASTER. 1983. Diel haul-out patterns of Weddell seal (*Leptonychotes weddelli*) females and their pups. *Canadian Journal of Zoology* 61:2084–2086.
- TURNER, J., J. S. HOSKING, T. J. BRACEGIRDLE, G. J. MARSHALL, AND T. PHILLIPS. 2015. Recent changes in Antarctic sea ice. *Philosophical Transactions of the Royal Society of London, A: Mathematical, Physical and Engineering Sciences* 373:20140163.
- VÁZQUEZ-MEDINA, J. P., T. ZENTENO-SAVÍN, AND R. ELSNER. 2006. Antioxidant enzymes in ringed seal tissues: potential protection against dive-associated ischemia/reperfusion. *Comparative Biochemistry and Physiology, C. Toxicology & Pharmacology* 142:198–204.
- WHITE, M. G., AND U. PIATKOWSKI. 1993. Abundance, horizontal and vertical distribution of fish in eastern Weddell Sea micronekton. *Polar Biology* 13:41–53.

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