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Breath-hold capacities and circadian dive rhythmicity shape optimal foraging strategies in a polar marine mammal, the Weddell seal (*Leptonychotes weddellii*)

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Air-breathing vertebrates must balance their response to diel shifts in prey accessibility with physiological thresholds and the need to surface after each dive. Weddell seal (*Leptonychotes weddellii*) dive behaviors were tracked across the year under rapidly-changing light regimes in the Ross Sea, Antarctica (~ 75-77°S). This provides a 'natural experiment' with free-living seals experiencing 24-hrs of light (Polar Day), light/dark cycling, and continuous darkness (Polar Night). The Weddell seal's temporal niche switches from nocturnal diving in the summer to diurnality for the remainder of the year. Rhythmicity in dive efforts (depth, duration, post-dive surface recuperation, bottom time, and exceeding physiologic thresholds) is stronger and more closely circadian during times of the year with light/dark cycling compared with Polar Day or Night. With light/dark cycling, animals also make the most extreme dives (those that far exceed the calculated aerobic dive limit, cADL) significantly earlier than solar noon. Offsetting the longest dives that require longer surface recuperation times from mid-day allows animals to maximize total dive time under high-light conditions conducive for visual hunting. We identify an optimal foraging strategy to exploit a diel preyscape in a highly-seasonal environment, while balancing tradeoffs imposed by physiological thresholds in a diving mammal.

Selective pressures in an animal's environment are reflected in the behavioral and physiological tactics employed to ensure survival and reproduction, ultimately shaping life histories. Optimal foraging strategies are used to maximize an animal's net energetic gains, avoid predation risks, and/or mitigate intraspecific competition for resources[1,2]. To best achieve optimality, temporally aligning behaviors and physiologies to anticipate daily environmental changes provides an adaptive advantage, that may improve caloric returns. Such diel rhythmicity is driven by endogenous circadian 'master clocks' and peripheral oscillators regulating daily shifts in metabolic processes. Intrinsic rhythms often deviate slightly from 24-h, and extrinsic cues (referred to as zeitgebers or 'time givers') further entrain activities to be more precisely circadian with geophysical time[3]. The most universal zeitgeber across taxa is photoperiod and light/dark cycling[4].

In the absence of light/dark cycling, the benefits of circadian organization become uncertain and perhaps even disadvantageous[3,5,6]. For example, high-latitude organisms endure long spans of the year with Polar Day (continuous light; sun does not set) or Polar Night (continuous dark; sun does not rise). Yet, even without light/dark cycling, daily rhythms in ambient light intensity remain, but the magnitude of such rhythms becomes attenuated at higher latitudes. Among polar vertebrates, there is substantial inter-specific variation in rhythmicity under constant light regimes. For instance, the lack of photoperiodic zeitgebers results in the loss of circadian rhythmicity in Svalbard reindeer (*Rangifer tarandus*), with animals' body temperatures and activities becoming arrhythmic or 'free-running' (i.e., drifting from 24-h)[7]. Rhythmic behaviors can also be influenced by shifts in activity budgets associated with energetically costly life history events. For example, reproductive efforts and increased activity associated with chick-rearing can diminish circadian rhythms in little auks (*Alle alle*)[8], or attendance activities can be partitioned in species with biparental care, such as the thick-billed murre (*Uria lomvia*)[9]. Similarly, there may be ontogenetic shifts

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in activity patterns, such as in the Great Grebe (*Podicephorus major*) where adults exhibit daily oscillations in foraging activities but juveniles dive throughout the day, presumably to compensate for immature dive abilities and lower prey capture and processing efficiencies[10]. Seasonal transitions in photoperiod translate to local productivity, and the need to take advantage of ephemeral forage and/or prey in regions with a short growing season may prompt animals to intensively feed at all hours[11]. In contrast, other species, such as some arctic migratory birds[12], ground squirrels (*Urocitellus parryii*)[13], and polar bears (*Ursus maritimus*)[14] all maintain circadian rhythms when the sun is constantly above the horizon throughout the summer's Polar Day.

Adding further complexity, marine predators exploit three-dimensional habitats with daily, synchronous movements of prey between the lit surface waters and unlit deep sea (in diel vertical migrations, DVM)[15]. Zooplankton ascend to feed in shallow surface layers at night, but increased light intensity prompts a mass descent through the water column during daylight to avoid predation[16]. DVM behaviors often 'cascade' through multiple trophic levels and taxa, driven by predator-prey interactions[17]. An animal's response to daily shifts in prey accessibility within the water column is constrained by physiological thresholds, and the need to balance the increased energetic expenditures of traveling to greater depths with energetic gains acquired from successful foraging[18,19]. This is especially relevant to central-place foragers such as marine mammals that must return to the water's surface for air after each dive[20,21].

Marine mammals have a suite of adaptations to extend underwater dive durations, including large endogenous oxygen (O_2) stores amassed from large blood volumes up to ~3× the size of terrestrial mammals of similar size, high packed red blood cell volumes (~1.5× that of terrestrial mammals), and elevated blood hemoglobin (~1.5–2×) and muscle myoglobin (~5–10×) concentrations[22]. To prolong the use of on-board O_2 stores during dives, O_2 is partitioned through peripheral vasoconstriction to prioritize its use at anoxia-intolerant organs, and animals become brady-cardic and drop their body temperature to depress metabolic rates[21]. On longer dives, once aerobic thresholds are exceeded and ATP-production relies more heavily on anaerobic glycolysis, lactate production increases exponentially[23,24]. This necessitates longer post-dive surface recuperation time to clear anaerobic byproducts from circulation, ultimately decreasing the total time spent underwater foraging. Therefore, frequently exceeding the aerobic dive limit (ADL) is generally considered inefficient. The vast majority of dives remain aerobic in nature[24] with limitations on dive durations imposed by the magnitude of O_2 stores and their management and use rates[19].

While relatively rare, dives that exceed aerobic thresholds are functionally significant. When foraging, the decision to remain at depth is made based on patch quality[25]. To forage optimally, animals should make longer, deeper dives in rich patches with the most successful returns. In such areas, animals could benefit from exceeding their ADL when the energetic gains of exploiting a rich prey patch outweigh the cost of longer post-dive surface recuperation times. This is particularly relevant when feeding on spatially and temporally ephemeral prey. However, time at depth can't be extended indefinitely, and even in the richest prey patches, dives will ultimately be terminated due to finite O_2 limitations[25] and respiratory drive[26]. Marine mammals generally dive longer and deeper during mid-day[27,28] and pinnipeds further increase dive efforts during their long post-molt foraging trips when rapid mass recovery is prioritized[29–31]. However, to date, there has been relatively little effort to distinguish the role of physiological capacity in diel behaviors[28,31] when prey may be concentrated into rich patches at specific times of day, particularly when ambient light regimes (and presumably prey behaviors) change drastically throughout the year.

In this study, we test for intrinsic and extrinsic factors governing dive behavior through a 'natural experiment' with free-ranging animals exposed to Polar Day and Night (continuous light, LL and dark, DD, respectively) and varying light/dark (LD) cycling across the year. Tradeoffs between O_2 conservation and energetic gains, motivating optimal foraging strategies may also be accentuated in Weddell seals (*Leptonychotes weddellii*) in

Erebus Bay, Antarctica, as this is the southernmost population of the world's southernmost living mammal experiencing some of the most profound seasonal changes in environment[32]. This species is a highly proficient diver, reaching depths up to 904 m and a maximum recorded dive duration of 96 min[33] nearly 4–5× their estimated ADL, making Weddell seals a particularly tractable system to assess how physiological plasticity affects chronobiology. We demonstrate that in addition to a seasonal phase inversion, Weddell seals exhibit significant diel and circalunar organization across numerous indices of dive effort (depth, duration, post-dive surface duration, bottom time that is indicative of foraging, and approaching/exceeding aerobic thresholds). This was made possible due to long (~10 months) and complete dive records that span LL, LD, and DD phases of their annual cycle, and provide the opportunity for a comprehensive assessment of periodicity in dive behaviors. We show that the Weddell seal's dive rhythmicity is attenuated in the absence of LD cycling, and animals exhibit stronger temporal organization of dive depths than physiologically constrained dive durations. Along with greater rhythmicity in behaviors, the Weddell seal's most 'extreme' dives are offset from mid-day during times of the year with LD cycling. We posit that physiological dive thresholds may act as a chronodisruptor, but preferentially keeping dives close to the ADL mid-day while making the longest dives outside this time window would prioritize shorter surface time and maximize total dive time under optimal foraging conditions. We shed light on how animals can balance the inherently conflicting nature of O_2 conservation with diel variation in patch depth and quality.

Results

Of sixty-two adult Weddell seals instrumented at Ross Island (~77°S, 165°E) or the Victoria Land coastline (~76°S, 162°E), three dive records were excluded from further analyses due to tag failures or less than one week of transmissions. The remaining fifty-nine (Fig. 1; 50F: 9M) instruments collected 8913 seal days of behavioral data throughout the western Ross Sea. Data were collected via satellite transmission ($n = 49$) or archived and physically recovered from the instrument ($n = 10$). The physically recovered instruments were particularly valuable as they represent complete records without satellite transmission loss and these were used for finer-scale tests of rhythmicity. Animal body mass at the time of tag deployment averaged 306.4 ± 9.9 kg ($n = 59$) and mean calculated aerobic dive limits (cADLs) derived from the measurement of endogenous oxygen stores were 19.1 ± 0.2 min ($n = 54$). All dive activities are shown in McMurdo local time (New Zealand Standard time; NZST), where local noon is at ~12:45–13:00 h.

Seasonal phase inversion in activity and haul-out rhythms

Weddell seal haul-out timing changed significantly over the course of the year (Fig. 2, note non-overlapping 95% confidence intervals; *see* Supplementary Table 1 and Supplementary Fig. 1 for additional information on competing Bayesian circular mixed-effect models). At the beginning of tag deployments in the austral summer, Weddell seal haul-outs occurred primarily during the daytime (starting at NZST $08:58 \pm 00:42$ 95% CI and ending at $21:03 \pm 00:26$ h) through the end of March (Day of Year, d86). Correspondingly, the number of dives made and proportion of time spent diving was greater at night at the start of tag deployments (Fig. 3; GAMM, Number of Dives: Day of Year $F = 310$, $P < 0.001$, Time $F = 274.6$, $P < 0.001$; %Dive Time: all Day of Year × Time interactive effects $P < 0.001$).

Seals then abruptly transitioned to nocturnal haul-outs starting at NZST $22:34 \pm 00:24$ h each day and continuing through the night to $03:45 \pm 00:26$ h. For the remainder of the year, animals instead spent the most time diving mid-day. In addition to timing, Weddell seal haul-out durations also changed across the year (GAMM, $F = 38.25$, $P < 0.001$). Haul-outs were the shortest mid-winter, when daily dive time and total number of dives were highest. Total dive time and number of dives decreased toward the end of instrument deployments as animals returned to the breeding colonies and/or pupping, concomitant with a return to daytime haul-outs in mid-October (day 291, haul-outs from $09:56 \pm 01:27$ to $21:31 \pm 01:10$ h). Taken together, Weddell seals exhibited a seasonal phase
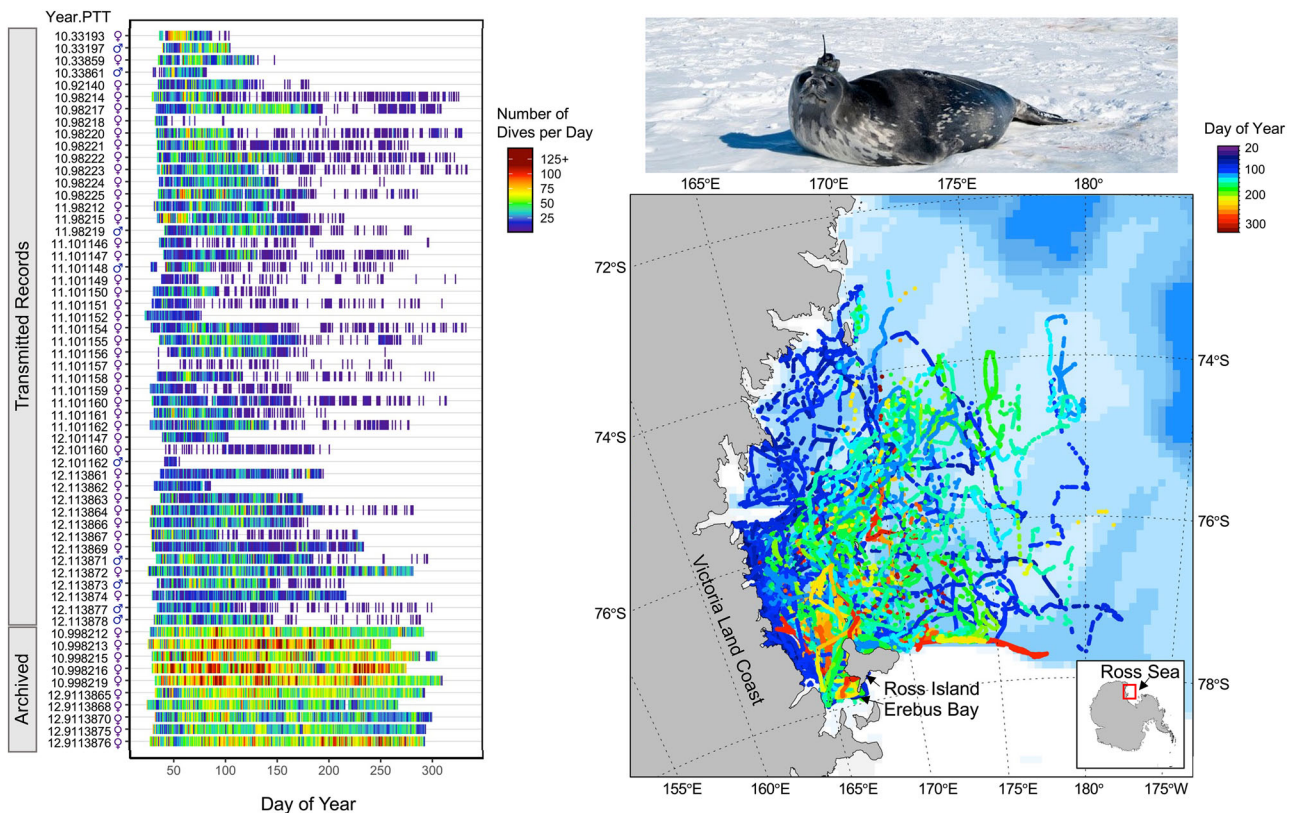
Fig. 1 | Transmitted and archived Weddell seal dive records. (*Left*) Behavioral dive data were collected across the year, either from CLS Argos satellite transmission or through physical recovery of the instrument with archived records. Each record shows one individual seal (Year and PTT identifier noted), animal sex, and the number of dives recorded. (*Right*) Weddell seals instrumented from Ross Island,

Erebus Bay, and the Victoria Land Coast utilized the western Ross Sea; each point shows the location of a dive across the year. Locations were further used to calculate solar and lunar characteristics the animals experienced. For further information on habitat utilization of animals in this study see Goetz et al. [30]. Photo credit: Dan Costa; Antarctic map from the 'CCAMLRGIS' package. n_{seals} = 59; n_{dives} = 281,268.

inversion, changing their dive activities from nocturnal during the summer, to diurnal for the remainder of the year.

Diel and seasonal shifts in dive indices correspond with photoentrainment

Dive efforts (depth, duration, post-dive surface duration, bottom time) and the extent to which animals pushed physiological limits (dive duration:cADL, the proportion of dives exceeding the cADL) were all significantly greater during mid-day, with peaks of all indices' means centered around solar noon (NZST 13:00–13:20 h) as compared with shallower and shorter dives during nighttime (Fig. 4; Table 1). All aspects of dive behavior increased during the spring, coinciding with the return of daylight and increasing photophase.

Indeed, solar cycles and presumably light levels appeared to be strong factors driving diurnal rhythms in Weddell seal dive behaviors across the year (Fig. 5). All aspects of dive effort (depth, duration, post-dive surface duration, bottom time) and the extent to which animals pushed physiological limits (dive duration:cADL, the proportion of dives exceeding the cADL) exhibited a steep increase, on average, at twilight as the sun rose in the sky from −18° to 0° (or conversely, efforts decreased as the sun set from 0° to −18°). Dive efforts were significantly greater during daylight hours (solar altitude ≥ 0° above the horizon) than in darkness (solar altitude < −18°), and reached a maximum at solar noon (when the azimuth approached ± 180° or 'due north').

Offsetting dives that greatly exceeded physiologic limits from mid-day and solar noon

Weddell seals rarely made their longest dives that exceeded their cADL to the greatest extent during mid-day (Fig. 6). Instead, these typically occurred significantly earlier (compared to average duration dives), before solar noon.

This pattern was particularly evident during times of the year with LD cycling. Dives increased in duration as light levels increased, up to approximately the Weddell seal's cADL (i.e., ~15–25 min in duration) and depths between ~300–500 m with 50–60% bottom time. On days with LD cycling, dives rarely exceeded the cADL by more than ~30% during mid-day (Fig. 6) and/or when the sun was highest in the sky (Fig. 7; overall GAMM statistics shown in Supplementary Table 2). Conversely, the (relatively rare) longest dives that were more than double the length of the cADL were made when the sun was lower in the sky. Offsetting the most extreme dives from mid-day, in turn, also kept longer post-dive surface durations (7–>8 min) earlier in the day rather than during peak solar conditions. Temporal partitioning of dives (by hour and solar altitude) throughout the day under LD conditions was less pronounced in dive depth than in dive duration, post-dive surface time, bottom time, and dive duration:cADL ratios. Patterns often did not hold during constant LL or DD conditions.

In the absence of sunlight, lunar cycles shaped dive behaviors

The impacts of lunar cycles were superimposed upon diel rhythms in dive behaviors but were most distinct in darkness. Both dive depths and durations increased during the full moon (Fig. 8; Supplementary Table 3; lunar phase × day/twilight/night, dive depth: F = 84.0, P < 0.001; duration: F = 80.789, P < 0.001), particularly during nighttime (when the sun was at least 18° below the horizon). This was presumably driven by increased illumination (lunar illumination × day/twilight/night, dive depth: F = 133.2.0, P < 0.001; duration: F = 71.4, P < 0.001; Supplementary Fig. 2 for other indices of dive effort). Indeed, without solar illumination, the full moon appeared to shift the peak in dive efforts to 17:14–17:17 h. This was also evident by visual observation of recovered records (Fig. 9; i.e., note band of increased dive depth and duration and disruption of diel cyclicity at day
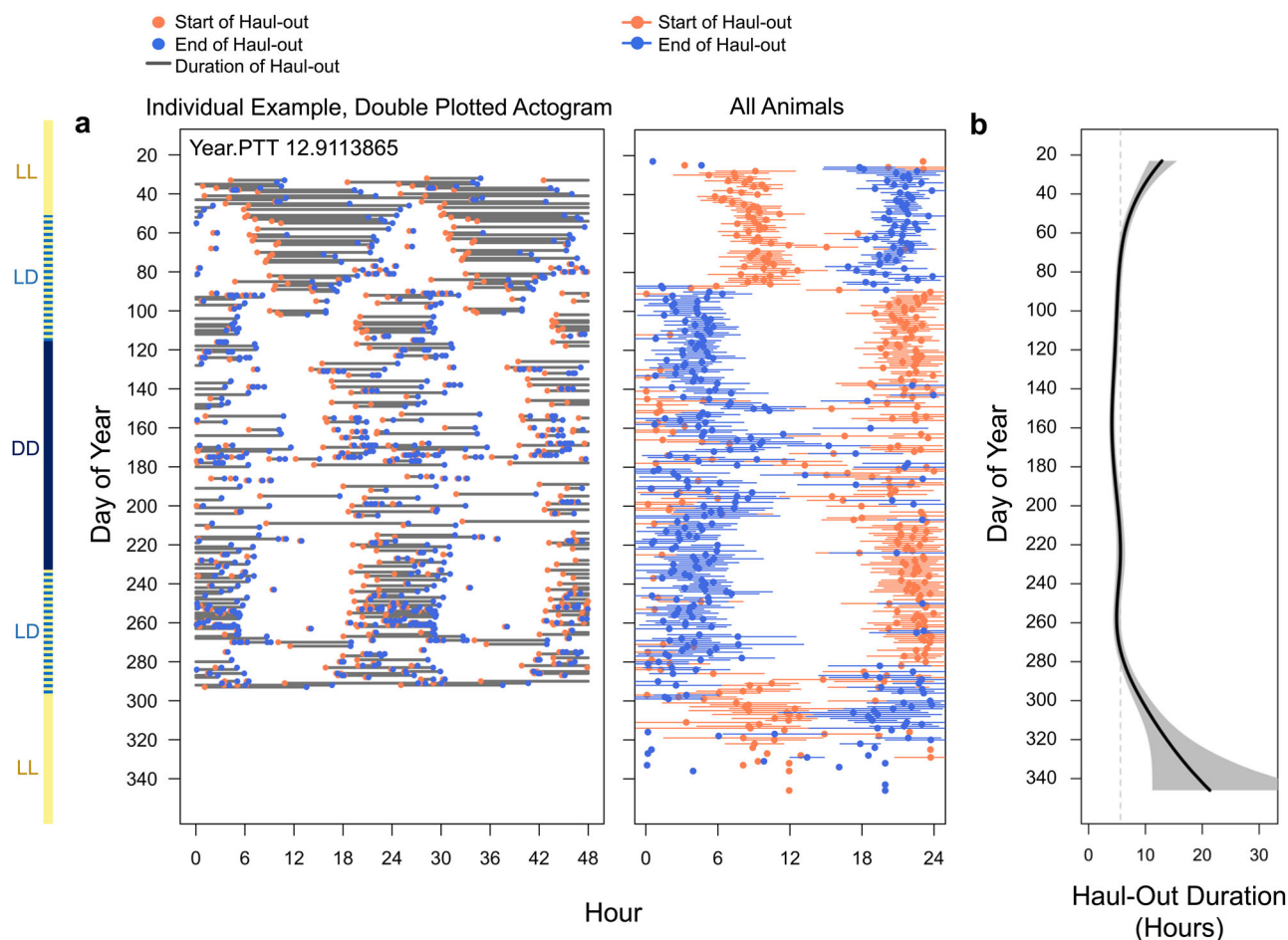
Fig. 2 | Seasonal phase inversion in haul-out timing. a (*Left*) An example of the daily haul-out activities of an adult female Weddell seal across the year, represented as a double-plotted actogram. Data shown are from a physically recovered instrument without transmission loss. (*Right*) Weighted circular mean ± 95% confidence interval (CI) start and end times for seal haul-outs across the year showing a phase inversion in which haul-out timing 'switches' from daytime to nighttime, and then returns to daytime again the next summer. Weddell seal haul-out durations **b** also changed across the year. GAMM shows the mean, with gray shading for the 95% CI; dashed line denotes the overall mean across tag deployments. Light regime (LL, LD, DD) is shown at *left*. All activities are shown in McMurdo local time (New Zealand Standard Time; UTC + 12). n_{seals} = 59; $n_{haul-outs}$ = 8,616.

~125, 155, 185, 215 in actograms). As with solar illumination, seals also made deeper and longer dives when the moon's altitude was higher and when positioned directly north (Supplementary Table 3), further demonstrating that lunar illumination is a significant driver of dive behavior in polar darkness.

Geophysical time, solar and lunar phases, and intrinsic factors all explained variation in dive behaviors

The extrinsic (geophysical time, solar, and lunar characteristics) and intrinsic (sex, mass) factors outlined in this study explained the variation in dive behaviors to different extents. The most parsimonious models included day of year, and time of day or solar azimuth (Table 1; Supplementary Table 3). Light regime, solar altitude, and then lunar phase and illuminated fraction of the moon were also included in top-ranked models and accounted for significant variation in dive depths. The illuminated fraction of the moon and lunar phase explained more variation in dive durations than did solar altitude. Animal sex improved models explaining variation in dive depths with males making shallower dives. In contrast, dive durations, dive duration:cADL ratios, and the proportion of dives exceeding the cADL were significantly greater for animals that were more massive at the time of instrument deployment. Mass at the time of deployment was the greatest contributing factor explaining the probability of animals exceeding the cADL, while extrinsic factors influenced when the longest dives that greatly exceeded the cADL occurred.

Physiological constraints and absence of light zeitgebers attenuated behavioral periodicity

Weddell seal dive efforts exhibited substantial rhythmicity that generally remained close to a 24 h period for most of the year. However, the strength of patterns varied across the year (Figs. 9, 10; LME at 15-d intervals, peak normalized power ($P_N$max) depth: $F_{1,156}$ = 11.0, P = 0.001; $P_N$max duration: $F_{1,156}$ = 24.3, P < 0.001; LME by light regime, $P_N$max depth: $F_{4,28.1}$ = 28.0, P < 0.001; $P_N$max duration: $F_{4,28.4}$ = 13.4, P < 0.001). In LL and DD conditions, more animals exhibited arrhythmic dive behaviors (depth and duration), rhythms that differed from 24 h, and/or low-amplitude or weakly significant rhythms (Fig. 10). In contrast, during LD cycling, Weddell seals exhibited the greatest rhythmicity (i.e., highest $P_N$max) in their dive behaviors at ~d60–120 (March/April) and again at d225–270 (mid-August/October). During periods with LD cycling, all individuals had high-amplitude circadian rhythms that were entrained to precise 24-h circadian periods in dive depths (highest peak in power (or tau; τ) range d90: 23.87–24.24 h; d225–255: 23.41–24.49 h) and durations (τ range d225–270: 23.27–24.30 h). Further supporting physiological constraints to dive rhythmicity, dive depths exhibited significantly greater rhythm strength ($P_N$max) than durations (Fig. 10; LME at 15-d intervals, $F_{1,316}$ = 16.8, P = 0.001; LME by light regime, $F_{1,67}$ = 26.9, P < 0.001), and all other indices of dive effort (Supplementary Fig. 3). While weaker than circadian rhythms, there was also significant circalunar organization of Weddell seal dive efforts closely approximating the lunar month of 29.5 days (Supplementary
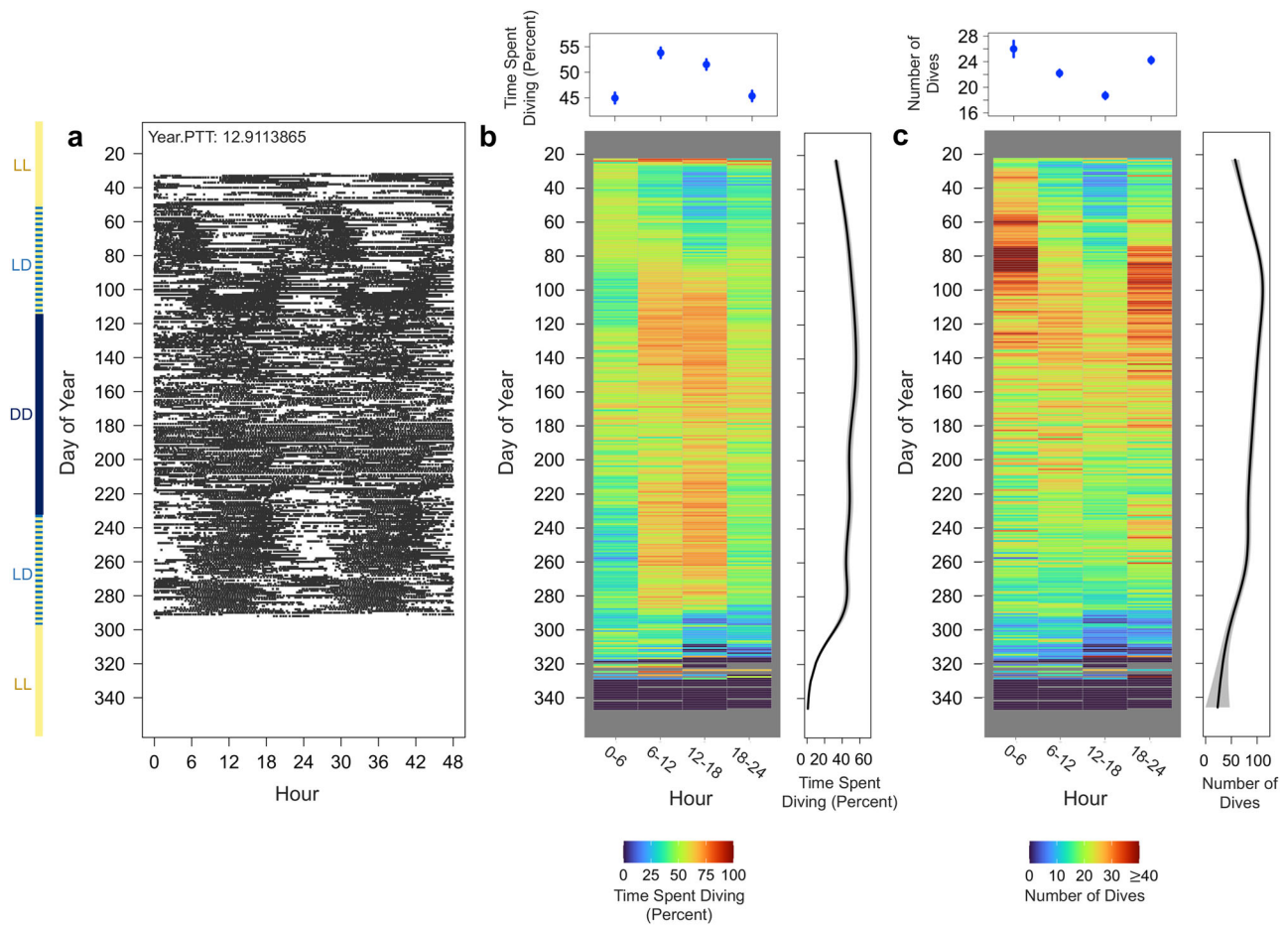
Fig. 3 | Time that Weddell seals performed their dives changed across the day and year. a An example of the daily diving activity of one adult female Weddell seal across the year represented as a double-plotted actogram. Data shown are from a physically recovered instrument without transmission loss; each point marks the start time of an individual dive. **b** The percentage of time spent diving and **(c)** number of dives across the year determined from instrument 'summary' statistics that were collated and transmitted in six-hour time blocks independent of light levels. *Top* shows the mean ± 95% confidence interval for each activity in each time block from GAMMs. *Right* in each panel shows GAMMs with one dimensional smoother by day of the year only when data from all time hour time blocks were available for a given day to avoid biases; gray shading shows a 95% confidence interval. Light regime (LL, LD, DD) is shown at *left*. All activities are shown in McMurdo local time (New Zealand Standard Time; UTC + 12). n_{seals} = 57; $n_{summary\ blocks}$ 0:00–6:00 = 8204; 6:00–12:00 = 8194; 12:00–18:00 = 8157; 18:00–24:00 = 8124.

Table 4; depth $\tau = 28.4 \pm 0.7$ days, $P_N\max = 0.010 \pm 0.003$; duration $\tau = 27.6 \pm 0.8$ days, $P_N\max = 0.006 \pm 0.001$).

Discussion

This study addresses the conflict between the depletion of endogenous O_2 stores and energy gains in a marine mammal's diel preyscape. DVM drives prey masses deeper within the water column during daylight hours best for visual hunting[15], but may also push air-breathing vertebrates past their inherently limited aerobic dive capacities during foraging efforts. While extending dives and pushing physiologic capacities could result in greater prey acquisition and energetic gains, it also burdens the animals with increased locomotory costs[34], and after exceptional dives marine mammals require longer surface recuperation times to repay O_2 debts and clear anaerobic byproducts[23,24]. While there have been numerous studies suggesting animals push physiologic limits at certain times in the year[31], or due to reproductive investments[29], we show that there are also strategic times of the day when animals should dive more conservatively (i.e., close to the cADL), to maximize total dive time during optimum hunting conditions. Conversely, animals may preferentially make their longest dives, requiring longer surface recuperation periods when foraging conditions are relatively unfavorable for visual hunting. Optimizing dive behaviors relative to ambient illumination is likely to be most important during days that experience the greatest variation in light conditions – that is, when there is light/dark cycling. The Weddell seal, an exceptional diver and the world's

southernmost living mammal[20,32], exhibits a multitude of shifts in foraging efforts that appear to optimally align physiologically constrained dive capacities with environmental cues.

There was a prominent phase inversion in haul-out timing, with Weddell seals hauling-out during the day during the austral summer and then switching toward primarily being hauled-out at night during the remainder of the year[35]. Such temporal niche switching is considered to be relatively rare in free-living mammals[3,36]. However, many high-latitude fish species in the Arctic, including arctic cod (*Boreogadus saida*) exhibit reverse DVM (remain shallow during the early hours and travel to depth at night) under 24-h daylight and revert to DVM once light-dark cycling resumes[16,37]. In the Antarctic summer, zooplankton cease DVM activities in favor of continuous feeding at ice edge phytoplankton blooms[38,39]. Whether seasonal changes in DVM behaviors ultimately cascade up to higher trophic levels remain unresolved, as there have been few studies of vertical migration of fish in McMurdo Sound. However, cameras borne by Weddell seals have been used to track shifts in the depths that predominant prey species, Antarctic silverfish (*Pleuragramma antarcticum*) and Antarctic cod (i.e., toothfish; *Dissostichus mawsoni*) are encountered[40]. Even when the sun is continuously above the horizon, both fish species were observed at deeper depths during mid-day; however, Antarctic silverfish appeared to respond to light intensity more than cod[40]. Similar seasonal shifts in haul-out timing have also been observed in other Antarctic pinniped species (i.e., crabeater seals, *Lobodon carcinophagus*)[27].
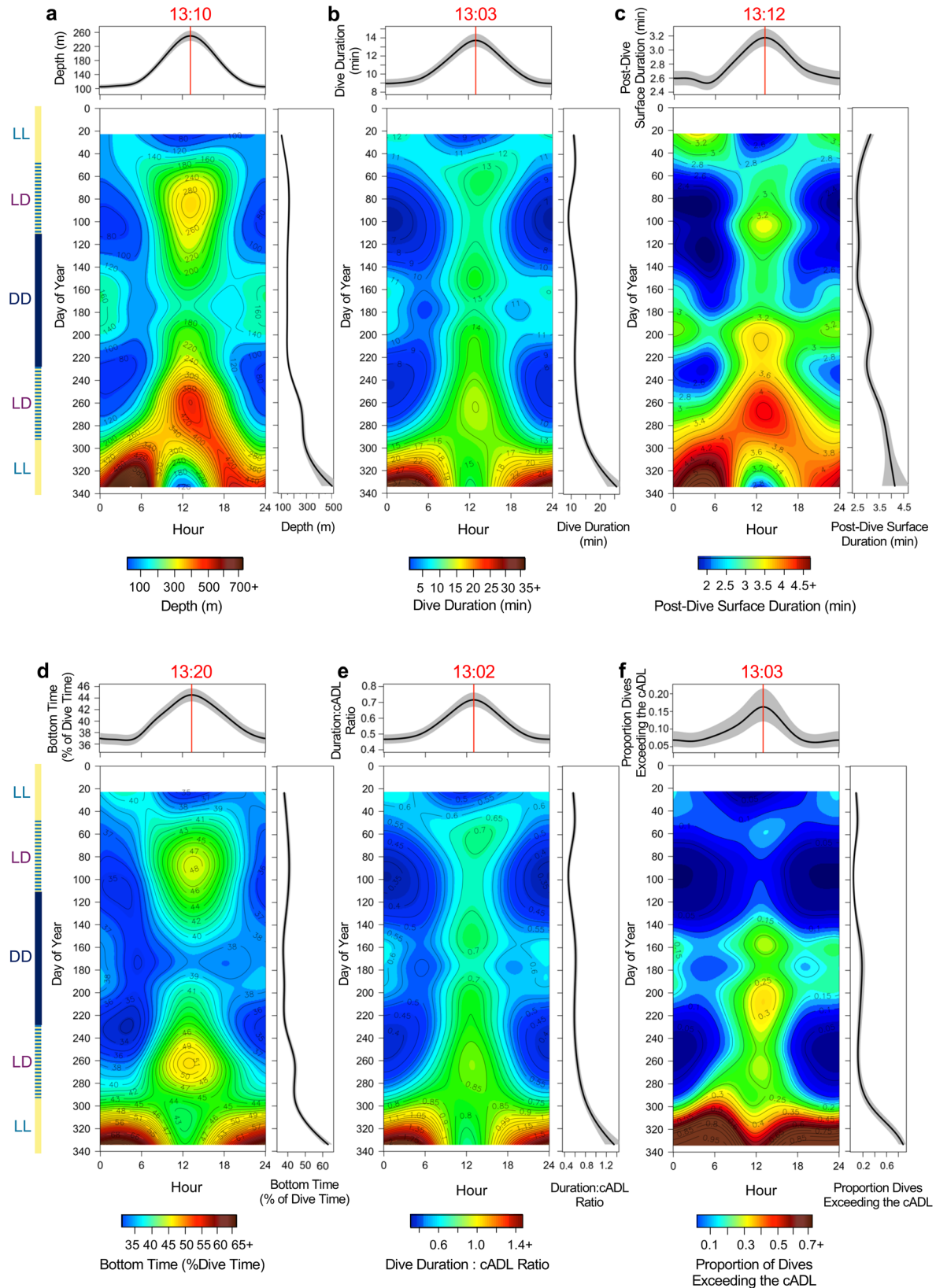
Fig. 4 | Indices of dive effort exhibited diel and seasonal variation. Two-dimensional GAMMs show that dive efforts: **a** depth, **b** dive duration, **c** post-dive surface duration, **d** bottom time, **e** dive duration:cADL ratio, and the **f** proportion of dives exceeding the cADL were greatest at approximately solar noon (*Top*; GAMMs with one dimensional smoother showing dive effort by hour, gray shading shows 95% confidence interval and red line denotes the timing of peak activity). 2-D models represent Day of Year + Hour + (Day of Year × Hour). Note that solar noon is at ~12:45–13:00 h in McMurdo Sound and all dive activities are shown in McMurdo local time (New Zealand Standard Time; UTC + 12). Indices of dive effort all significantly increased in late spring (*Right* in each panel shows GAMMs with one dimensional smoother by day of the year; gray shading shows a 95% confidence interval). Light regime (LL, LD, DD) is shown at *left*. **a–d**: n_{seals} = 59; n_{dives} = 281,268; **e, f**: n_{seals} = 54; n_{dives} = 272,984.

Table 1 | Subset of top-ranked models explaining variation in dive efforts

Model	R^2	AICc	ΔAIC_C	Log likelihood	df
Depth ~					
Day of Year + Solar Azimuth + (Day of Year × Solar Azimuth) + Sex	0.193	720,279.2	0	−360,131.6	8
Day of Year + Solar Azimuth + (Day of Year × Solar Azimuth)	0.195	720,288.0	8.8	−360,137.0	7
Day of Year + Time of Day + (Day of Year × Time of Day)	0.192	720,384.4	105.2	−360,185.2	7
Time of Day (h) × Light Regime (LL/LD Fall/DD/LD Spring/LL next summer)	0.163	728,895.1	8615.9	−364,439.5	8
Solar Azimuth	0.115	733,844.4	13,565.2	−366,918.2	4
Light Regime (LL/LD Fall/DD/LD Spring/LL next summer)	0.033	738,211.7	17,932.5	−369,098.8	7
Solar Altitude	0.094	741,766.2	21,487.0	−370,879.1	4
Lunar Phase + Solar Altitude	0.094	741,818.6	21,539.4	−370,904.3	5
Day/Twilight/Night	0.058	745,052.6	24,773.4	−372,521.3	5
Lunar Phase + Day/Twilight/Night	0.059	745,065.6	24,786.4	−372,526.8	6
Fraction of Moon Illuminated + Day/Twilight/Night	0.058	745,080.1	24,800.9	−372,534.0	6
Daylength	0.012	746,636.2	26,357.0	−373,314.1	4
Dive Duration ~					
Day of Year + Time of Day (h) + (Day of Year × Time of Day) + Mass	0.129	558,724.0	0	−279,354.0	8
Day of Year + Solar Azimuth + (Day of Year × Solar Azimuth) + Mass	0.130	558,750.0	26.0	−279,367.0	8
Day of Year + Time of Day (h) + (Day of Year × Time of Day)	0.089	558,831.7	107.7	−279,408.8	7
Light Regime (LL/LD Fall/DD/LD Spring/LL next summer)	0.022	563,668.1	4944.1	−281,827.0	7
Daylength	0.008	568,034.5	9310.5	−284,013.2	4
Solar Azimuth	0.050	569,883.8	11,159.8	−284,937.9	4
Fraction of Moon Illuminated	0.001	570,436.3	11,712.3	−285,214.2	4
Lunar Phase	0.001	570,460.6	11,736.6	−285,226.3	4
Solar Altitude	0.026	577,769.7	19,045.7	−288,880.8	4
Post-Dive Surface Duration ~					
Day of Year + Mass	0.008	608,017.2	0	−304,003.6	5
Light Regime (LL/LD Fall/DD/LD Spring/LL next summer)	0.008	609,678.5	1661.3	−304,832.3	7
Daylength	0.002	610,477.7	2460.5	−305,234.9	4
Mass	<0.001	610,899.5	2882.3	−305,445.8	4
Year	<0.001	610,911.7	2894.5	−305,450.9	5
Sex	0.001	610,913.5	2896.3	−305,452.7	4
Fraction of Moon Illuminated	<0.001	611,046.0	3028.8	−305,519.0	4
Lunar Phase	<0.001	611,058.6	3041.4	−305,525.3	4
Day of Year + Solar Azimuth	0.022	612,500.0	4482.8	−306,245.0	5
Day of Year + Time of Day (h)	0.022	612,561.2	4544.0	−306,275.6	5
Day/Twilight/Night	0.009	613,013.4	4996.2	−306,501.7	5
Fraction of Moon Illuminated + Day/Twilight/Night	0.010	613,191.2	5174.0	−306,589.6	6
Lunar Phase + Day/Twilight/Night	0.010	613,200.6	5183.4	−306,594.3	6
Solar Altitude	0.014	614,694.4	6677.2	−307,343.2	4
Solar Azimuth	0.011	615,476.4	7459.2	−307,734.2	4
Bottom Time (%) ~					
Day of Year + Solar Azimuth + (Day of Year × Solar Azimuth) + Year	0.055	1,967,584	0	−983,784.0	8
Day of Year + Solar Azimuth + (Day of Year × Solar Azimuth)	0.036	1,967,629	45	−983,808.5	6
Day of Year + Time of Day (h) + (Day of Year × Time of Day) + Year	0.052	1,968,193	609	−984,088.6	8
Lunar Phase + Solar Altitude + Lunar Phase × Solar Altitude	0.025	1,979070	11,486	−989,529.1	6
Solar Altitude	0.024	1,980,456	12,872	−990,224.9	3
Time of Day (h) × Light Cycle	0.027	1,981,043	13,459	−990,514.5	7
Solar Azimuth	0.019	1,990,190	22,606	−995,091.9	3
Fraction of Moon Illuminated + Day/Twilight/Night + Fraction of Moon Illuminated × Day/Twilight/Night	0.017	1,990,897	23,313	−995,440.5	8
Daylength	0.005	2,013,636	46,052	−100,6815	3
Light Regime (LL/LD Fall/DD/LD Spring/LL next summer)	0.004	2,013,718	46,134	−100,6853	6

Table 1 (continued) | Subset of top-ranked models explaining variation in dive efforts

Model	R^2	AICc	ΔAIC_C	Log likelihood	df
Dive Duration:cADL Ratio ~					
Day of Year + Time of Day (h) + (Day of Year × Time of Day) + Mass	0.112	543,264.9	0	−271,624.5	8
Day of Year + Solar Azimuth + (Day of Year × Solar Azimuth) + Mass	0.113	543,286.3	21.4	−271,635.1	8
Day of Year + Time of Day (h) + (Day of Year × Time of Day)	0.084	543,308.3	43.4	−271,647.1	7
Light Regime (LL/LD Fall/DD/LD Spring/LL next summer)	0.018	548,119.2	4854.3	−274,052.6	7
Daylength	0.009	552,360.5	9095.6	−276,176.2	4
Solar Azimuth	0.049	554,072.8	10,807.9	−277,032.4	4
Fraction of Moon Illuminated	0.001	554,646.6	11,381.7	−277,319.3	4
Lunar Phase	0.001	554,681.7	11,416.8	−277,336.9	4
Day/Twilight/Night	0.016	560,439.6	17,174.7	−280,214.8	5
Solar Altitude	0.028	561,819.8	18,554.9	−280,905.9	4
Proportion of Dives Exceeding the cADL ~					
Mass	0.039	1,457,144	0	−728,569.0	3
Year	0.009	1,457,459	315	−728,725.6	4
Sex	0.006	1,457,461	317	−728,727.4	3
Fraction of Moon Illuminated	<0.001	1,457,900	756	−728,947.2	3
Lunar Phase	<0.001	1,457,920	776	−728,957.0	3
Lunar Phase × Day/Twilight/Night	0.001	1,458,052	908	−729,021.2	5
Daylength	0.015	1,464,413	7269	−732,203.7	3
Solar Altitude	0.003	1,471,532	14,388	−735,763.0	3
Solar Azimuth	0.016	1,471,599	14,455	−735,796.3	3

Generalized Additive Mixed-Effect Models demonstrating the relationship between indices of dive effort (depth, duration, post-dive surface duration, bottom time as a percentage of total dive duration, the dive duration-to-cADL ratio, and the probability of a dive exceeding the cADL) with geophysical time, intrinsic factors, and solar and lunar cycles. All models included individual animal PTT as a random effect. Models were evaluated based on variance explained, the smallest Akaike Information Criterion corrected for small sample size (AICc), and Log Likelihood. Note that Time of Day and Solar Altitude, and Day of Year and Lunar Phase/Fraction of the Moon Illuminated were not included in the same models due to multicollinearity. For all models evaluated see Supplementary Table 3.
Bold headers show the dive index that is predicted (dependent variable) from intrinsic, geophysical, and environmental variables.

In late summer, Weddell seal distribution shifts landward, and animals exhibit strong fidelity to remnant fast-ice in sheltered areas of McMurdo Sound (i.e., Cape Armitage, the base of the Erebus Glacier Tongue) to avoid predation by killer whales (*Orcinus orca*) that gain access to the region as the sea ice deteriorates[41]. During this time, female Weddell seals are intensively foraging and quickly recuperating body mass after weaning their pups[42,43], yet it remains unknown whether the change in the timing of daily foraging activities is a strategy to temporally evade predation pressures. Whether because of a lack of strong selective pressure to align foraging efforts with prey DVMs, the preference to follow activities of prey displaying reverse DVM, temporal partitioning to minimize predation risk by killer whales, or any combination thereof, daytime haul-outs are likely advantageous because solar irradiation and warmer ambient temperatures facilitate warmer skin temperatures for more rapid hair re-growth during the annual molt[44,45]. Keeping such energetically costly life history events succinct would likely reduce total metabolic overhead[46].

In addition to strong circadian patterns in when animals preferred to dive, there was also significant circadian organization in the magnitude of dive efforts (i.e., depths, durations, resultant post-dive surface recuperation times, bottom times, and encroachment on physiologic limits). Circadian oscillations were much stronger in dive depths than in durations, perhaps reflective of finite aerobic capacities constraining flexibility in breath-hold behaviors. This supports the notion that physiologic thresholds may, through their interaction with extrinsic features such as DVMs, act as chronodisruptors in central-place foragers that must return to the water's surface at the end of each dive. Circadian rhythmicity was strongest when light/dark cycling occurred during the fall and spring, and organization became attenuated during the Polar Day (LL, summer) and Polar Night (DD, winter). Without solar illumination, lunar cycles became more important in structuring dive efforts (depths, durations, etc). While less is

known about biological rhythms through the Antarctic winter, lunar phase and altitude drive zooplankton movements throughout the Arctic winter. This has been coined 'lunar vertical migrations' (LVM)[47] with rhythmic periods lasting 29.5 days rather than in circadian (24-h) cycles. In this study, the Weddell seal's circadian rhythmicity with solar cycles was much stronger than periodicity tracking lunar phases, likely due to the much greater light intensity of the sun compared with the moon. The impacts of lunar illumination with the full moon were primarily apparent once the sun had receded below the horizon (i.e., in the absence of sunlight).

Effective use of cues to 'anticipate' when more intensive activity begins would allow the animals to physiologically prepare for deeper and longer dives for more successful foraging[36]. Such preparation might include decreased body temperatures, rhythmic gene expression and activities of metabolic enzymes, and/or suppressing digestion to depress metabolic rates[48]; all would sustain longer dives. However, the animal's endogenous circadian rhythms may also vary throughout the year. For example, in continuous daylight during the austral summer, the Weddell seal's circulating melatonin levels either have weak or absent circadian oscillations[49,50]. The breakdown of circadian organization in behaviors under continuous light or dark conditions has been hypothesized to allow animals to sync phase with the light/dark cycle quickly when it resumes[7], and transitions between light regimes occur most rapidly in high-latitude environments[51]. Weddell seals and other marine mammals may use photoperiodic cues directly, or alternatively, the predator's behaviors may merely synchronize to the endogenous rhythms and resultant behaviors of their prey (i.e., masking)[52].

Net energetic gains from foraging activities may also vary diurnally. For example, crepuscular foraging tends to be most profitable for predators, as both diurnal and nocturnal prey are active[53] and may be a time of day when prey is more abundant and easily accessible without the need to expend more energy on longer and deeper dives. However, there is evidence that

Fig. 5 | Strong photoentrainment of dive behaviors. Weddell seal dive effort parameters (**a**, **b** depth; **c**, **d** dive duration; **e**, **f** post-dive surface duration; and **g**, **h** bottom time as a percentage of total dive time; $n_{seals} = 59$; $n_{dives} = 281,268$), and relative to the calculated aerobic dive limit (**i**, **j** dive duration-to-cADL ratio, and **k**, **l** the proportion of dives that exceeded the cADL; $n_{seals} = 54$; $n_{dives} = 272,984$). All dive efforts and the extent to which animals pushed physiologic thresholds increased with solar altitude as the sun rose above the horizon (*left*). Note that when the solar altitude angle is ≥ 0° this is taken to be daytime (*yellow*), 0 to −18° is considered twilight (*light blue*), and at <−18° the sun is well below the horizon at nighttime (*dark blue*). Similarly, dive efforts increased as the solar azimuth changed with the sun positioned directly north on the horizon at solar noon (*right*; angles shown as degrees with 0 denoting south. *Yellow* = approaching solar noon with the sun positioned north, *light blue* = sun to the east/west on the horizon, *dark blue* = sun positioned south at solar midnight). *Dashed line* denotes mean; and GAMM shows the model fit (*solid black line*) ± 95% confidence interval (*gray shaded region*).
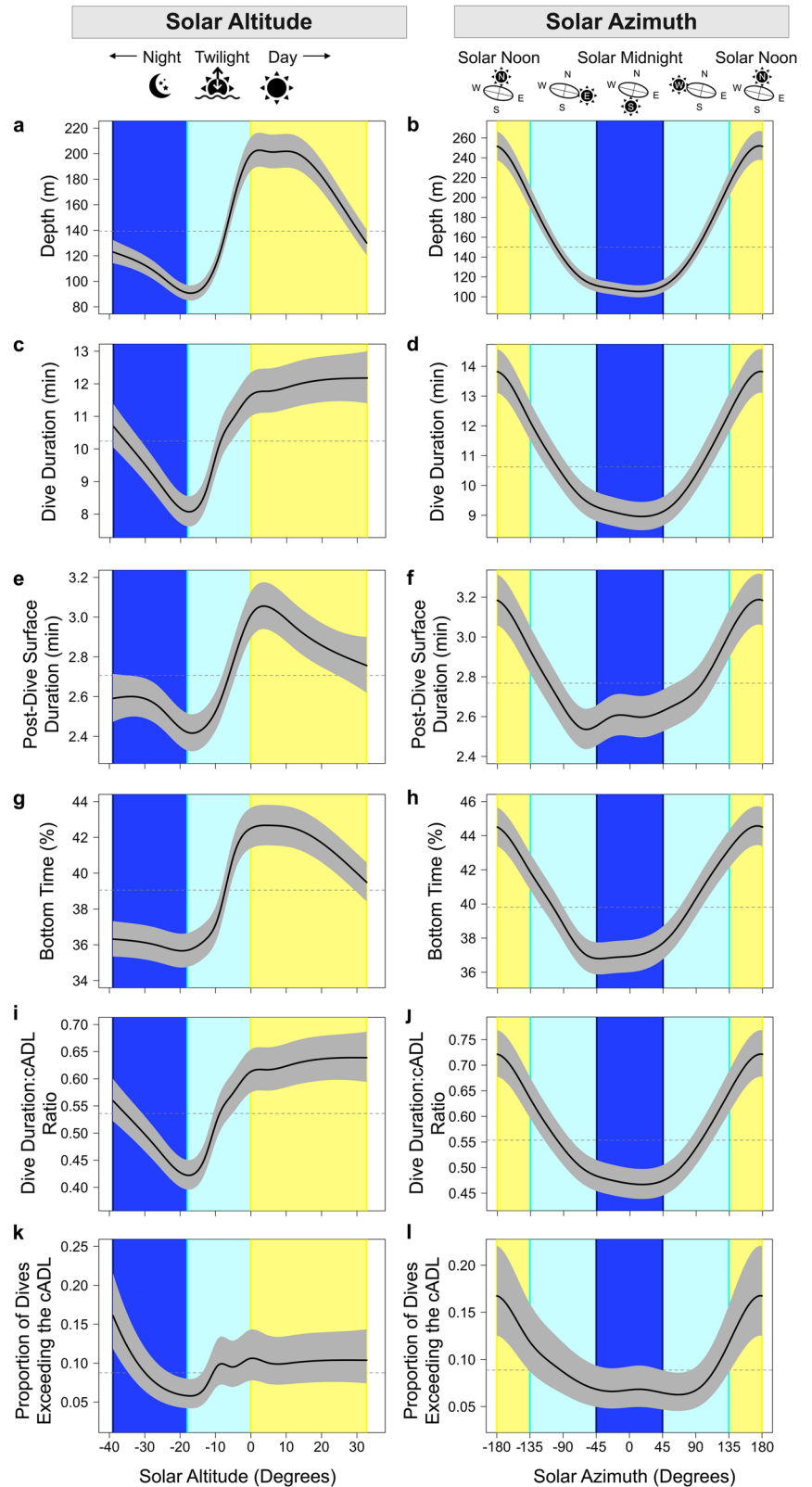
Weddell seals are visual predators with higher prey capture rates during daylight than in darkness: they use strategic maneuvers to provide back-lighting before striking prey and have sensitive eyes for underwater low-light conditions, including more rod photoreceptors in the retina and large pupil areas[54,55]. Weddell seals also exhibited strong photoentrainment in this study, with marked increases in dive efforts as the sun rose during twilight hours. In addition to changes in solar position during twilight, there are large

changes in irradiance and light's spectral composition (with lower wavelengths <500 nm) at these times, and solar azimuth across the day can also serve as a prominent zeitgeber to entrain circadian clocks and aid in compass navigation, influencing animal behaviors[53]. The seals' preference to increase dive efforts during daylight hours rather than foraging at night when prey would be shallower in the water column suggests that they may realize higher net energetic gains when foraging primarily during daylight
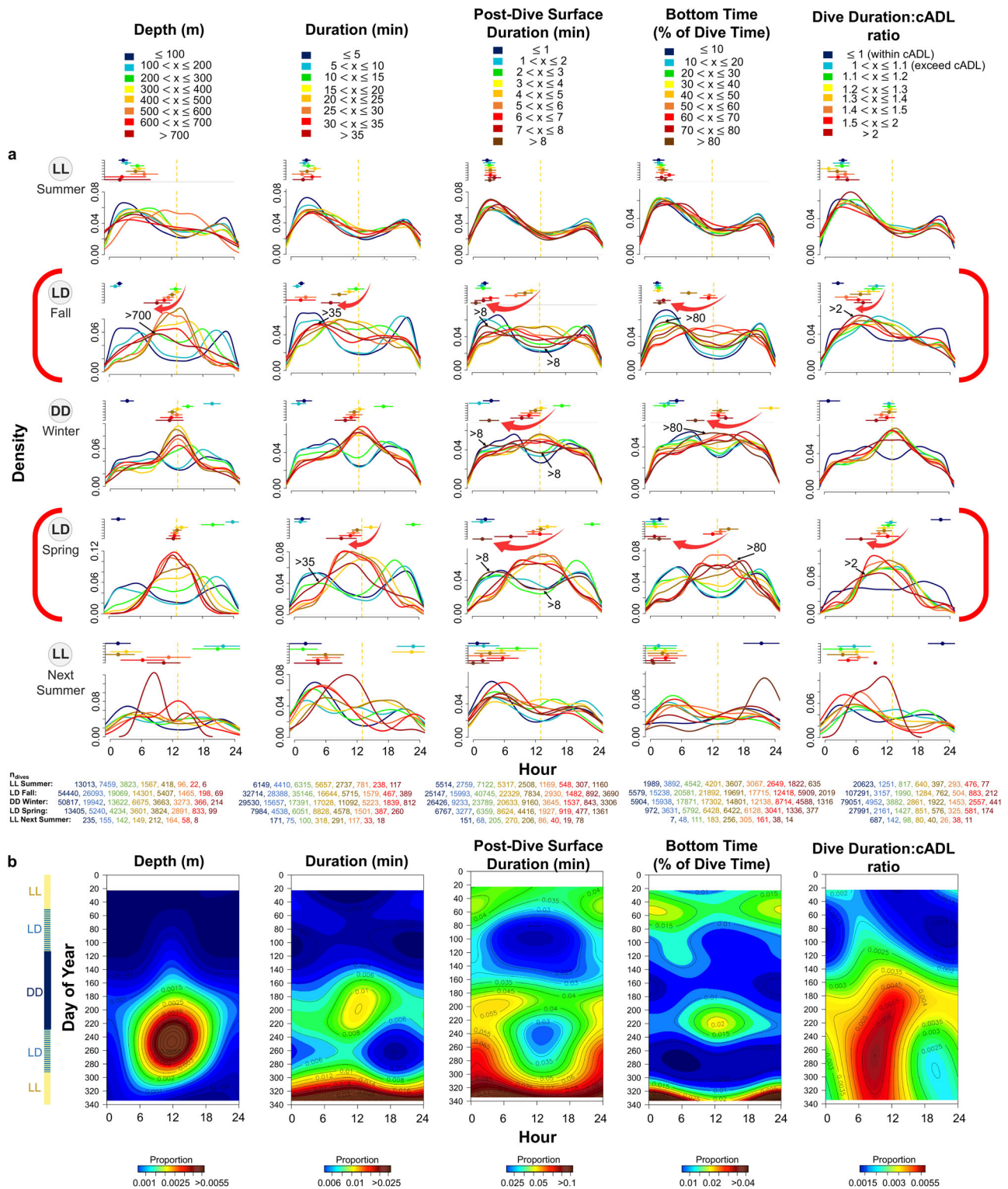
Fig. 6 | During times of the year with LD cycling, the longest dives that far exceeded the cADL and the longest post-dive surface times were offset from mid-day. a Density plots showing the local time of day that dives were made for increasing dive depths, durations, post-dive surface durations, percent bottom time, and dive duration:cADL ratio across the year's changing light regimes. At *top* of each plot are the weighted circular mean ± 95% CI by dive class (as defined in the top legend); red arrows denote that the most extreme dives were made significantly earlier in the day compared with dives of average magnitude (i.e., non-overlapping 95% CI's). Patterns were particularly prominent during times of the year with LD cycling (red brackets). Vertical dashed yellow lines show solar noon at 13:00 local time in

McMurdo Sound (New Zealand Standard Time; UTC + 12). Sample sizes are noted below. **b** 2-D plot from binomial GAMMs specifically showing the probability of the most extreme dives (i.e., dives classified as >700 m depth, >35 min duration, >8 min post-dive surface duration, >80% bottom time, dive duration:cADL ratio >2) occurring across the day (local time) and year. The longest dives and post-dive surface recuperation durations, and dives that exceeded the cADL to the greatest extent were made earlier in the day and were offset from solar noon. Note that because the proportion of dives that overall exceeded the cADL is a binomial function this is the same pattern as in Fig. 4.
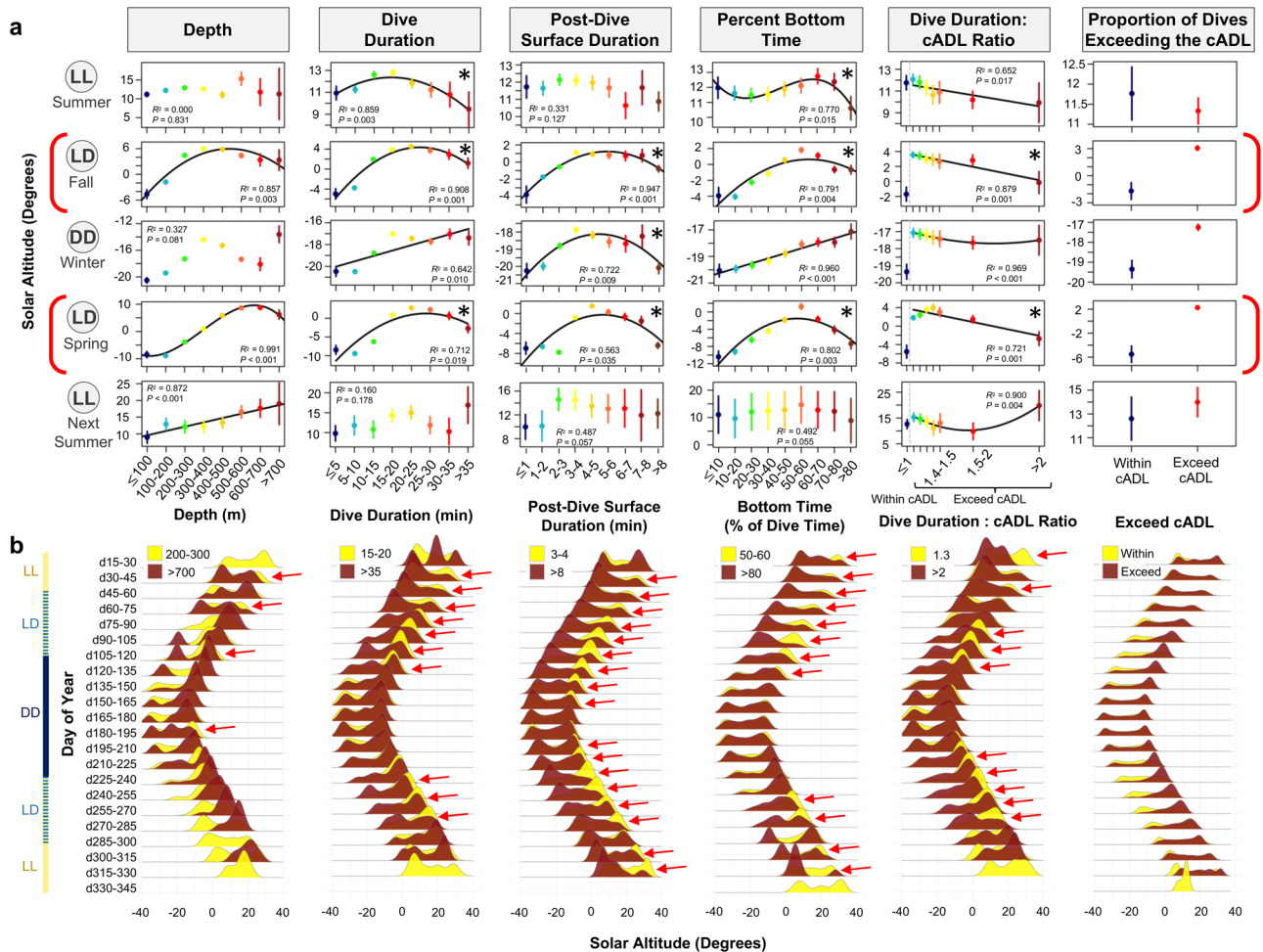
Fig. 7 | During times of the year with LD cycling, the most extreme dives occurred when the sun was lower in the sky. a During LD conditions (*red brackets*), all indices of dive effort increased as solar altitude increased until mid-level classes. However, the most extreme dives occurred when the sun was lower in the sky. These patterns were often not present under LL or DD conditions. Mean ± 95% CI solar altitude is shown from GAMM models testing for differences by dive classification group, with individual ID as a random effect. Best-fit order polynomial curves, as determined using AICc were fit to each. For dive duration:cADL ratios, curves were only fit to points where the ratio >1; Curves could not be fit for the proportion of dives greater than the cADL (a binomial). *Asterisks* mark instances that dives of the most extreme class were made when the sun was significantly lower in the sky relative to dives of average effort. **b** Density distributions depicting the solar altitude that average dives

were made (*yellow*) compared with the most extreme dives (*dark red-brown*) for 15-day intervals. The most extreme dives were consistently made when the sun was lower in the sky during times of the year with LD cycling (*red arrows* mark distributions shifted toward lower solar altitude; dive duration, surface duration, % bottom time, dive duration:cADL ratio); patterns were weaker for dive depths; dives exceeded the cADL overall more often when the sun was higher in the sky as most dives mid-day were 1.1–1.3× the cADL. Note that density plots are shown because Day of Year and Solar Altitude could not be included in the same GAMM models due to collinearity. n_{dives} are the same as in Fig. 6, with the addition of the proportion of dives that exceeded the cADL (within, exceed: LL Summer – 20623, 3961; LD Fall – 107291, 8792; DD Winter – 79051, 18068; LD Spring – 27991, 6095; LL Next Summer – 687, 435).

hours despite the added energetic costs to reach greater depths coinciding with prey DVMs.

Early in the year, many of the animals were near the Erebus Bay breeding colonies where dives would be constrained by shallow local bathymetry[30], and mean dive depths during peak daylight hours reached ~200 m. All indices of foraging effort were higher in the spring, and at this time of year, dives reached ~400 m depth on average during mid-day, well into the mesopelagic, disphotic zone (euphotic depth within the Ross Sea is between 9 and 82 m in summer[56]). Weddell seal mid-day dive depths throughout the year coincide with depth layers where larger cohorts of adult silverfish are typically found (200–400 m)[57]. Weddell seals also use physical features on the underside of the sea ice as visual landmarks to navigate back to breathing holes[58]. Hunting during daylight hours may minimize the time required to find illuminated breathing holes during ascent and thus allow animals to devote a greater proportion of the dive to pursuing prey. Indeed, this study also suggests greater foraging efficiencies by significantly greater bottom times (as a percentage of total dive time) mid-day. While there

remains substantial variation in such large behavioral datasets, the extent that temporal and light cycle characteristics accounted for variation in behavior in this study was similar to the variation accounted for in habitat use models[30].

More effective foraging when there is ambient light would also provide a potential proximate mechanism driving the Weddell seal's behavioral preference to make their deepest and longest dives offset from mid-day during times of the year with light/dark cycling. Under LD conditions there would be stronger pressures for Weddell seals to concentrate their dive durations around the ADL during peak foraging (daylight) hours. Indeed, mid-day and when the sun was highest in the sky, dives remained ~1–1.3× the cADL, demonstrating that even as animals increased their foraging efforts (and slightly exceeded the cADL) they only did so by amounts that were unlikely to significantly increase post-dive recuperation times. Because there is an exponential relationship between anaerobic dive durations and surface recovery time, more extreme dives require disproportionately longer recovery times (or a subsequent series of shorter aerobic dives)[24,59]. Thus,
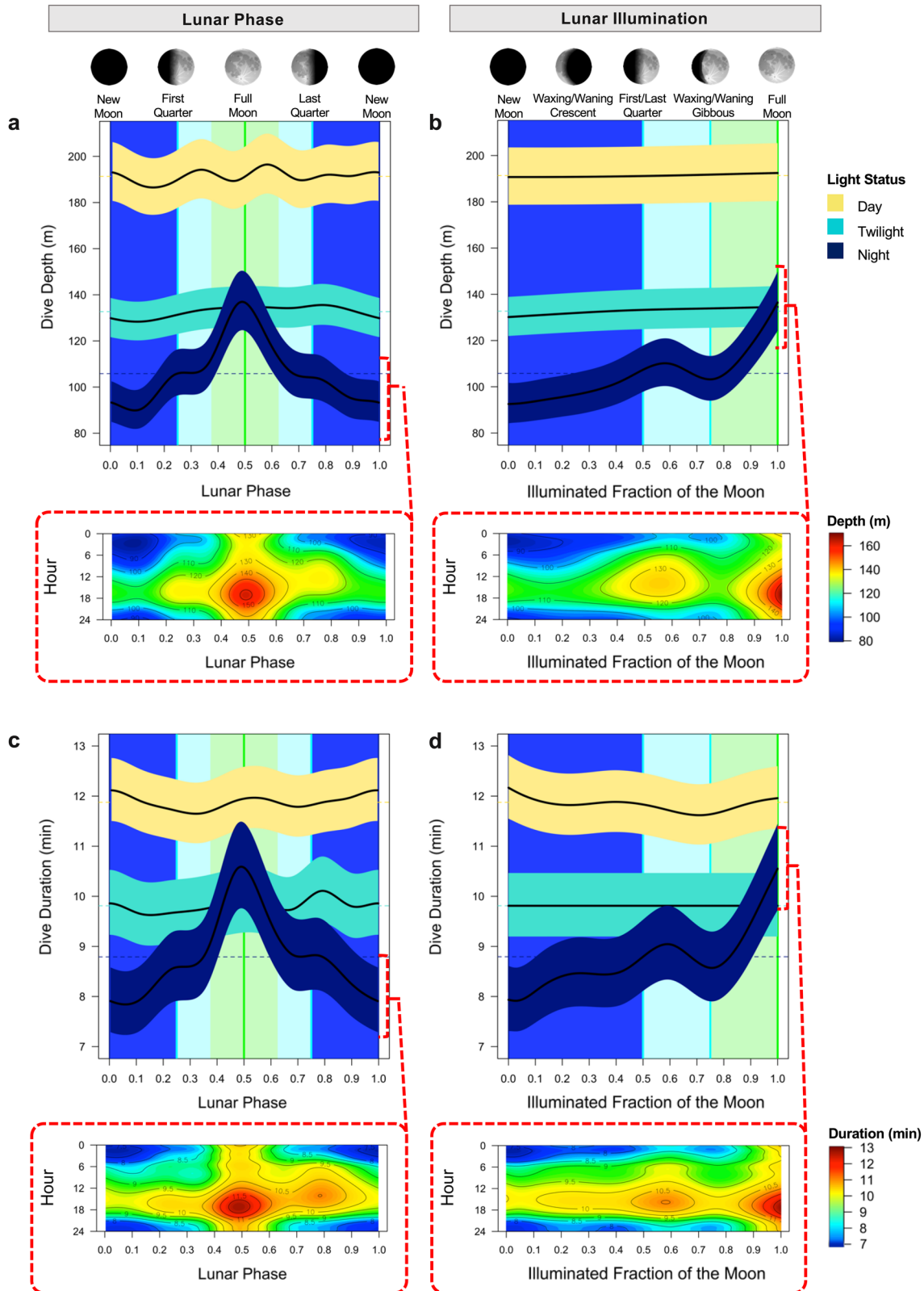
Fig. 8 | In darkness, lunar phase and illumination shaped dive behaviors. Weddell seal dive depths (**a**, **b**) and durations (**c**, **d**) increased during the full moon (*left*; lunar phase was 0.5 at the full moon) when a greater fraction of the moon was illuminated (*right*). Lunar impacts on dive behaviors were most notable at nighttime (when the sun was at least 18° below the horizon; note that this can be at any hour during the winter Polar Night). Insets *framed in red* focus on nighttime dives only and show that the full moon and illumination increase dive depths and durations at all hours (in New Zealand Standard Time; UTC + 12). n_{seals} = 59; n_{dives} day = 91,913; twilight = 126,268; night = 63,087.
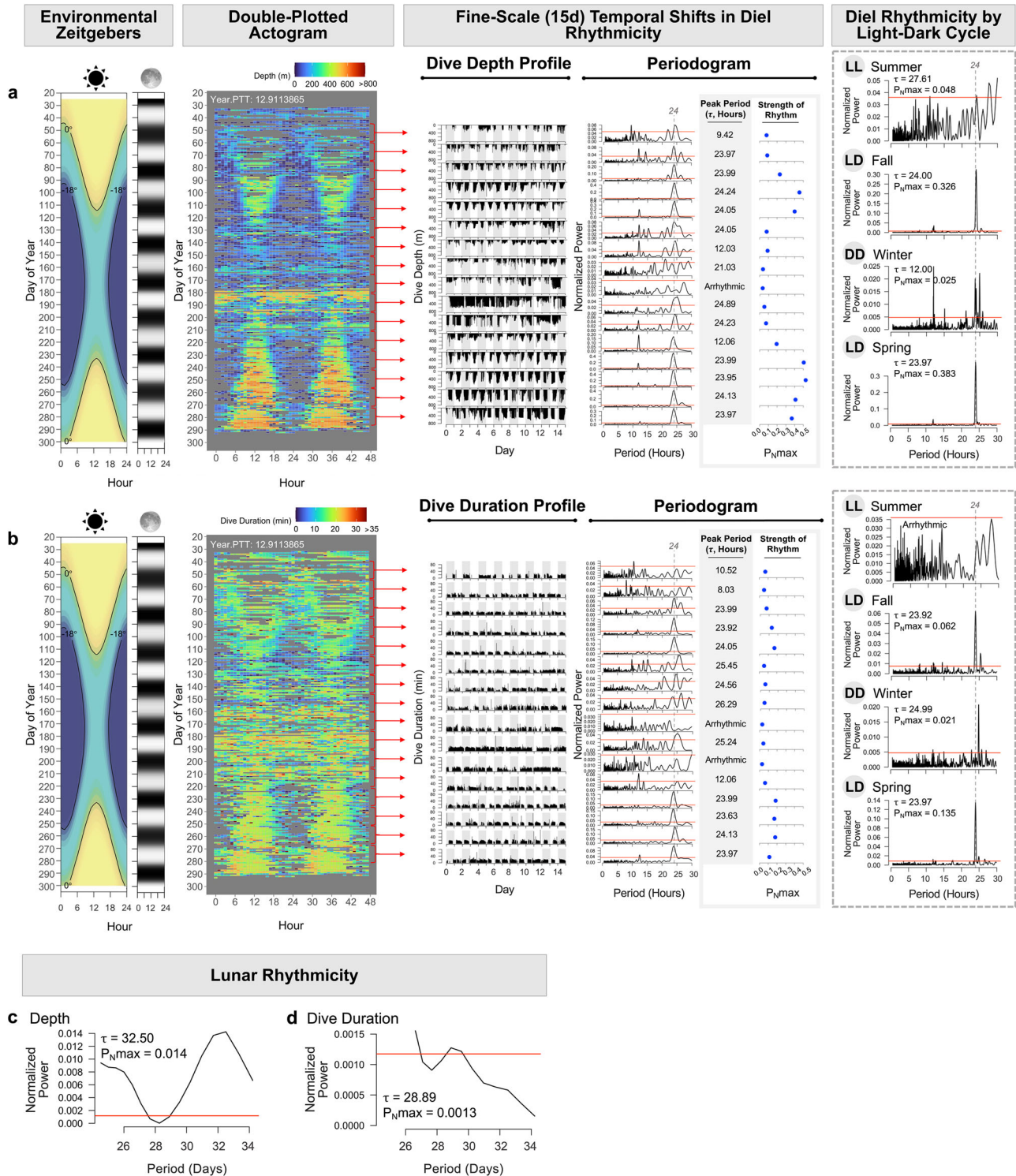
Fig. 9 | A representative analysis of periodicity showing greater rhythmicity in dive depth than duration. a Dive depth and **b** duration for Weddell seal PTT 12.9113865 after instrument recovery (n = 13,636 dives). Solar (*yellow* = solar altitude >0°, *light blue* −18 to 0°, *dark blue* < −18°) and lunar (*black* = new moon, *white* = full moon) environmental zeitgebers derived from seal positions from respective study year are denoted. Dive behaviors changed across the day and year, displayed in double-plotted actograms with each cell representing the mean depth or duration for that respective hour. All dive activities are shown in McMurdo local time (New Zealand Standard Time; UTC + 12). Note 'banding patterns' with greater dive depths and durations, particularly at ~d125, 155, 185, and 215 during the full moon and DD conditions. Dive profiles for 15 days (alternating gray and white backgrounds show alternating days) were used to construct Lomb–Scargle periodograms for fine-scale temporal shifts in diel rhythmicity; note different scales for normalized power (P_N). The dominant frequency (tau) between 0.5 and 30 h and the strength of the rhythm ($P_N$max) were extracted from each periodogram when it exceeded the significance threshold (*red line*). Additional periodograms were constructed after grouping all dives by light regime (light-light LL; light-dark cycling LD in Fall and Spring separately; dark-dark DD); and for all dives to discern circalunar rhythms between 24.5 and 34.5 days for **c** depth and **d** duration.
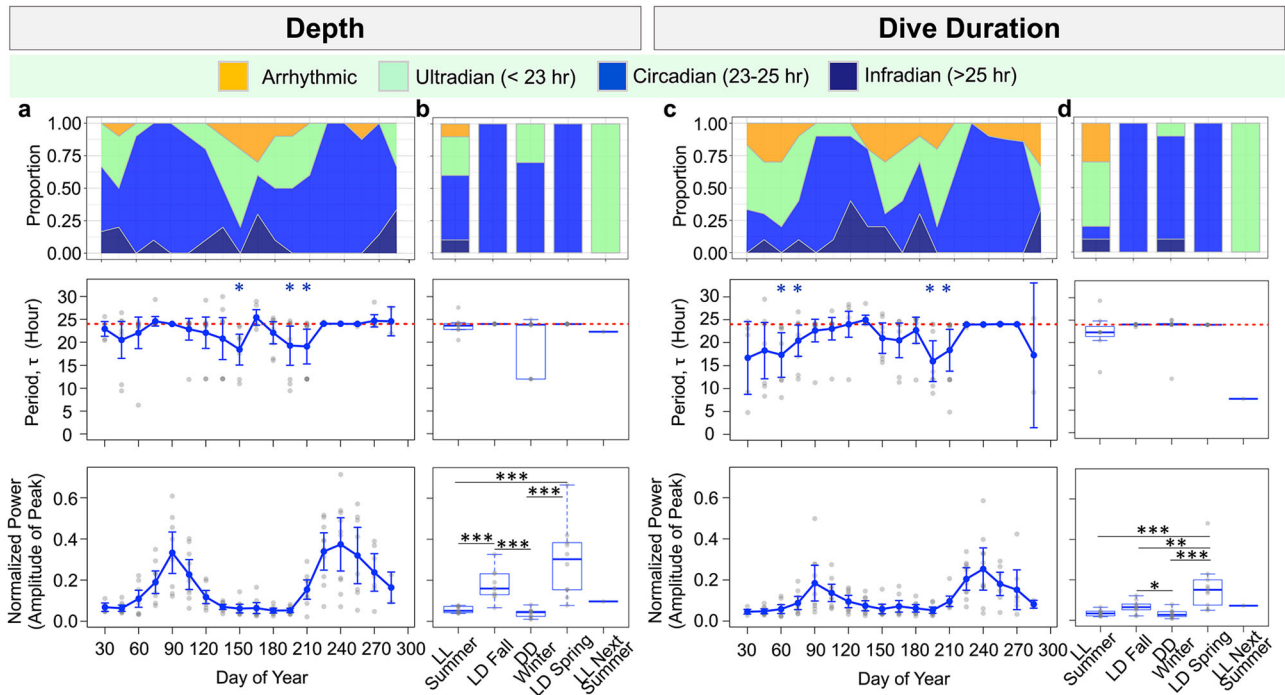
Fig. 10 | Attenuation of circadian rhythmicity without light-dark cycling. The proportion of animals exhibiting arrhythmic, ultradian, circadian, or infradian dive rhythmicity, period (only when exceeding significance thresholds), and normalized power ($P_N$max) of the peak taken from Lomb–Scargle periodograms constructed for (**a, c**) fine-scale 15-day intervals and with all dives combined by light regime (**b, d**) for dive depth (*left*) and duration (*right*). Analyses were only performed on recovered dive records without transmission loss ($n = 10$). Scatterplots depict the mean ± 95% confidence interval; *asterisk* denotes timepoint where the period was significantly less than 24-h. n_{seals}, d30 = 6, d45–240 = 10, d255 = 8, d270 = 7, d285 = 3. Boxplots encompass the interquartile range, the center line denotes the median, and whiskers encompass the range of values; * signifies $P < 0.05$, **$P < 0.01$, ***$P < 0.001$. n_{seals}, LL, LD Fall, DD, LD Spring = 10, LL next summer = 1. 'LL next summer' was omitted from statistical analyses due to low sample size.

even though most of the Weddell seal's dives remain aerobic or close to the ADL in nature, the timing that animals make the relatively few but 'extreme' long dives would disproportionately influence daily foraging efforts[19,24].

Because making dives that exceed the ADL would reduce the total amount of time animals could spend diving (Fig. 11)[19,60], they are generally thought to be less efficient from an Optimal Foraging Theory perspective. Thus, based on Optimal Foraging Theory, we predict that it would be disadvantageous to make dives far exceeding the ADL during times of the day when more light enters the water column, and hunting would be aided by greater visibility. And this was indeed reflected in the seal's dive behaviors. Under LD conditions, Weddell seals spent the most time diving during mid-day, and the longest duration dives with the longest post-dive surface times were made earlier in the day and/or when the sun was lower in the sky. Still, there are numerous documented examples of marine mammals such as northern and southern elephant seals (*Mirounga angustirostris; Mirounga leonina*)[31,60,61] and beaked whales (*Ziphius cavirostris*)[62] consistently exceeding their cADLs, and additional instances when it would be advantageous for animals to surpass physiologic thresholds[60,63].

There are likely to be strong selective pressures for plasticity both in physiology and behaviors in response to patchy or ephemeral prey. It may be energetically favorable for an animal to exceed its aerobic capacity, if that enables the capture of a particularly large and calorically dense prey item or if the area otherwise has low prey biomass[25,64]. Another factor in balancing the optimal timing to exceed physiologic thresholds is prey handling and processing times. For example, Weddell seals are known to terminate dive bouts after catching a large toothfish (1–2 m in length; ~70–90 kg), since it requires hours to remove spines and be-head before consumption[65,66]. It may be advantageous for a seal to exceed its ADL in hunting a toothfish because processing time at the surface could coincide with the breakdown of anaerobic byproducts. The net reward of this energy-dense prey item (15% fat and 9.4 kJ g^{-1} wet mass)[67] will likely outweigh the additional costs of lost foraging time. Conversely, a seal does not necessarily have to push physiologic limits to attain greater energetic

returns if a toothfish is encountered early in a dive[65]. Long dives can also serve as an exploratory endeavor or for predator avoidance, and may not always conclude with higher rewards[68]. Dive behaviors are also known to change as animals return to the breeding colonies each year when females prepare for parturition and males establish underwater mating territories[29,30].

Throughout this study, we have compared dive durations to the cADL as determined through measurements of tissue O_2 stores. While the tight correspondence between O_2 stores and the 'lactate threshold' ADL has been validated specifically in Weddell seals[23], there are many additional complexities in diving physiology that we are unable to monitor using current remote technologies. Temporal shifts in O_2 stores and/or diving metabolic rates may occur across the year. We have shown previously that hemoprotein concentrations and endogenous O_2 did not change overwinter in these same skip-breeding Weddell seals[42,69]. However, the dive response is 'graded', and diving metabolic rate has substantial inter-dive variation[24,70,71] that we could not measure. Therefore, the cADL may be underestimated for some dives and it may not be possible to distinguish whether many of those mid-day dives that were ~1–1.3× the cADL were anaerobic versus actually aerobic. Nevertheless, this study's most extreme, long dives appear to be strategically timed and are well beyond practical physiologic thresholds (>2× cADL) even when accounting for variability in metabolic control.

In summary, we demonstrate that the selective pressures environmental zeitgebers place on dive behaviors driving circadian patterns can be at odds with physiological thresholds imposed on dive capacities in pelagic-foraging marine mammals. We provide evidence that Weddell seals strategically perform their most extreme dives well before solar noon. The longest dives that far exceeded aerobic thresholds were preferentially placed such that they did not overlap with optimum conditions for visual hunting, presumably to prevent prolonged surface recuperation times and to maximize the total time spent diving mid-day. The prioritization of remaining close to physiological thresholds, specifically at solar noon, likely impacts the
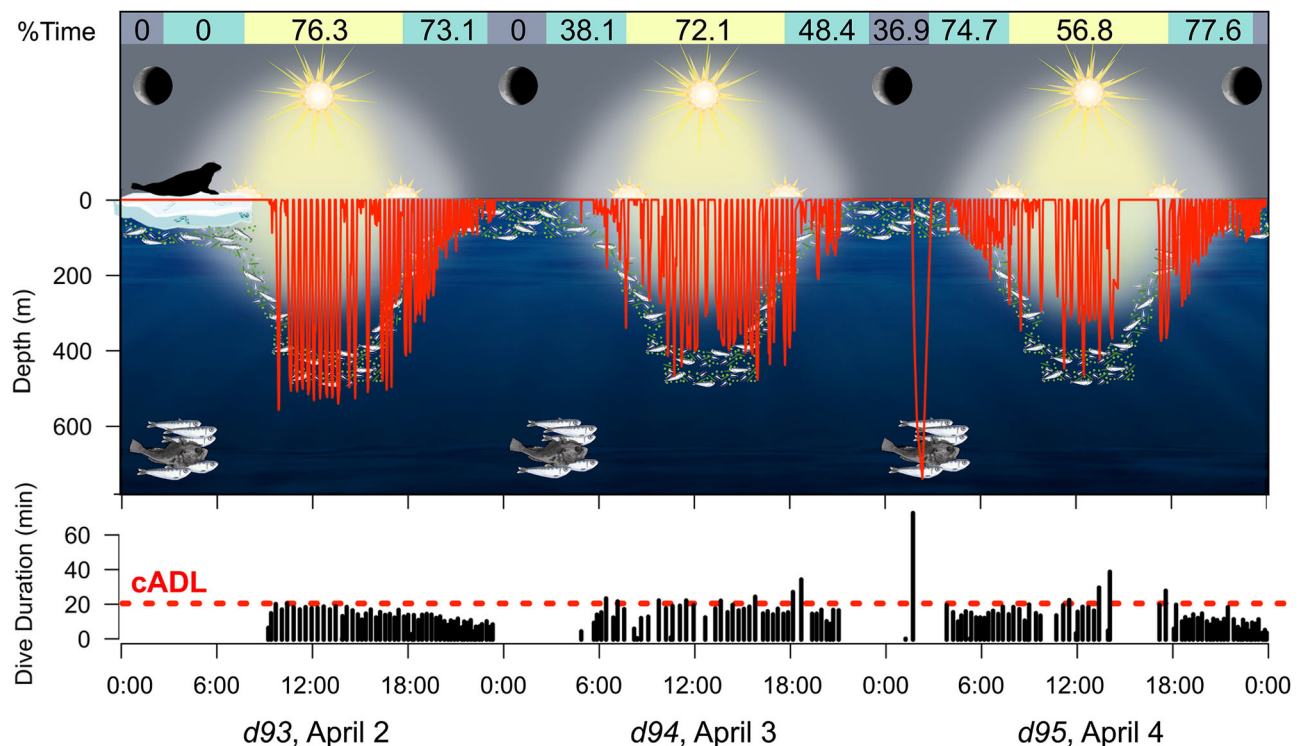
Fig. 11 | Timing of the most extreme dives in an optimal foraging theory framework. (*Top panel*) A representative record from PTT 12.9113865 demonstrates that most dives occurred during twilight and daytime, with dive depths and durations increasing mid-day (d93, d94) when there is light-dark cycling. The percentage of time spent diving is shown, separated into categories: night (*blue*), twilight (*cyan*), and daytime (*yellow*). Dive durations (*bottom panel*) stayed close to the cADL (*denoted by red dashed line*) during peak daylight hours to maximize the total time that could be spent diving (i.e., 76.3% and 72.1% of daytime). The most extreme dives, with the longest durations that greatly exceeded the cADL were significantly misaligned from daylight hours. Thus, recuperation times did not disrupt the intensive dive activity that occurred mid-day (in d94 or d95). However, if a dive exceeded the cADL mid-day, the animal had to spend longer at the surface to clear anaerobic byproducts, reducing the total time spent diving during optimal daylight foraging conditions (in the middle of d95).

extent to which diving vertebrates can follow and exploit diel resources within the water column. The magnitude of diel rhythms and the temporal partitioning of the longest dives within the day were strongest during times of the year with light/dark cycling. Conversely, these patterns were dampened under constant light or darkness. This work highlights the balance between utilizing foraging strategies that are most advantageous in a diel preyscape and the energy and time costs of pushing physiological limitations in a diving mammal.

Methods
Animal handling and instrument deployment
We have complied with all relevant ethical regulations for animal use. All work and animal handling protocols were approved by the University of Alaska Anchorage and the University of California Santa Cruz Institutional Animal Care and Use Committees (all authors and project participants were based at these institutions at the time all fieldwork was conducted). The research was authorized under National Marine Fisheries Service Marine Mammal Protection Act permit 87-1851-04 and Antarctic Conservation Act permits while at McMurdo Station.

Sixty-two post-molt adult Weddell seals (52F: 10M) were captured on the fast-ice along the McMurdo Sound region, Antarctica in Erebus Bay (~77°S, 165°E) and the Victoria land coastline (~76°S, 162°E) in January and February 2010–2012[30]. Females were either confirmed (through demographic records) or presumed to be skip-breeders that did not produce a pup during the study year because they were fully molted[72,73]. Animals were sedated with an initial intramuscular administration of ~1.0 mg/kg tiletamine/zolazepam HCl. Following a 10–15 min induction period, animals were captured via hoop net, and additional intravenous administration(s) of ketamine and diazepam (~0.2 mg/kg and 0.012 mg/kg, respectively) were given as needed to keep animals sedated while eupneic.

All animals were outfitted with Conductivity Temperature Depth-Satellite Relay Dive Loggers (CTD-SRDLs) weighing 600 g from the Sea Mammal Research Unit (University of St. Andrews, St. Andrews, Scotland) and a VHF transmitter (Sirtrack, Inc.) to facilitate relocation. Instruments were attached to the fur (CTD-SRDLs on the head; VHFs on the flank) using 5 min epoxy (Loctite® or Devcon®)[29,30]. Data were transmitted as compressed dives to the Collecte Localisation Satellites, Advanced Research and Global Observation Satellite System (CLS ARGOS)[74]. These instruments are programmed to relay an unbiased sampling of dives, and transmitted dives exhibit the same seasonal and hourly patterns as transmitted and recovered dives combined (Supplementary Fig. 4). Ten instruments were recovered with full dive records (i.e., without satellite transmission loss) the following year. Recovered records were used for analyses whenever possible.

Calculation of the aerobic dive limit
Animals were weighed using a tripod and hanging scale (except for one animal where body length and girth were used to estimate mass following Castellini and Kooyman[75]). Blood and muscle O$_2$ stores were measured to calculate an aerobic dive limit (cADL) in 54 of these same animals[42,69] as described in Shero et al. (2015; 2022)[42,69]. Blood was collected from the extradural vein into EDTA (for hematology) or heparinized vacutainers (for blood volume). Hematocrit (Hct; packed red blood cell volume) was determined by whole blood centrifugation, and blood hemoglobin concentrations were measured using the cyanomethemoglobin assay (using a UV/Vis Beckman series 530 spectrophotometer, Beckman Coulter, Inc.; at $\lambda = 540$ nm). Blood volume was measured using the Evan's Blue dye technique. After a pre-injection blood sample was collected, 0.5–1.2 mg kg^{-1} of Evan's Blue dye was administered into the extradural vein; doses were determined gravimetrically prior to injection and the syringe was flushed to ensure complete delivery. Injections were followed by three consecutive

blood draws ~10 min apart (exact time of blood draws were recorded). These samples were centrifuged and plasma background absorbance values were measured at λ = 740 nm; this was subtracted from the dye's optical density at λ = 624 nm. Dilution of the dye relative to the initial injectate was used to calculate plasma volume as described in Foldager & Blomqvist[76] and El-Sayed et al.[77].

Blood volume (BV) was calculated as:

$$BV(L) = \frac{\text{Plasma Volume(L)}}{(100 - \text{Hct})/100} \quad (1)$$

Muscle myoglobin concentrations were determined from a tissue biopsy collected from the *Longissimus dorsi* primary swimming muscle, following Reynafarje 1963[78] and modified for microwell format following Prewitt et al.[79]; samples were run in quadruplicate alongside lyophilized myoglobin horse standard and previously assayed pinniped samples (on a Molecular Devices SpectraMax 340 microplate reader; at λ = 538 and 568 nm to account for any hemoglobin contamination).

Total body oxygen (TBO$_2$) stores were calculated as the summation of lung, blood, and muscle O$_2$ stores. Lung O$_2$ stores were calculated as $V_i \times 0.15\text{FO}_2$, where V_i is the estimated diving lung volume (in liters) and is taken to be $0.5 \times 0.1(\text{total body mass})^{0.96}$. This assumes that lung volume is at 50% of total capacity when animals initiate a dive, and 0.15FO$_2$ is the partial pressure of O$_2$ in the lungs[21]. Blood O$_2$ stores were calculated from hemoglobin, Hct, and blood volume assuming that: (1) Hemoglobin has an O$_2$ carrying capacity of 1.34 mL O$_2$ g^{-1} [hemoglobin], (2) arterial blood is 33% of total blood volume; 66% of blood is in the venous system, (3) in the arterial system the maximum O$_2$ saturation possible is 95%, and the minimum saturation is 20% after O$_2$ has been offloaded at other tissues, (4) venous blood has 5% less volume than the starting arterial O$_2$ stores and can be extracted to zero[22,23,80]. Muscle O$_2$ stores were calculated for each animal assuming that myoglobin also had an O$_2$ carrying capacity of 1.34 mL O$_2$ g^{-1} [myoglobin] and that the animal's muscle mass was 38% of lean body mass[22]. Body composition was determined using the tritiated water (HTO) dilution technique as described in Shero et al.[81], with lean body mass taken to be fat-free tissue. Each animal's diving metabolic rate (DMR) was estimated from 1.6× Kleiber[82,83]. The calculated aerobic dive limit (cADL; in minutes) was determined as TBO$_2$ stores (in mL O$_2$) divided by DMR (mL O$_2$ min^{-1}).

Haul-out and summary data for activity budgets
Animals were determined to be hauled-out when the instrument was dry for >10 min; the haul-out ended when the tag was wet for >40 s[74]. Each instrument also constructed a 'summary record' for every 6-h time period. It contained statistics including the number of dives taken, and the proportion of time spent diving. These summary records provide a more complete overview of animal activity budgets because they are compilations of all the recorded activities and remain unbiased to satellite transmission conditions.

Dive processing for vertical foraging activity
From dive records, the day of instrument deployment and recovery were excluded from analyses. Erroneous dives that were >1.5× the Ross Sea maximum bathymetry (ETOPO 1), >5400 s in duration, >2000 m depth, had vertical travel speeds >4 m/s, had duplicate timestamps, or within-dive timestamps associated with the mid-depths that decreased across the dive were also removed. For finer-scale analyses of shifts in dive attributes, dives were retained if the underwater event lasted for 4× the sampling interval and depth resolution of data loggers, or ≥ 16 s in duration and to depths ≥ 12 m. The maximum post-dive surface times were 9 min, after which instruments were programmed to trigger a haul-out. This 'cap' was not present in the physically recovered records, and thus all surface times >9 min were trimmed to 9 min to ensure comparability with transmitted records. Bottom time was calculated as the percentage of the total dive time that was spent at ≥ 80% of the maximum depth for a given dive[84]. All times

are reported as local time in the study area (New Zealand Standard Time; UTC + 12).

Tracklines, and lunar and solar attributes
Position records associated with each individual dive were filtered using a speed filter (locations must have been <15 km h^{-1} from the previous horizontal position). Tracklines were interpolated at 2 h intervals using forward-looking particle filtering models and accounting for ARGOS class-specific position errors as described in Goetz et al.[30]. Of all dives, 98.8% remained within 15 degrees of longitude in this study; 53.2% occurred within just 3 degrees of longitude (i.e., resolution within 12 min). Solar and lunar characteristics were calculated from the coordinates and timestamps from each dive using the 'suncalc' package in R[85]. This included daylength, solar azimuth (position along the horizon measured from 0° when directly south and 135° is the northwest, 180° when the sun is directly north), and solar altitude (degrees above the horizon). Daylight was considered to be when the solar altitude was ≥ 0° (i.e., above the horizon), 0 to −18° at twilight, and <−18° at nighttime. To determine how dive behaviors differed by light regime, behavioral data were also grouped by days of 24-h daylight (LL; summer), days with both light and dark cycles (LD; with the sun above and below the horizon, fall and spring), and days of 24-h darkness (DD; winter when the sun never rose above the horizon and remained <0°) at the McMurdo Station field site. We use the labels: "LL", "LD", "DD" as defined above for readability and to retain standard chronobiologic terminology. We note that wild animals would not experience constant illumination as would occur in the laboratory. Rather, our definition of "LL" and "DD" refers to the sun being constantly above or below the horizon, respectively. Lunar characteristics derived from timestamps and animal positions included lunar phase (with values ranging from: 0 at the new moon, 0.25 at the first quarter moon, 0.5 at the full moon, 0.75 at the last quarter moon), the proportion of the moon illuminated, and lunar altitude.

Periodicity in dive effort
Lomb–Scargle periodograms were used to test for rhythmicity in dive behavioral parameters, as this method is particularly robust to unequally sampled data such as is typical of biotelemetric datasets[86]. For recovered records only (*n* = 10), periodograms were constructed for each animal for 15-day non-overlapping time windows for the determination of relatively fine-scale shifts in activity rhythms. To determine how rhythmicity may shift with light conditions, periodograms were also constructed for each animal with dives divided into light categories the animal experienced throughout the year (LL summer, LD fall, DD winter, LD spring, LL next summer). Each light category was only included in periodogram analyses if there were at least 10 full days of activity data[87]. Circalunar behavioral organization was analyzed with periodograms constructed for the entire tag deployment. All periodograms were constructed using R package 'lomb' with a period set between 0.5 to 30 h for determination of circadian rhythms and between 24.5 and 34.5 days for circalunar rhythms, an oversampling factor of 5[88], and significance set as alpha = 0.01 with standard normalization[89]. The peak periodogram was randomized 10,000 times for a more robust p-value estimation.

For daily organization of dive behaviors, the highest peak in power (or tau; τ) at 24 h (±1 h; 23–25 h range) was taken as the circadian period estimate. When the highest peak in power was <23 h, this was taken to be ultradian, or >25 h taken to mean that activities were organized with infradian rhythmicity. For determination of longer effects of lunar cycles, τ between 24.5 and 34.5 days was taken to be circalunar. When no peaks in power exceeded the significance threshold, activities were determined to be arrhythmic. The peak normalized power ($P_N$max) was also extracted as a measure of rhythm strength.

Statistics and reproducibility
We assessed temporal shifts in behavioral rhythmicity throughout the study. Generalized additive mixed-effect models (GAMMs) were used to characterize non-linear temporal shifts in dive behaviors using the 'mgcv'

package in R (4.3.1). Restricted maximum likelihood (REML) was used for smoothing parameter estimation with a cubic regression spline with shrinkage for physiological and extrinsic variables. The shrinkage term provides a means to remove unimportant model variables by allowing the degrees of freedom to shrink to zero. Time of day (in decimal hours), lunar phase, and solar/lunar azimuth were included in models with a cyclic cubic regression spline to wrap the smallest and largest values; this was not used for day of year because there was a gap in data at the end of the year. For example, Dive Duration ~s(Day of Year, cubic regression spline with shrinkage) + s(Time of Day, cyclic cubic spline) with individual ID included as a random effect in all models; for full candidate model descriptions see Supplementary Table 3. Finally, binomial GAMMs were fit to determine when the most extreme dives were most likely to be made throughout the day. Model fit was explored for homoscedasticity of residuals and the best-fit models were identified using the Akaike Information Criterion corrected for small sample size (AICc; in the 'MuMIn' package) and significance of variables at alpha < 0.05 determined in 'lmerTest'. Shifts in timing were calculated by creating a circular vector using a 24-h clock; circular means are presented.

When predicting the time of day that haul-outs were made (i.e., the dependent variable was circular), a Bayesian circular mixed-effect model based on the projected normal distribution was used in 'bpnreg' with the Markov Chain Monte Carlo (MCMC) sampler set to 10,000 iterations with a burn-in of 1000 and a lag of 3, and uninformative priors. We note that the bpnreg package sets the priors for all covariates and the intercept to a Normal(0, 10,000) distribution; other distributions could not be used. However, the lack of precision on the normal distribution that the package uses as a default should generally avoid constraining the posterior distribution. Models were specified as: Time of day (converted to radians using a 24-h clock) ~ $PN(\mu, \Sigma)$ and $\mu = \beta^1_0 + \beta^1_1 \times X_1 + \beta^2_0 + \beta^2_2 \times X_2 + \varepsilon_{individual}$, with the random effect of the individual described as $\varepsilon \sim Normal(0, \sigma^2)$. If animals did not exhibit a preference for haul-out timing, then the timestamps provided for the haul-out start and end would not have been different. Thus, models tested whether 'start/end' of the haul-outs (categorical co-factor) improved model fit; see Supplementary Table 1 for all candidate models. Bayesian models were examined for convergence and the best fit was determined by Deviance Information Criterion and Watanabe-Akaike Information Criterion (DIC and WAIC; in 'bpnreg').

Sample sizes included 62 instrumented seals, of which 59 behavioral datasets were retained for further temporal analyses. Each seal repeatedly made dives (mean: 4767 ± 638 standard error) throughout the instrument deployment. While this type of ecological fieldwork does not permit true replicates, the individual was always treated as a random effect to account for repeatedly measured dives. The study was carried out, with seals instrumented, over three consecutive years.

Reporting summary
Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability
All metadata on the individual animals, and tracking and diving data are archived and available through the United States Antarctic Program Data Center (USAP-DC) at the permanent link: https://doi.org/10.15784/600025[90]. Additional source data linking dive behavioral data to solar and lunar attributes, physiological status, and periodogram outputs are provided at https://doi.org/10.15784/601835[91].

Code availability
This study did not involve the use of custom code. All packages and commands used are cited in the "Methods" section in the text.

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Author contributions
M.R.S., J.M.B., D.P.C., and K.T.G. conceived the study. All authors performed project fieldwork and deployed instruments. K.T.G. programmed and prepared instruments and analyzed animal tracklines, and M.R.S. measured aerobic capacities and performed circadian analyses. M.R.S. wrote the manuscript and all authors edited and approved the manuscript.

Competing interests
The authors declare no competing interests.

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