



RESEARCH ARTICLE

SLEEP

Brain activity of diving seals reveals short sleep cycles at depth

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Sleep is a crucial part of the daily activity patterns of mammals. However, in marine species that spend months or entire lifetimes at sea, the location, timing, and duration of sleep may be constrained. To understand how marine mammals satisfy their daily sleep requirements while at sea, we monitored electroencephalographic activity in wild northern elephant seals (*Mirounga angustirostris*) diving in Monterey Bay, California. Brain-wave patterns showed that seals took short (less than 20 minutes) naps while diving (maximum depth 377 meters; 104 sleeping dives). Linking these patterns to accelerometry and the time-depth profiles of 334 free-ranging seals (514,406 sleeping dives) revealed a North Pacific sleepscape in which seals averaged only 2 hours of sleep per day for 7 months, rivaling the record for the least sleep among all mammals, which is currently held by the African elephant (about 2 hours per day).

Across the animal kingdom, sleep is critical for energy conservation, immune function, memory, and learning (1). Disruptions to sleep, including obstructive sleep apnea and shift work, negatively affect human health (2, 3). By comparison, diverse sleeping habits among wild animals reflect adaptations to resolve conflicts between sleeping or feeding while avoiding predation and exhaustion (4–6). In response to these trade-offs, cows sleep-chew, horses sleep-stand, ostriches sleep-stare, and frigate birds sleep-fly (7–10).

Marine mammals face unique challenges in obtaining adequate daily sleep (11). Most of them feed underwater and breathe at the ocean surface, where predators typically attack (12). Activity budgets of mammals at sea reflect the balance between these survival needs, which often push the animals toward physiological extremes such as large body size, prolonged activity, and enhanced oxygen stores (13). For example, northern elephant seals (*Mirounga angustirostris*) travel >10,000 km during 7-month-long foraging trips. Seals minimize time at the surface (~2 min between 10- to 30-min dives) to reduce predation risk by killer

whales and white sharks while maximizing foraging time (12, 14–16). They also feed around the clock on small prey to satisfy the energy requirements associated with their large body size (17). Given these ecophysiological demands, a long-standing question has been when, where, and how do seals sleep at sea?

A new tool to detect sleep at sea

We developed a new submersible system to record brain activity (electroencephalogram, EEG) and heart rate (electrocardiogram, ECG) concurrently with dive depth and motion of elephant seals at sea [Fig. 1E; (18)]. These sensors identified sleep states [rapid eye movement (REM) sleep and slow-wave sleep (SWS); figs. S1 to S3 and table S2], swimming effort (stroke rate), and three-dimensional (3D) diving behavior in freely moving female juvenile seals ($n = 13$ seals) (18). We recorded sleep in a controlled laboratory environment ($n = 5$ seals) and in the wild ($n = 8$ seals) at four locations, including on the beach, in shallow water, offshore along the continental shelf (depth <250 m), and in the open ocean (depth >250 m; table S1). EEG recordings allowed us to pair sleep states with diving behavior recorded in time-depth profiles for juveniles over multiple days at sea (104 sleeping dives). We used these sleep signatures to estimate sleep patterns across >3 million dives by 334 free-ranging adult females over prolonged trips at sea (514,406 sleeping dives across 53,581 recording days).

On a typical sleeping dive, seals transitioned from an awake glide into SWS. Although asleep, they could maintain their upright posture for several minutes (Fig. 1 and movie S1). These results underscore the importance of EEG in assessing sleep state (18). As seals

shifted from SWS to REM sleep, sleep paralysis resulted in a loss of postural control. Seals turned upside down and drifted downwards in a “sleep spiral.” Sleep spirals tightened from a median diameter of 7.5 ± 7.9 m [median $\pm$ interquartile range (IQR)] at 71 ± 97 s (median $\pm$ IQR) in SWS to 3.3 ± 3.5 m loops at 40 ± 29 s in REM (Fig. 1). Sleep spirals consisted of two to 13 consecutive 360-degree loops at 82 to 377 m depth. On the continental shelf, seals slept motionless on the ocean floor at 64 to 249 m depth.

The predation risk of sleep at sea

Among marine mammals, unihemispheric sleep (SWS in only one hemisphere) allows captive cetaceans and otariids (fur seals and sea lions) to swim and keep one eye open during sleep (11, 19). This suggests that cetaceans and otariids can sleep while monitoring predators (20, 21). Unihemispheric sleep has not been detected in captive true seals (family *Phocidae*) such as elephant seals (22). Similarly, our study did not reveal sleep asymmetry between hemispheres (<2-fold difference). This suggests that true seals use an alternative solution to mitigate predation risk. This study experimentally confirms the hypothesis (22, 23) that in the absence of unihemispheric sleep, elephant seals’ extreme diving abilities allow sleep deep below the ocean surface, out of view of visual predators.

The sleep paralysis that co-occurs with REM sleep would make seals especially vulnerable to predation (1). REM is often minimized for aquatic mammals because the accompanying paralysis can also prevent access to air (22). In captive fur seals confined to water, REM is virtually eliminated (24). Elephant seals at sea reduce REM sleep, as is seen in captive fur seals and true seals in water (24–27), but unexpectedly exhibit a large proportion of REM [$26.5 \pm 5.0\%$ (mean $\pm$ SD) in total sleep time overall and $29.1 \pm 4.3\%$ of at-sea total sleep time; table S3]. This compares to 11%, 6%, 5%, and 1% in aquatic sleep for captive Caspian seals, harp seals, walruses, and fur seals, respectively [(22, 24–27); see the materials and methods].

Our at-sea deployments occurred during late spring, when juvenile seal aggregations attract predators (14). While transiting over the continental shelf, juvenile seals alter their swimming behavior to avoid predation (28). Unexpectedly, we found that seals slept proportionally more on the continental shelf than in the open ocean (Figs. 2 and 3A). One seal performed up to 36 consecutive sleeping dives on the continental shelf but fewer than five at sea. This suggests that seals can safely sleep at depth despite elevated coastal predation risk.

Finding time to sleep at sea

Without unihemispheric sleep allowing continuous vigilance, seals are vulnerable and

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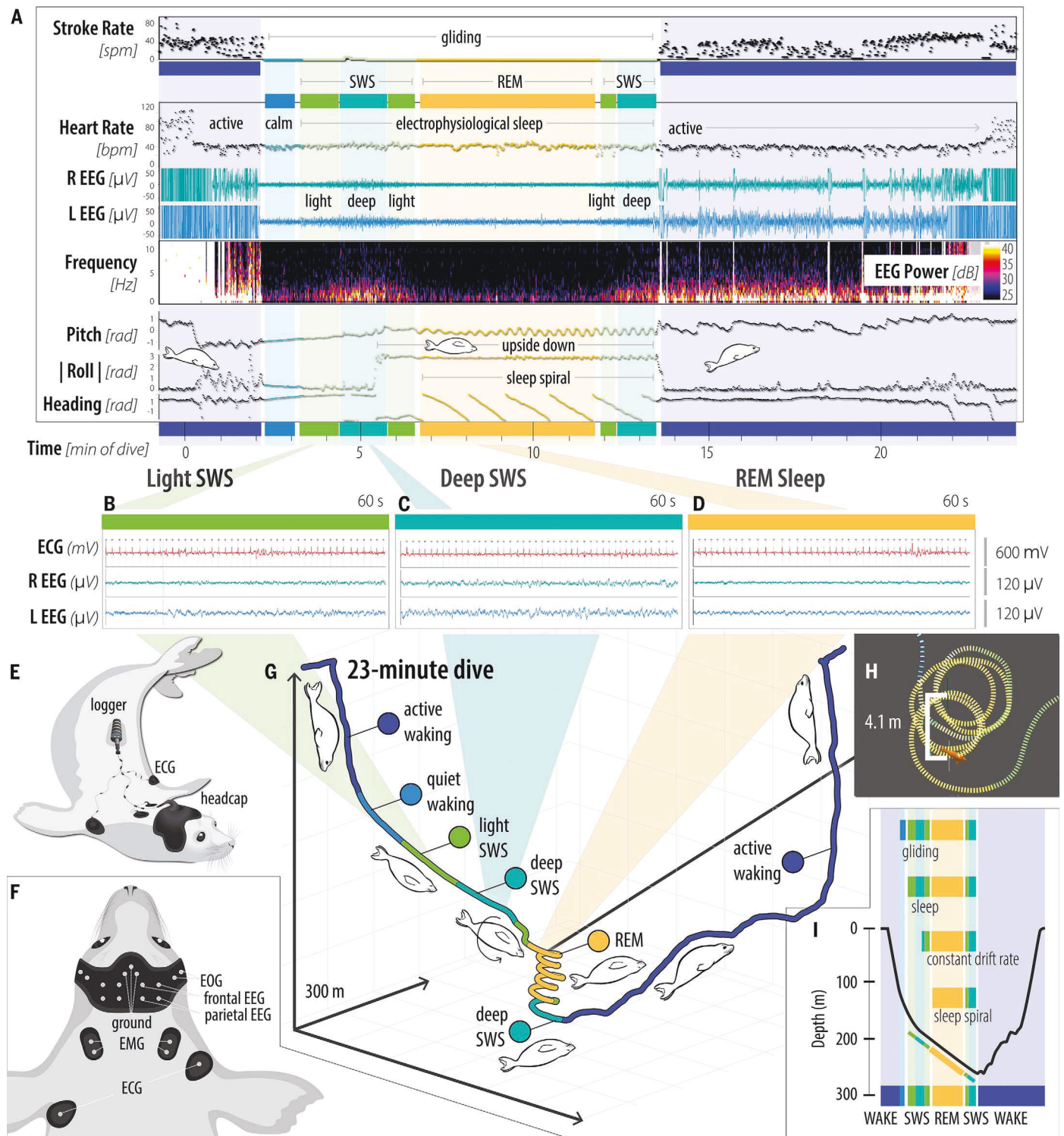


Fig. 1. 3D drift dive sleep patterns. (A) A 23-min sleeping dive showing stroke rate [strokes per minute (spm)], heart rate [beats per minute (bpm)], left (L) EEG (μ V), right (R) EEG (μ V), L EEG spectrogram [power (dB) for frequency (Hz) over time], pitch (radians), roll (absolute value; radians) and heading (radians), and time (minutes of dive). (B to D) Raw EEG and ECG signals during the transition to light SWS (B), deep SWS (C), and REM (D). During SWS, high-voltage, low-frequency slow waves are present. During REM, low-voltage, high-frequency EEG activity co-occurs with

rate variability. (E) EEG logger configuration demonstrating headcap and logger placement. (F) Schematic demonstrating placement of electrodes for electrooculogram (EOG), EEG, ECG, and electromyogram (EMG). (G) 3D dive profile color-coded by sleep state: Active waking is shown in dark blue, quiet waking in light blue, light SWS in light green, deep SWS in teal, and REM in yellow. (H) Top view of sleep spiral. (I) Depth over time showing nested durations of gliding, electrophysiological sleep, constant drift rate, and spiraling.

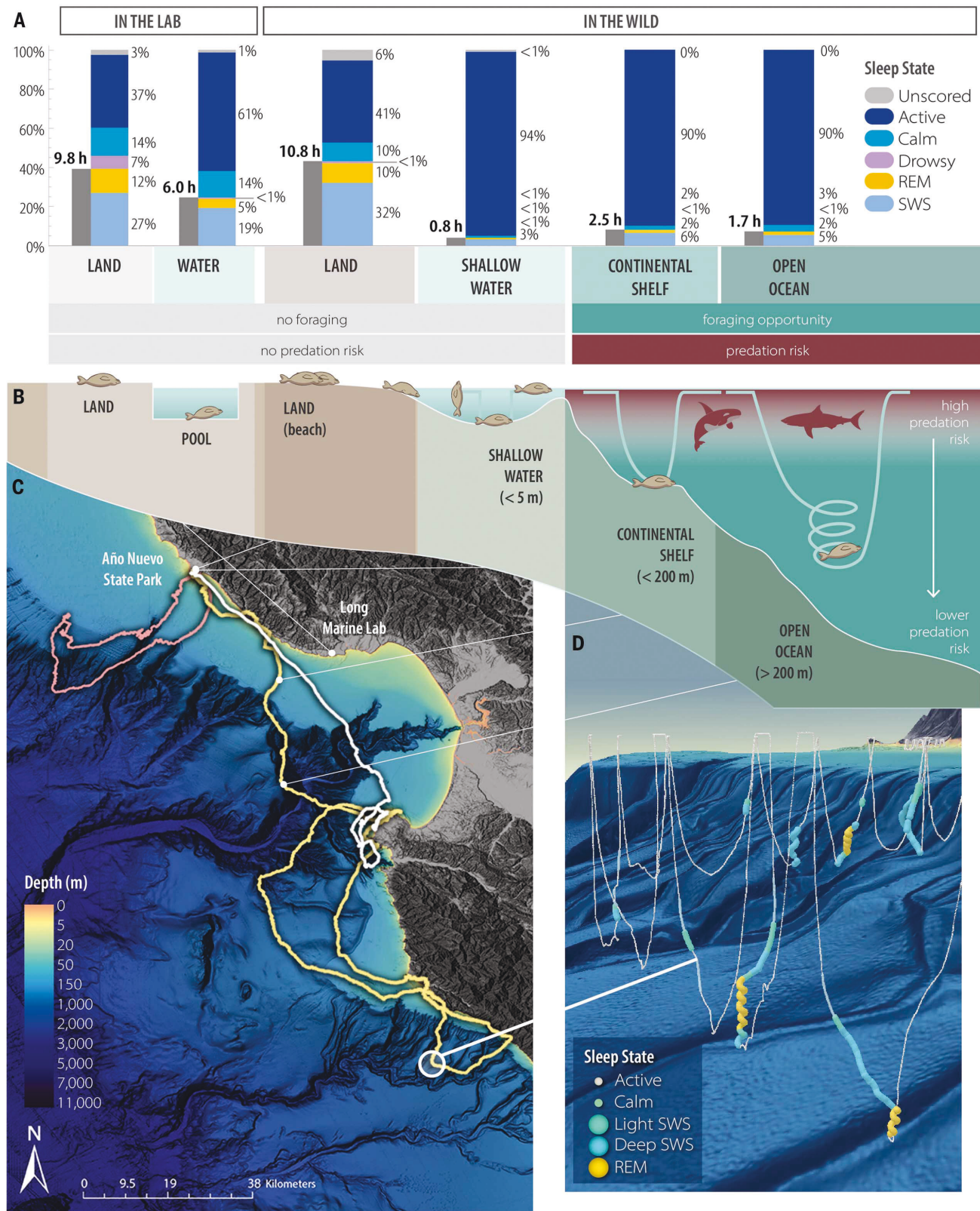


Fig. 2. Sleep patterns from land to sea. (A) Daily sleep quotas for seals in the laboratory (on land and in the pool) and in the wild (on land, in shallow water, on the continental shelf, and in the open ocean), including active waking (dark blue), calm (lighter blue), drowsiness (purple), REM sleep (yellow), and SWS (light blue). REM sleep totals include certain and putative REM (see “REM scoring” section in the

supplementary materials). (B) Schematic showing the resting postures of seals in each habitat, including seals resting on the ocean floor on the continental shelf and drifting in the open ocean. (C) 2D map with bathymetry showing georeferenced dead-reckoned tracks for three animals recorded at sea. (D) 3D map demonstrating sleeping dive sequence, including the sleeping dive from Fig. 1.

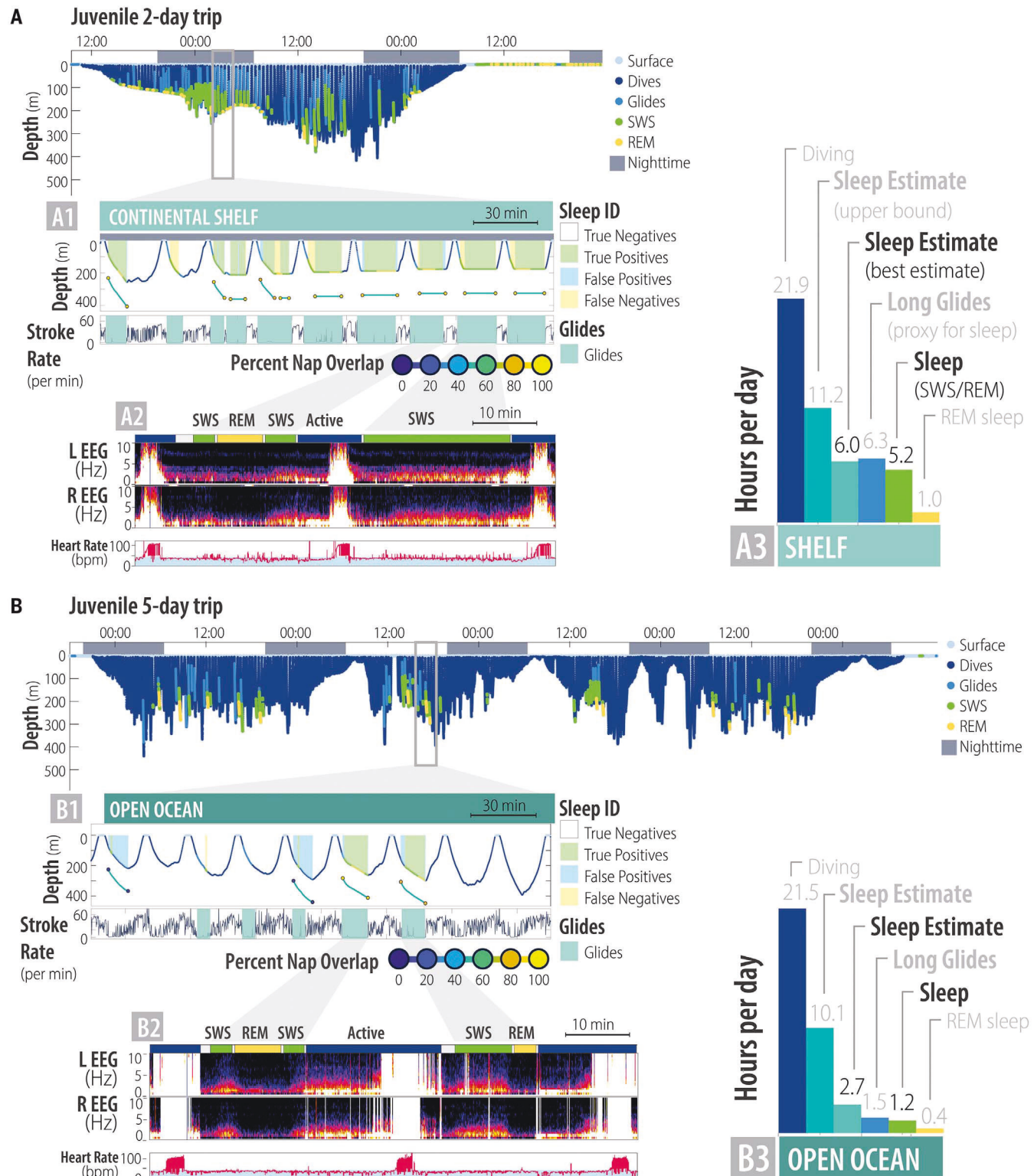


Fig. 3. Sleep identification model performance. Time-depth records for two juvenile seals (**A** and **B**) are colored to indicate surface intervals (light blue), dives (dark blue), glides (blue), SWS (green), and REM sleep (yellow). In panels (A2) and (B2) display EEG spectrograms and heart rate for two adjacent sleeping dives. Panels (A3) and (B3) quantify daily activity budgets (or provide estimates) in hours per day of diving, sleep estimates (upper bound – unfiltered sleep ID; best estimate/lower bound includes only sleep ID segments that meet filter criteria), gliding (long glides >200 s), sleeping (both SWS and REM), and REM sleep.

demonstrate sleep identification accuracy (false positives in blue, false negatives in yellow, and true positives in green). Panels (A2) and (B2) display EEG spectrograms and heart rate for two adjacent sleeping dives. Panels (A3) and (B3) quantify daily activity budgets (or provide estimates) in hours per day of diving, sleep estimates (upper bound – unfiltered sleep ID; best estimate/lower bound includes only sleep ID segments that meet filter criteria), gliding (long glides >200 s), sleeping (both SWS and REM), and REM sleep.

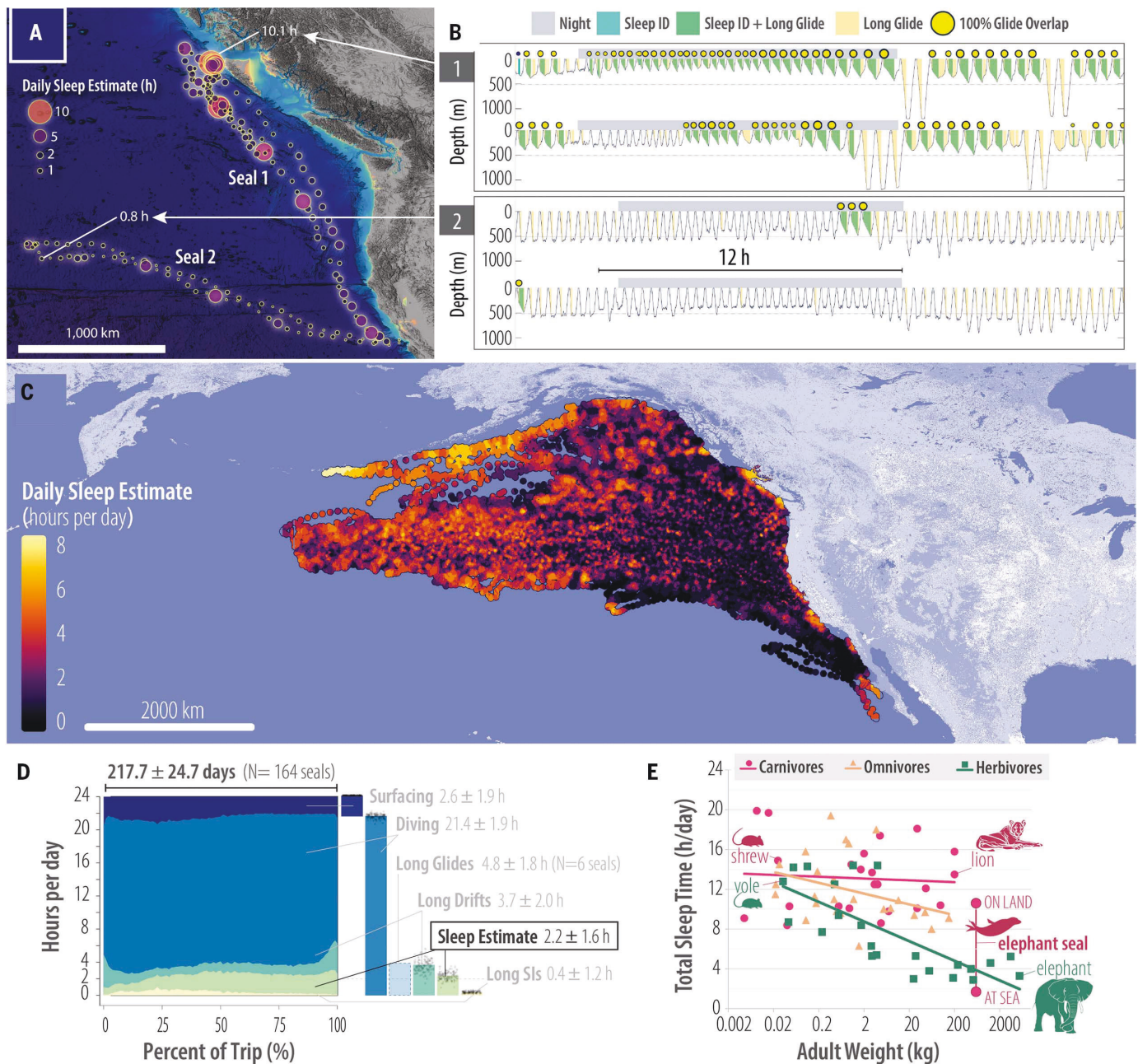


Fig. 4. Estimating daily sleep for 334 adult females. (A) Map showing estimated sleep (hours per day) for two of 15 seals instrumented with stroke rate loggers (basemap matches bathymetry legend in Fig. 2). Each circle represents 1 day, with circle size and color reflecting daily sleep (hours per day). (B1 and B2) Time-depth records for two 24-hour days far from shore (B1) and close to Vancouver Island (B2), demonstrating the difference in sleep during pelagic versus coastal foraging. Yellow dots and green shaded regions above dive profiles indicate identified sleep segments that 100% overlap with a long glide segment (yellow and blue shading represent false negatives and false positives, respectively). (C) Map with spatially averaged daily sleep estimates clipped to the extent of tracking data (1 point per seal day) across 342 good-quality tracks from 267 adult females. Note

the higher sleep time along the coast and foraging grounds. (D) Daily activity budgets for long postmolt foraging trips ($n = 164$ seals) including surface intervals, diving, long glides, long drifts, sleep estimates (filtered long drifts), and long surface intervals. Sleep estimates demonstrate low sleep time throughout the trip. (E) Comparative figure showing total sleep time in terrestrial mammalian carnivores, omnivores, and herbivores [reprinted with permission (1)]. Extremes of sleep time on land and at sea from EEG recordings in juveniles (Fig. 2) are plotted for comparison. Sleep durations for other mammals are based on behavior and/or EEG in the laboratory and/or wild. Differences in recording location (laboratory versus wild) and sleep identification technique (EEG versus behavior) complicate sleep quantification and direct comparison.

unable to actively transit during sleep to maximize foraging efficiency. Between heightened predation risk and lost foraging opportunities, we expected sleep to be strongly restricted at sea. Supporting this hypothesis, we discovered

that seals' daily sleep time was >5 times higher on land than at sea (Fig. 2). Seals slept up to 14 hours/day on land [10.8 ± 3.0 hours/day (mean $\pm$ SD)] but as little as 0 hours/day at sea (1.7 ± 0.7 hours/day; tables S3 and S4).

After returning from 2 to 3 days at sea, seals remained on land for 18 to 43 hours, sleeping up to 53.3% of each hour before returning to shallow water (fig. S4). This moderate sleep rebound was comparable to the daily patterns

of other seals at the colony (fig. S4), suggesting that this relatively short multiday trip did not incur a notable sleep debt.

Substantial fluctuations in sleep duration allow birds to prioritize migration and breeding for several days (5, 10). As mammals, elephant seals similarly partition strategies over long time scales, sacrificing sleep at sea to support the energy requirements associated with their large size and deferring sleep until they leave the water and are on land with no predators. Seals in laboratory settings show modest differences between total sleep time on land and water (24, 25). Here, we demonstrate greater extremes in total sleep time for wild seals that are necessary to balance sleep with the need to replenish the energy stores of a large, highly mobile predator at sea.

Mapping range-wide sleep patterns at the population level

Using the paired electrophysiological and time-depth signatures of SWS and REM sleep from instrumented seals (Figs. 1 and 2), we developed a high-accuracy sleep identification algorithm that identified segments of inactivity characterized by low vertical speed and acceleration from time-depth data (93% accuracy; Fig. 3 and figs. S5 to S7). This algorithm allowed us to estimate sleep quotas for 334 adult seals from their diving data recorded over several months at sea [$n = 170$ short trips (74.6 ± 9.5 days) and $n = 164$ long trips (217.7 ± 24.7 days)] (Fig. 4). These analyses indicated that daily sleep quotas were likely to be universally low (1.1 ± 1.1 hours/day for short 70-day trips and 2.2 ± 1.6 hours/day for >200-day trips) (Fig. 4).

Expanding this analysis to the population level, we can map range-wide sleep patterns to identify critical habitats for protecting wild seals while they sleep at sea. These “sleep-scapes,” which are based on 342 foraging trips by seals across the North Pacific (Fig. 4C), reveal the same unexpected sleep patterns as in juvenile EEG records. That is, seals slept more while closer to the coastline despite greater predation risk (Fig. 4B1) (14). Because coastal foragers consume fewer, larger prey (17), our findings suggest that these seals must either expend more energy hunting for larger prey or require more time to rest and process such prey. Although the coastal water column may harbor more predators, the continental shelf may also facilitate sleep by providing shelter from predators and relative proximity to the surface. These findings and the resulting sleep-scape aid in identifying critical habitats that may guide coastal conservation efforts for wild animals.

By connecting locomotion with different forms of sleep (SWS versus REM) in northern elephant seals, the present study provides conclusive evidence of sleep during drift dives

(23, 29, 30). Furthermore, these unique recordings of brain activity for a wild, free-ranging marine mammal at sea show that sleeping at depth allows seals to drift safely in and out of sleep paralysis. However, these respites are short, because the large body size [456 to 687 kg (min-max adult female arrival breeding mass); (37)] of this elite diver that forages and sleeps in the dark must be sustained by near-constant foraging at sea. Sleep patterns interpreted from the dive records of hundreds of seals revealed only 2 hours/day of sleep for months, rivaling the record for the least sleep among mammals [the African elephant at 2 hours per day; (32)]. Both this method (applying sleep signatures from a small sample to reveal population-level patterns) and these findings (a detailed understanding of sleep for a highly mobile, large mammal) provide opportunities for understanding sleep’s function, evolution, and pathology across mammals, including in humans.

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SUPPLEMENTARY MATERIALS

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Materials and Methods

Figs. S1 to S7

Tables S1 to S5

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Movie S1

MDAR Reproducibility Checklist

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Sleeping deep

Sleep is essential, but not all mammals live in environments where long periods of time asleep are possible. Marine mammals encounter especially challenging conditions for sleep when they are at sea. Using advanced remote monitoring techniques, Kendall-Bar *et al.* found that wild northern elephant seals can sleep for less than 2 hours per day at sea and do so while diving to depths of around 300 meters. Unlike other marine mammals, they enter full REM sleep, with accompanying paralysis, but they do so at depths below those occupied by their predators. —SNV

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