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MARINE BIOLOGY

Forced into an ecological corner: Round-the-clock deep foraging on small prey by elephant seals

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Small mesopelagic fishes dominate the world's total fish biomass, yet their ecological importance as prey for large marine animals is poorly understood. To reveal the little-known ecosystem dynamics, we identified prey, measured feeding events, and quantified the daily energy balance of 48 deep-diving elephant seals throughout their oceanic migrations by leveraging innovative technologies: animal-borne smart accelerometers and video cameras. Seals only attained positive energy balance after feeding 1000 to 2000 times per day on small fishes, which required continuous deep diving (80 to 100% of each day). Interspecies allometry suggests that female elephant seals have exceptional diving abilities relative to their body size, enabling them to exploit a unique foraging niche on small but abundant mesopelagic fish. This unique foraging niche requires extreme round-the-clock deep diving, limiting the behavioral plasticity of elephant seals to a changing mesopelagic ecosystem.

INTRODUCTION

The mesopelagic zone (200 to 1000 m deep) is a poorly studied ocean ecosystem despite the ecological importance of the incredible abundance of small fishes (<10 cm, <10 g), which dominate the world's total fish biomass (1, 2). Until now, observational difficulties have precluded research into the role of small fishes in marine food webs, especially as prey for large organisms. Elephant seals (*Mirounga* spp.) are key top predators within mesopelagic ecosystems (3) that primarily forage on small and abundant mesopelagic fishes (e.g., myctophids) to meet their energy requirements (4–7). In contrast, large deep-diving toothed whales forage on bigger prey, such as mesopelagic squids or demersal fishes at higher trophic levels (8–14). For example, sperm whales [50,000 kg body mass (15), two orders of magnitude larger than female elephant seals] are known to feed on large squids (e.g., jumbo squids <2 m, <50 kg) (9, 13, 14). This suggests an evolutionary trade-off between the advantage of greater diving abilities and the disadvantage of greater absolute metabolic requirements, both associated with large body size (14, 16).

On the basis of allometry alone, larger marine mammals can dive longer because oxygen stores scale proportionally to mass and metabolic rate scales with mass$^{0.75}$ (14, 16). That is, larger animals have a lower metabolic rate relative to their mass than smaller animals, in addition to having larger overall oxygen stores, enabling them to prolong their deep dives to find profitable prey (e.g., maximize energy acquisition per prey) (14). However, a larger body size is also associated with higher absolute food requirements (16). Therefore, a fundamental biological question arises: How does body size constrain prey selection in the mesopelagic environment?

To address this question, we studied female elephant seals by leveraging data from animal-borne smart accelerometers and video cameras that implement onboard programs for efficient data storage.

Together, these innovative tools propel the field of biology forward by switching the research paradigm from inferring where predators find prey by investigating where they go to directly measuring predator-prey interactions in the deep ocean.

Leveraging advanced bio-logging tools to measure feeding in elephant seals

We collected data from 48 adult female northern elephant seals *M. angustirostris* during their 2-month postbreeding oceanic migrations in the Northeast Pacific Ocean between 2011 and 2018. We addressed the postbreeding short migrations (cf., 7-month postmolting long migrations) because the body mass recovery after breeding is critical in their annual life cycles to determine whether they will pup again in the next breeding year, ultimately affecting the population dynamics (17).

Elephant seals are extreme in nearly every aspect of their foraging ecology and are particularly noteworthy for their outstanding physiological diving capacities (18), which allow them to continuously dive, for long periods of time (20 min on average, >100 min at maximum) and deep (500 m on average, >1500 m at maximum) with only a few minutes breathing at the surface (19). We measured several complementary foraging variables using data loggers attached to seals: (i) seal locations using the Argos satellite tracking system (19), (ii) feeding events from smart mandible accelerometers that implement onboard data processing to record the number of jaw motion events every 5 s (7), (iii) prey size/type (e.g., fish or squid) from a newly developed smart video system that ensures efficient memory allocation by an onboard program with three implemented triggers (day/time, depth, and timing by first feeding-related acceleration signals in each dive) (4), and (iv) at-sea buoyancy change to infer body lipid store gains each day, which is a key measure of energetic balance in individual animals (19). Months-long monitoring of at-sea body condition changes is only possible in elephant seals that conduct the key drift dive behavior [rest motionless at depth (20)], which provides a unique opportunity to study marine ecosystem dynamics from the perspective of energetic balance in top predators (19, 21–25). In total, we obtained 221,512 dives with more than 5 million feeding events and energetic balance indices for more than 3500 days from 48 seals and 48.2 hours of underwater videos

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from 15 seals (table S1). We hypothesized that continuous deep diving is necessary for elephant seals to feed on enough small-sized fishes and to maintain their comparatively small body size among deep-diving marine mammals. This hypothesis entails that the small-fish prey resource is not viable for marine mammals with a larger body size. Testing this hypothesis will resolve a decades-long mystery about why elephant seals dive continuously and use the unique deep foraging niche. More broadly, our work will shed new light on how body size functions as an ecological constraint in marine mammals, in which body mass ranges widely between species and within species through sexual dimorphism.

RESULTS AND DISCUSSION
Continuous foraging on small fish to achieve positive energy balance

Seals migrated across the Northeast Pacific Ocean and foraged at depths matching the distinctive diel vertical movements of mesopelagic prey (Fig. 1, A and B) (7). Foraging depths did not vary with bathymetry; seals mainly foraged at around 400 to 600 m depths in open mesopelagic waters (far shallower than the bathymetry of 2000 to 6000 m) (Fig. 1C), where seawater temperature decreases below 5°C and oxygen concentration reaches the minimum (i.e., oxygen minimum zone <20 μmol kg^{-1}) (Fig. 1D) (26). Despite the considerable geographical variation in elephant seal foraging grounds (Fig. 1A), the daily number of feeding event showed little fluctuation throughout migrations and were most frequent in the middle of migrations (Fig. 1, E and F; mean 24.5 ± 5.7 feeding signals per dive, 62.8 ± 5.7 dives per day).

Our animal-borne video observations demonstrated that most seals foraged predominantly on small fish (e.g., myctophids) and, occasionally, squid in deep open waters (i.e., pelagic foraging; Fig. 2, fig. S1, movies S1 and S2, and table S1) [also see (4)]. Rare exceptions to this pelagic foraging strategy were observed in three seals (table S1) that extensively foraged in the benthic habitat of coastal regions (i.e., benthic foraging; Fig. 2, fig. S1, and movies S3 to S5). This benthic foraging is an uncommon strategy that appears to confer a higher energetic reward by feeding on larger demersal fishes (Fig. 2 and movies S4 and S5), but it is likely also associated with a higher risk of predation by killer whales (Orcinus orca) and white sharks (Carcharodon carcharias) (27).

Given that their primary prey is small, we hypothesized that seals must consume a large quantity of prey each day to achieve positive energy balance. To test this hypothesis, we characterized the relationship between the number of feeding event [as a proxy of the number of prey consumed (7)] and foraging time-activity budgets (Fig. 3A). Foraging time was defined as the proportion of time spent in foraging dive cycles (i.e., dive duration plus post-dive surface time) per day, where each foraging dive was defined as a nonresting dive that included at least five feeding events (26). Most data points showed that seals spent over 80% of the day foraging and had 1000 to 2000 feeding events per day (Fig. 3A). More foraging time was associated with exponentially more feeding events (Fig. 3A). We then quantified the effects of foraging time and the number of feeding event on at-sea buoyancy change (i.e., drift rate change), which is an index of body lipid gains per day (Fig. 3B). We found that seals must spend most (80 to 100%) of the day (i.e., 24-hour period) foraging to achieve a sufficient number of feeding event for positive energy balance (Fig. 3B, fig. S2, and table S2).

Body size constraints on mesopelagic prey selection

Our results imply that the key driving force that leads elephant seals to forage at great depths is the abundant fish that dominates total fish biomass worldwide (1, 2). The less frequent feeding events at the beginning and end of migrations (Fig. 1, A and E) likely reflect higher traveling speeds to/from open waters (19) to avoid predation near the coast (27) and reach foraging grounds. In the middle of the migration, the number of feeding event was consistently around 1000 to 2000 per day (Fig. 1E) regardless of geographic location (Fig. 1A), suggesting that mesopelagic fish are distributed relatively uniformly throughout the Northeast Pacific Ocean. Occasionally, seals had up to 4000 feeding events per day (Fig. 1A), but this was rare and patchy, possibly related to mesoscale activity (e.g., fronts and eddies) as recently suggested (23).

A recent ship-based survey showed that mesopelagic fish density increases from near-surface water to 400 to 600 m (28), which matches the primary foraging depths of female elephant seals during both daytime and nighttime (Fig. 1, B and C). This suggests that the deep-diving capabilities of elephant seals (18) allow them to exploit profitable depths that are inaccessible to other shallow-diving (<250 m) marine mammals such as dolphins, porpoises, and fur seals (Fig. 4A and table S3) (29–31). These shallow-diving species can only feed on myctophids during the night when the fishes exhibit diel vertical movements toward the ocean surface.

On the other hand, most deep-diving (>1000 m) marine mammals, including toothed whales (e.g., beaked whales, sperm whales, and pilot whales), routinely reach the mesopelagic depths where myctophids are common (Fig. 4A) but feed on less abundant large squid or demersal fish (8–14). Their deep dives are regularly interrupted for several hours by extended surface time and a series of shallow dives (32–35), making these toothed whales less frequent deep divers compared to elephant seals that continue to dive deep without extended surface intervals or shallow dives even after diving deeper than 1000 m (7). Notably, the body mass of these deep-diving toothed whales (2000 to 50,000 kg) is one (or two) order(s) of magnitude larger than that of female elephant seals (350 kg) (Fig. 4B and table S3). This implies that body mass [∝metabolic demand (16)] relative to foraging depth [∝travel cost (14)] is a key factor limiting the targeting of small mesopelagic fish by large toothed whales; such small prey in deep waters would be far less cost-effective as a main prey resource for the large whales (Fig. 4B). These interspecies comparisons highlight that elephant seals are unique frequent deep divers that forage on abundant small prey not exploited by other deep-diving marine mammals, a unique ecological niche in the open ocean.

Intraspecific sex differences appear to support the body size constraints on mesopelagic prey selection. Elephant seals are characterized by extreme sexual dimorphism (i.e., 2000 kg male versus 350 kg female) (27). Previous studies found the complete absence of large male elephant seals in the offshore mesopelagic zone. Instead, males foraged in coastal benthic waters, where they accept higher predation risk in exchange for larger prey (27). Here, we estimated prey size based on our results that at least 1000 to 2000 feeding events per day are required to achieve positive energy balance in females (Fig. 3B and fig. S2). We used a field metabolic rate for female northern elephant seals (92 kJ min^{-1}) and a mean caloric value for mesopelagic prey (2837 kcal g^{-1} wet weight) (7), estimating the prey size to be 5.6 to 11.2 g (2). On the basis of the classic allometry that metabolic rate scales with the body mass$^{0.75}$ (16), we suggest that males of 2000 kg body mass would have to forage for 370% of each day based on the
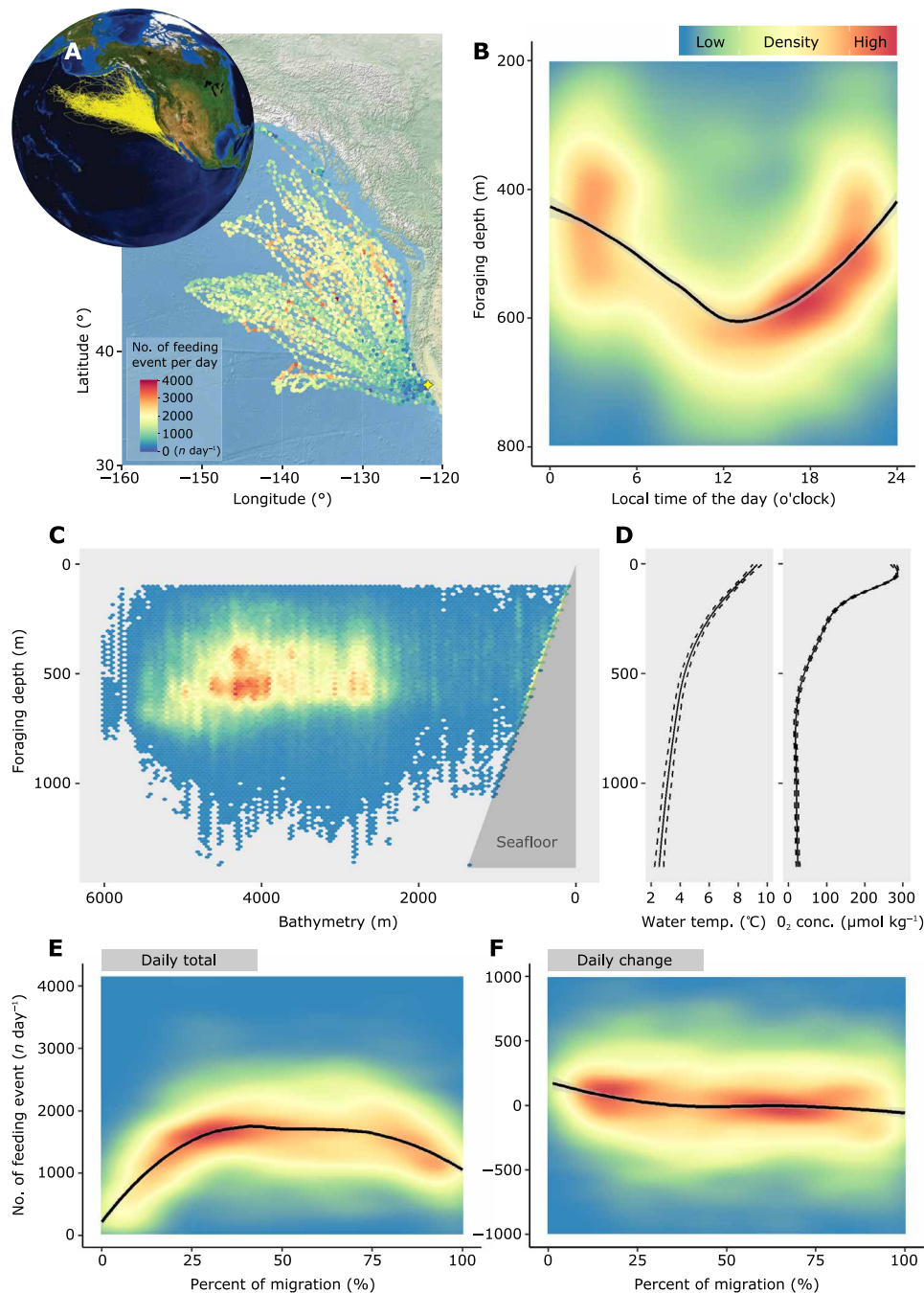
Fig. 1. Mandible accelerometers with satellite tracking quantify spatiotemporal foraging intensity in ocean-migrating female northern elephant seals. (**A**) Geographic distribution of number of feeding event along migration routes ($n = 48$ in 2011 to 2018 for this study), which is representative of our previously collected large dataset [$n = 209$ in 2004 to 2010; shown as yellow lines in the circular inset, replicated with permission from (69)]. Density distribution of foraging depths plotted against (**B**) time of the day and (**C**) bathymetry, and (**D**) aligned with water temperature and dissolved oxygen concentration. Density distribution of time-series (**E**) daily total number and (**F**) daily change in number of feeding event throughout migrations.

offshore prey availability, assuming that 350-kg females need to forage for 100% of each day [Fig. 3B and fig. S2; on the basis of the ratio (3.7) of body mass$^{0.75}$ between the males and females]. Therefore, our data suggest that the sexual size dimorphism and resulting energy requirements lead to intersex niche segregation; males simply could not make a living in the offshore mesopelagic zone.

To balance large body sizes and prey availability (prey size versus abundance), marine mammals have acquired diverse foraging strategies over evolutionary time scales. For example, deep-diving toothed whales use echolocation to find more profitable (but less abundant) prey and maximize energy acquisition per single prey (14). In contrast, baleen whales that include the world's largest animal (blue
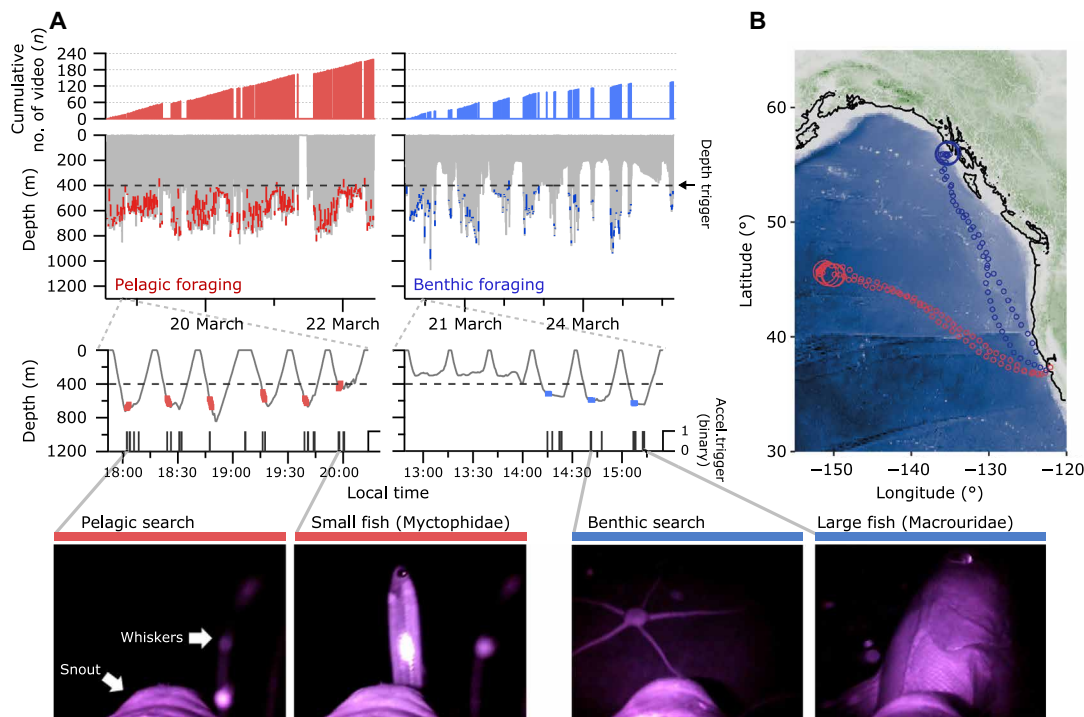
Fig. 2. Smart animal-borne video system confirms that seals predominantly forage on small fish in pelagic waters. (**A**) Pelagic foragers in red [observed in $n = 45$ of 48 seals, representative data for one seal (2017_U20)] encountered small fish, whereas benthic foragers in blue [observed in only $n = 3$ of 48 seals, representative data for one seal (2017_5712)] encountered large fish (table S1). (**B**) Along migration routes, the video recording locations (larger open circles) were located at the farthest points from the colony due to the delay timer of 36 days. As in (A), note that video was recorded for only 1 min per dive (red or blue segments on depth plot), when the criteria of depth (400 m) and acceleration triggers (black lines) were met. These trigger settings maximized the video coverage of foraging dives, under the limited video recording capacity of each tag (4 hours). See movies S1 to S5 for original movies, where seal's snout and whiskers are present in the camera frame, as noted in the bottom left still image. All prey footage lists are available in the Supplementary Materials (movies S2 and S5); the lists with higher resolution images are also available in the ADS (Arctic Data archive System) of the National Institute of Polar Research (https://ads.nipr.ac.jp/dataset/A20210316-001).
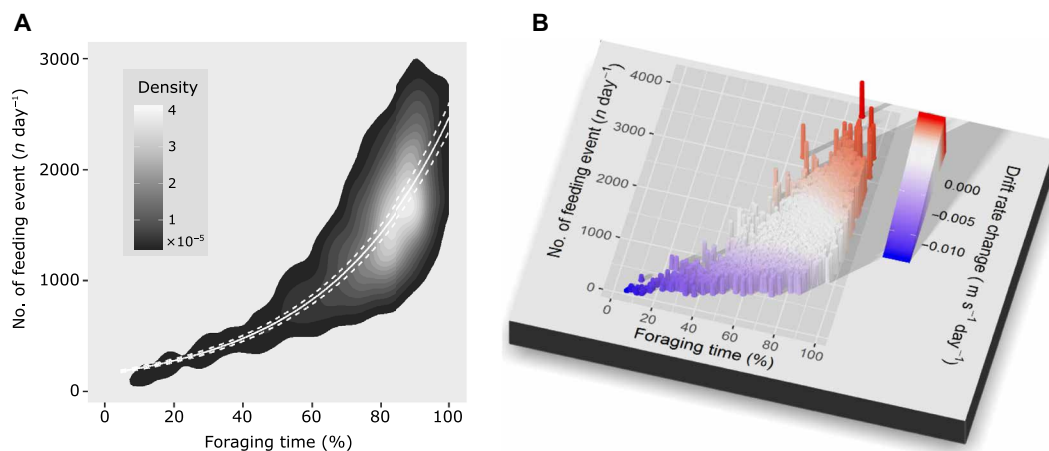

Fig. 3. Seals must spend most of the day foraging to achieve a sufficient number of feeding event for positive energy balance. (**A**) Density plot of foraging time versus number of feeding event, together with a fitted exponential curve from the 45 seals that adopted pelagic foraging on small fish. (**B**) 3D relationship of drift rate changes (i.e., index of lipid gain rate; z axis) projected against daily foraging time and the number of feeding event, showing how lipid gain depends on foraging time and success.

whale *Balaenoptera musculus*; Fig. 4) filter feed zooplankton to maximize the quantity of small prey acquired at shallow depths (*14*). We suggest that female elephant seals, which are not capable of echolocation or filter-feeding, found a unique evolutionary pathway to enhance diving abilities relative to their body mass, allowing them to dive continuously to the mesopelagic depths and maximize feeding opportunities on abundant small fishes. These results demonstrate the close relationships between body size, prey availability, and hunting capacity that shape the foraging guilds within marine mammals.
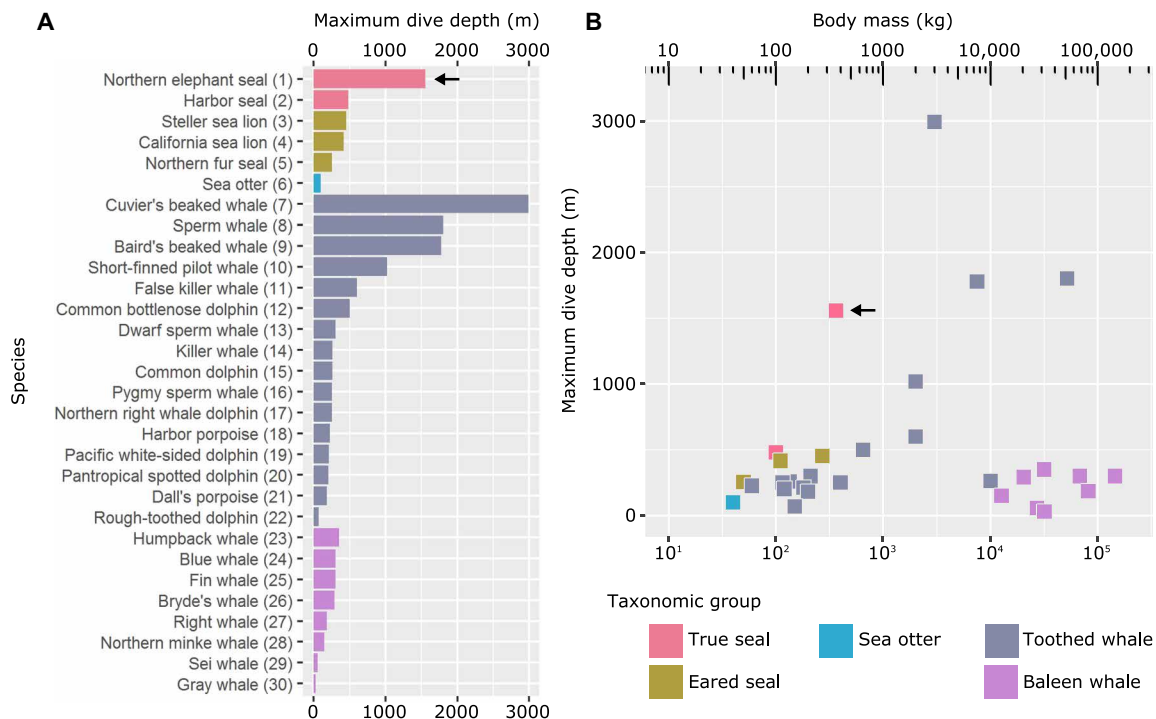
Fig. 4. Interspecies allometry highlights that female northern elephant seals have high physiological diving capacity relative to body mass. The maximum dive depth [as an index of physiological diving capacity (*15*)] of female northern elephant seals is (**A**) listed with all other diving mammals known to forage in the North Pacific and (**B**) plotted against body mass. A full species list and references are available in table S3.

Reliance on small fishes limits plasticity in foraging time

In return for adapting to a unique foraging niche, female elephant seals have a tight daily schedule, allocating almost the entire day to foraging (80 to 100%) to achieve positive energy balance (Fig. 3). This provides a quantitative answer to a decades-long mystery about why elephant seals dive continuously. The required duration of foraging activity limits the amount of time seals can allocate to other critical activities, such as resting or sleeping [1.4 ± 0.3 hour day^{-1}, inferred from calculated resting dive cycle time that includes non-active segments (*7, 20, 21*)]. These results indicate that they have limited flexibility to allocate more time to foraging. Because increasing foraging time is the primary countermeasure used by marine predators to compensate for reduced prey abundance (*17, 36–39*), we suggest that the narrow behavioral niche of elephant seals severely constrains their plasticity to buffer changes in mesopelagic fish biomass.

As climate change alters oceans worldwide, large marine endotherms are potentially vulnerable to changes in prey availability due to their high energetic demands (*12, 40, 41*). Elephant seals would not be an exception, because their round-the-clock deep foraging depends heavily on the high abundance and relatively uniform distribution of small mesopelagic fish. Recent studies suggest that the mesopelagic zone is undergoing physical changes (e.g., warming and deoxygenation) and will face the most prominent escalation in climate velocities than any other ocean depth layers by the end of this century, advocating the urgent need to study its ecosystem before it is too late (*1, 42*). This provides strong motivation to study the deep mesopelagic ecosystem (*42*), but it has been difficult owing to observational difficulties, with complex physical, biological, and

biogeochemical processes involved in this zone that bridges the sunlit ocean surface and the dark abyss (*1*).

We have achieved this study by leveraging technological advances throughout our 30-year monitoring program of northern elephant seal foraging behavior (*4, 5, 7, 19, 21, 22, 27, 43*). Behavioral plasticity is the first line of defense against a changing environment compared to evolutional adaptation, which involves genetic changes across generations (*12*). Therefore, we suggest that elephant seal foraging activity and lipid gain rate can trace future changes in mesopelagic fish abundance; for example, reduced prey abundance would lead to lower lipid gain per unit of foraging time (Fig. 3). In this way, elephant seals can be used as sentinels (*44*) to better understand how rapid climate change alters the little-known but ecologically important mesopelagic ecosystem.

MATERIALS AND METHODS
Field experiments
Fieldwork was conducted at Año Nuevo State Park, CA, USA (37°5′ N, 122°16′ W) on female northern elephant seals during the 2-month postbreeding foraging migration (February to May) from 2011 to 2018. Each seal was chemically immobilized with an intramuscular injection of Telazol (1 mg/kg; tiletamine hydrochloride and zolazepam hydrochloride, Fort Dodge Animal Health, Fort Dodge, IA, USA) using a standard protocol (*19*) to attach the data loggers and to collect body mass and morphometric measurements at the end of the breeding season. Upon return from their foraging migration (and before the annual molt), seals were chemically immobilized to recover the data loggers and to collect mass and morphometric

measurements. Forty-eight seals were equipped with a 0.5W ARGOS satellite transmitter (SPOT4, SPOT5, and MK10-AF: Wildlife Computers, Bellevue, WA, USA; conductivity-temperature-depth satellite relay data logger (CTD-SRDL): Sea Mammal Research Unit, St. Andrews, Scotland) on the head, a very high frequency (VHF) transmitter (ATS, Isanti, MN, USA) on the back, and a smart mandible accelerometer (Kami Kami Logger, Little Leonardo Co., Tokyo, Japan) on the lower jaw (7) using 5-min epoxy with high-tension mesh netting and cable ties. Also, 15 seals were equipped with smart video systems (i.e., depth- and acceleration-triggered video cameras, Little Leonardo Co., Tokyo, Japan) on the head or jaw as described in (4).

Data summary
In total, we studied 48 seals that carried mandible accelerometers with/without smart video systems (table S1): 38 seals carried only mandible accelerometers and 10 seals carried both mandible accelerometers and smart video systems. An additional five seals carried only smart video systems. Thus, mandible accelerometers recorded the data throughout migrations for 48 seals, and smart video systems recorded 48.2 hours of underwater videos for 15 seals (table S1) (4). All seals carried satellite transmitters and recorded at-sea locations throughout migrations.

Quantifying daily number of feeding event
We quantified the number of feeding event by analyzing data from smart mandible accelerometers (Kami Kami logger) based on our previous study (26). The Kami Kami logger ("Kami Kami" is an onomatopoeia to describe biting behavior in Japanese) has a depth (pressure) sensor (recorded every 5 s) and a single-axis longitudinal accelerometer that records the number of feeding-related acceleration signals every 5 s based on measurements of mandible acceleration sampled at a high rate (32 Hz; gain setting of ±3G). The mandible accelerometer has an onboard data-processing algorithm that processes 32 Hz raw acceleration data and records the number of feeding-related acceleration signals (i.e., feeding events) every 5 s, where the counts of feeding events range from 0 to 10 by programming the event duration threshold (0.5 s) (45). A depth threshold of >100 m was used when counting the number of feeding event in this study to focus on prey captures at depth, avoiding noise in the acceleration data that are potentially unrelated to feedings event near the surface (7). Last, we summed the number of feeding event on a daily basis, obtaining the daily number of feeding event (i.e., in units of n day^{-1}; e.g., Fig. 1). Overall, 2,481,041 data points included at least one feeding event per 5 s, and a total of 5,251,229 feeding events were recorded from 48 seals (table S1).

Quantifying foraging depth
We obtained foraging depth per feeding event. The foraging depth data were used, for example, to visualize two-dimensional (2D) kernel density distribution plots using the geom_density2d function in the ggplot2 package distributed via the open source software R (46) (Fig. 1, B and C) and time-series plots for each seal (fig. S1), together with corresponding bathymetric data that were obtained as described in the next section.

Obtaining bathymetric data along migration routes
We obtained bathymetric data based on the daily location of seals using the marmap package distributed via R (47). First, using the getNOAA.bathy function, we obtained all bathymetric information with the resolution of 6 min at longitudes of −180° to −100° and latitudes of 20° to 70°, which encompasses all seal locations. Then, we extracted the corresponding bathymetry using the get.depth function based on the daily locations of seals. The resulting bathymetric data were visualized with migration routes (Fig. 2B) and foraging depths (Fig. 1C and fig. S1).

Categorizing seals based on foraging strategies: Pelagic and benthic foraging
On the basis of Fig. 1C (2D kernel density distribution plot of 48 seals with mandible accelerometers) and fig. S1 (time-series plot per seal), we found that the majority of seals (45 of 48 seals) foraged in pelagic waters (corresponding bathymetry of >2000 m) (i.e., pelagic foraging; Fig. 2, fig. S1, and table S1). Rare exceptions to this pelagic foraging were found in three seals, which extensively used the benthic foraging habitat in coastal regions (i.e., benthic foraging; Fig. 2, fig. S1, and table S1). We confirmed that the two different foraging strategies were reflected in prey types, revealed by the smart video system as detailed in the next section.

Identifying prey size difference between pelagic and benthic foraging
We identified prey species by visually investigating videos from 15 seals that carried smart video systems (i.e., depth- and acceleration-triggered video cameras) as we recently described in (4). Here, we show more detailed results of two seals (2017_U20 and 2017_5712) from (4).

The two seals were identical in the technical aspects of study design and hence comparable in foraging behavior as follows: (i) both carried mandible accelerometers (table S1), (ii) both carried the same types of head-mounted video system with the same configurations as detailed in the next two paragraphs, and (iii) both recorded video data at the farthest points from the colony along the migration routes in the same study year of 2017 (Fig. 2B and table S1). However, the two seals foraged in different locations; 2017_U20 foraged in pelagic waters (i.e., pelagic foraging) as most other seals did (i.e., 45 of 48 seals with mandible accelerometers), whereas 2017_5712 foraged in coastal waters (i.e., benthic foraging) (Fig. 2, fig. S1, and table S1).

The video camera has a depth (pressure) sensor (recorded every 5 s) and a single-axis longitudinal accelerometer that detects fast head movements related to feeding events at depth. Also, the video camera has 4 hours of video recording capacity at 30 frames per second with an LED infrared-light flash, which should not be visible to elephant seals that have short-wavelength sensitive rod opsin (48), allowing us to noninvasively view their prey captures even in the deep dark mesopelagic waters. Note that 4 hours of video recording capacity was allocated into batches of 1-min-long video files to achieve efficient data allocation and maximize prey encounters, as detailed below.

The video camera started a 1-min recording after three implemented triggers, (i) delay timer, (ii) depth trigger, and (iii) acceleration trigger, as detailed in our previous study (4) (also see Fig. 2A for examples). In the current study, the delay timer was set at 36 days to target the farthest migration locations from the breeding colony (see Fig. 2B). The depth trigger was set at 400 m to target mid-mesopelagic depths (400 to 600 m), where most feeding events occur (see Fig. 1C). Therefore, (i) after 36 days from departure, the video camera started video recordings only when (ii) seals reached depths deeper than 400 m and (iii) the first fast head movement was detected in each dive (Fig. 2A). Note that the triggers were valid

only once in a single dive (i.e., only a 1-min video was recorded per dive, as shown in Fig. 2A).

We obtained 214 and 132 video files for 2017_U20 and 2017_5712, respectively (346 video files totaling approximately 6 hours). All prey footage lists for the two seals are available in the Supplementary Materials (movies S2 and S5); the lists with higher resolution images are also available in the ADS (Arctic Data archive System) of the National Institute of Polar Research (https://ads.nipr.ac.jp/dataset/A20210316-001). They have 1-s (i.e., 30 frames) clips of prey footages to play in slow motion on repeat, and each clip starts playing from a cueing frame that shows the clearest and most representative prey footage. Although it was difficult to identify detailed prey species due to halation and blurred prey footage in many cases, we identified the family (or genus) of several fish prey species based on previous reports of elephant seal prey (e.g., Myctophidae for pelagic foraging and Macrouridae and Sebastidae for benthic foraging) (4, 5, 43). Furthermore, prey identification was sufficient to classify prey as fish or cephalopods (with the rare exception of unidentified prey footage including bioluminescence in pelagic foraging) and importantly inform the general trend of prey size differences between pelagic and benthic foraging (movies S2 and S5). As highlighted in the supplementary videos, pelagic foraging is characterized by searching for prey in open mesopelagic deep waters to mainly forage on small fish (e.g., Myctophidae, i.e., myctophid or lanternfish) (Fig. 2 and movies S1 and S2). On the other hand, benthic foraging is characterized by searching for prey near the seafloor to forage on larger fish (e.g., Macrouridae) (Fig. 2 and movies S3 to S5). As complementary information, some squids (but rarely) were found in pelagic foraging (movie S2) as reported in our previous studies (4, 5).

The majority of seals adopted pelagic foraging (n = 45 of 48 seals with mandible accelerometers; Fig. 1C and fig. S1), confirming that small mesopelagic fish are the most important diet of female elephant seals as we recently reported (4, 5). Additional video footage and detailed information are available in our recent report (4).

Calculating dive cycle time per dive
Each dive was defined using a minimum depth of 10 m as in our previous study (45). Then, we calculated dive cycle time per dive as the sum of dive duration and post-surface time, where some (but rare) extended post-surface time over 300 s was rounded to 300 s, as in our previous study (26).

Calculating foraging time
From all dives, we extracted two distinctive types of dives with different purposes: (i) drift dives when seals are resting and/or sleeping (20–22) and (ii) foraging dives (45). Drift dives were defined as detailed in the next section "Calculating daily changes in drift rate as the index of net energy balance". Foraging dives were defined as the nondrift dives that included more than five feeding events (26). Then, we calculated "daily foraging time (%)" as follows

$$\frac{\text{Total foraging dive cycle time (hours)}}{24 \text{ hours}} \times 100$$

where 100% indicates that seals allocated all day to foraging dive cycles (i.e., dive duration plus post-dive surface time). Note that the calculated foraging time does not include daily drift dive cycle time [i.e., resting or sleeping time that includes nonactive (probably sleeping)

segments (7, 20)], which was relatively short (1.4 ± 0.3 hours daily for grand mean) but physiologically vital for animals (21).

Calculating daily changes in drift rate as the index of net energy balance
As an index of net energy balance as per our previous study (19), we calculated "drift rate change" as detailed below. We calculated the drift rate (in m s^{-1}; the vertical rate of passive descent while drifting through the water column during the drift dives), which has strong correlations with animals' buoyancy (i.e., body density) and hence with the amount of body lipid stores (i.e., % lipid tissue in animals' body) (21, 24). Therefore, the daily change in drift rate (in m s^{-1} day^{-1}) informs us of the net gain rate in body lipid stores, where the positive and negative values indicate lipid store increases (i.e., positive energy balance) and decreases (i.e., negative energy balance), respectively (19, 23, 25).

To calculate drift rate per drift dive, we applied a custom-written automated algorithm that processes time-series data of depth from mandible accelerometers based on our previous studies as follows (19, 22): A drift phase should (i) have no depths less than 100 m (to minimize the effect of gases in the lungs on buoyancy), (ii) be longer than 20% of the total duration of the drift dive, (iii) have little variance in depth change rate during the entire drift phase (i.e., mean squared residual should be less than 3 m^2), and (iv) have drift rates <−0.1 m s^{-1} [i.e., seals' buoyancy stays negative in the 2-month postbreeding migrations based on our previous studies (19, 22)]. We visually confirmed that the automated algorithm effectively extracted actual drift phases and calculated drift rates (19, 22). Then, we fitted a cubic spline to the drift rate time-series data using a built-in function interpolate2 in IGOR Pro v. 6.04 (WaveMetrics Inc., Lake Oswego, OR, USA) to estimate the daily drift rate values and finally obtain daily changes in drift rate (m s^{-1} day^{-1}) as daily net energy balance, as per our previous studies (19, 22).

Visualizing daily net energy balance against foraging activity in 3D
The daily values of foraging time, number of feeding event, and drift rate changes were integrated to visualize in 3D (Fig. 3B), showing how drift rate change (i.e., net energy balance) depends on foraging time and success. The 3D figure (Fig. 3B) was created based on the results from a generalized additive mixed model (GAMM), with drift rate change as a response variable and foraging time and number of feeding event as explanatory variables, including individual as a random effect (table S2), by using the gam function in the mgcv package distributed via R (49). We implemented a random effect by using the "re" smoother option, as suggested for simple, independent random effects (50). In Fig. 3B, the z axis (i.e., drift rate changes) was plotted based on predicted values from the GAMM model with the lowest Akaike's information criterion corrected for small samples (AIC$_c$) (table S2) projected onto observed x-y foraging coordinates (i.e., observed values of daily foraging time and number of feeding event in Fig. 3A).

Obtaining seawater temperature and oxygen concentration
We obtained seawater temperature and dissolved oxygen concentration data along depth through the World Ocean Database (https://www.nodc.noaa.gov/OC5/SELECT/dbsearch/dbsearch.html). From the database, we obtained all available profiling float data at longitudes of −160° to −120° and latitudes of 30° to 60° between February

and May of 2011 to 2018, which corresponds to where and when the study seals migrated (Fig. 1A and table S1). We integrated all obtained data together and visualized them as a function of depth using a generalized additive model with 95% confidence intervals using the gam function in the mgcv package distributed via R (Fig. 1D) (*49*).

Obtaining maximum dive depth information of marine mammals in the North Pacific

We compiled maximum dive depth information [as an index of physiological diving capacities (*15*)] on as many diving marine mammals in the North Pacific as could be found in the published literature (*15*, *32–34*, *51–68*) based on the species lists from two previous studies (*15*, *60*). We made our list based on two criteria: (i) We prioritized to use the maximum dive depth data from animal-borne electronic archival tags and (ii) we used the values in the previous lists (*15*, *60*) even if the values are not from animal-borne electronic archival tags (but from other source such as radio tags) in the case where we could not find any updated reports by animal-borne electronic archival tags. Our lists of species, maximum dive depths, and references are available in table S3. For the value of female northern elephant seals, note that we used the maximum dive depth of 1557.5 m obtained from our 48 seals with mandible accelerometers that recorded depth throughout migrations (table S3).

Obtaining body mass information of marine mammals in the North Pacific

Along with the maximum dive depth described in the last section, we collected body mass information from a previous study (*15*) (table S3). For the value of female northern elephant seals, note that we used a mass of 365 kg based on the mean departure and arrival mass of our 48 seals with mandible accelerometers; 365 = (325 + 406)/2 by rounding down to the nearest decimal (table S1 and S3).

Data presentation

Data are presented as arithmetic mean ± SD unless otherwise stated.

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