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Authors

Adachi, Taiki
Naito, Yasuhiko
Robinson, Patrick W
et al.

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Whiskers as hydrodynamic prey sensors in foraging seals

Taiki Adachi^{a,b,c,d,1}, Yasuhiko Naito^a, Patrick W. Robinson^d, Daniel P. Costa^{d,e}, Luis A. Hückstädt^{e,f}, Rachel R. Holser^e, Wataru Iwasaki^{b,g}, and Akinori Takahashi^{a,h}

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The darkness of the deep ocean limits the vision of diving predators, except when prey emit bioluminescence. It is hypothesized that deep-diving seals rely on highly developed whiskers to locate their prey. However, if and how seals use their whiskers while foraging in natural conditions remains unknown. We used animal-borne tags to show that free-ranging elephant seals use their whiskers for hydrodynamic prey sensing. Small, cheek-mounted video loggers documented seals actively protracting their whiskers in front of their mouths with rhythmic whisker movement, like terrestrial mammals exploring their environment. Seals focused their sensing effort at deep foraging depths, performing prolonged whisker protraction to detect, pursue, and capture prey. Feeding-event recorders with light sensors demonstrated that bioluminescence contributed to only about 20% of overall foraging success, confirming that whiskers play the primary role in sensing prey. Accordingly, visual prey detection complemented and enhanced prey capture. The whiskers' role highlights an evolutionary alternative to echolocation for adapting to the extreme dark of the deep ocean environment, revealing how sensory abilities shape foraging niche segregation in deep-diving mammals. Mammals typically have mobile facial whiskers, and our study reveals the significant function of whiskers in the natural foraging behavior of a marine predator. We demonstrate the importance of field-based sensory studies incorporating multimodality to better understand how multiple sensory systems are complementary in shaping the foraging success of predators.

deep ocean | mammal | sensory system | whisker | bio-logging

Underwater vision is limited for deep-diving predators. A gleam of bioluminescence is the primary light source in otherwise utter darkness (1). Consequently, sensory abilities that supplement or even substitute for vision have evolved in deep-diving predators. For example, toothed whales use active biosonar (i.e., echolocation) to locate prey at depth (2). Although pinnipeds have similar ecological demands (3), they appear incapable of echolocation (4). While deep-diving pinnipeds developed dark-adapted vision (4, 5), it is hypothesized that they use their vibrissae, also known as whiskers or sinus hairs, to locate prey by detecting and following hydrodynamic trails generated by those prey.

Do Deep-Diving Seals Use Whiskers to Find Prey in Nature? Although the term “vibrissae,” after the Latin *vibrio* (to vibrate), emphasizes the reception of vibration information, the significant function of pinniped whiskers, apart from the haptic function by direct touch (6), was only recently revealed. In the last 20 y, experiments with animals under managed care have demonstrated the importance of pinniped whiskers for detecting hydrodynamic vibrations of their prey. For example, captive, blindfolded harbor seals (*Phoca vitulina*) use their protracted whiskers to detect minute water movements (7). They followed the hydrodynamic trails behind moving objects that passed by at an earlier point up to several tens of seconds in time and 40 m in distance (8, 9). Also, the morphology of phocid whiskers includes a unique undulated surface structure that suppresses vibrations generated while swimming, increasing the signal-to-noise ratio (10–12). Finally, phocid vibrissae can sense mechanical vibrations from 10 Hz to 1,000 Hz, a surprisingly high range that includes the frequency content of hydrodynamic signals produced by swimming organisms (11). However, these previous studies were conducted in experimental settings with either isolated whiskers, artificial models, or captive animals under the deprivation of visual sensory input. A fundamental question remains: Do seals actually use the vibrissal system to locate prey under natural conditions?

Here, we show the contribution of whiskers to foraging by sensing the hydrodynamic cues of moving prey in deep-diving (200 to 1,000 m) female northern elephant seals (*Mirounga angustirostris*). Elephant seals are known to have highly sensitive whiskers appropriate for hunting moving prey in the dark (3, 13, 14). The vibrissal system of elephant seals is highly innervated. They have the highest number of myelinated nerve fibers (i.e., axons) per whisker of any mammal, including well-studied terrestrial whisker specialists (i.e., rodents) (*SI Appendix, Table S1*) (14–21). We recently quantified the natural

Significance

Unlike humans, most mammals have mobile facial whiskers, yet their natural movement and function are unknown due to observational difficulties, even in well-studied terrestrial whisker specialists (rodents). We report a remarkable case of whiskers contributing to mammal foraging in an extreme underwater environment: the deep, dark ocean. Our animal-borne video cameras revealed that elephant seals captured moving prey by sensing water movement. Their whiskers extended forward ahead of the mouth. Seals performed rhythmic whisker movement to search for hydrodynamic cues, a whisker movement homologous to terrestrial mammals exploring their environment. Based on direct observations, we show how deep-diving seals locate their prey without the biosonar used by whales, revealing another mammalian adaptation to complete darkness.

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The authors declare no competing interest.

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¹To whom correspondence may be addressed. Email: tadachi@ucsc.edu.

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foraging behavior of elephant seals. We found that they must feed on numerous small fishes (e.g., myctophids), requiring round-the-clock deep diving (mainly at 400- to 600-m depths) (3). Thus, studying free-ranging elephant seals provides us with a unique opportunity to reveal the contribution of whisker sensing to foraging success in nature. This work propels the field of sensory ecology of foraging forward by complementing previous studies on whisker specialists in captive conditions (13, 22–24). Our work resolves a decades-long mystery about how deep-diving seals locate prey in the darkness. Further, it reveals how the sensory abilities lead to foraging niche segregation in deep-diving animals.

Results and Discussion

Whisker Movements to Detect, Pursue, and Capture Prey. We report in situ whisker movements using a newly developed small, cheek-mounted video logger. The video logger has a light-emitting diode (LED) red/infrared-light flash, which is not visible to elephant seals due to the short-wavelength sensitivity of their rod opsin (5). This allowed us to noninvasively determine whether seals actively move (i.e., protract) their whiskers as they approach their prey (Fig. 1). We obtained 9.4 h of video data in total from five seals (mean \pm SD: 1.9 ± 1.2 h per seal), including three daytime and two nighttime recordings (Fig. 1A and *SI Appendix*, Fig. S1 and Table S2). Studies with captive seals showed that they protracted their whiskers while actively searching or following hydrodynamic trails (7–9, 24, 25). We inferred active prey sensing by scoring the video to determine biomodal whisker movement (retracted, whiskers closed backward; protracted, whiskers expanded forward) (Fig. 1D–G and *Movies S1 and S2*). Our results showed that elephant seals switch whisker states frequently during their dives (29 ± 13 times per dive) in response to both depth and presence of prey. The dominant cycle of whisker protract–retract switching (i.e., whisking cycle) has a median of 9.2 s (Fig. 1B, *a* and *C* and *SI Appendix*, Fig. S2 and *Movie S2*). Such rhythmic whisker movement is observed in diverse taxa, such as rodents whisking on land to explore the environment (26). The elephant seal’s whisking cycle is slower than the 0.05- to 1-s cycle (= 1 to 20 Hz in frequency) of terrestrial rodents (26). This is consistent with the mechanical limitations of movement in the denser marine environment (13).

At the start of dives, in shallower water, seals kept their whiskers retracted while there were no signs of prey (Fig. 1A and *G* and *SI Appendix*, Fig. S1 and *Movie S1*). During descent, as seals approached foraging depth (>200 m), they protracted their whiskers in front of their mouth (Fig. 1B). At deeper depths, which matched where prey appeared in the video (Fig. 2A), the duration of each whisker protraction event varied from 0.1 to 139.8 s. Prolonged whisker protractions, over 100 s, occurred only when prey appeared (Fig. 2B). Whiskers were protracted significantly longer when prey were present (38.4 ± 32.3 s) than when prey were absent (8.1 ± 9.6 s) ($P < 0.01$; Fig. 2B). Prey were present in only $0.14 \pm 0.12\%$ of the total video frames (Fig. 2A). Seals protracted their whiskers in all 26 events when prey appearance accompanied a feeding acceleration signal (Fig. 1A and *SI Appendix*, Fig. S1). Whisker protraction always occurred before prey appeared in the video (a median of 15.0 s before, ranging from 1.4 to 89.6 s) (*Movies S3 and S4*). The timing of prey capture events mostly matched the end of each prolonged whisker protraction (e.g., *Movie S4*). The last prey was seen in the video at 2.1 s before the end of whisker protraction (median value, with a minimum of 0 s). Only a single case shows an exceptionally long 39.2-s event; the seal likely fed on multiple prey and continued whisker protraction afterward,

maintaining the high sensitivity of the vibrissal system (*Movies S3 and S4*). These results show that seals used their whiskers to aid in searching, pursuing, and capturing prey. Regardless of the time of day (*SI Appendix*, Fig. S3), the percentage of time when whiskers were protracted increased with depth (Fig. 2A). This suggests that seals actively use their vibrissal system for prey sensing upon reaching the depth where they are likely to find prey (3). Seals mostly kept their whiskers retracted while ascending to the surface (Fig. 1A and *SI Appendix*, Fig. S1). We recorded one resting/sleeping “drift” dive where the seal kept its whiskers retracted throughout the dive (*SI Appendix*, Fig. S1, Seal ID U20). This is consistent with seals only protracting their whiskers when hunting, as seals do not forage during these drift dives (3), even though it reached 500-m depth.

Primary Role of Whisker Sensing in Foraging Success. Notably, bioluminescence [emitted by prey species, such as myctophid fish and squids (1, 3, 27)] occasionally appeared while seals protracted their whiskers (Fig. 1F and *Movie S4*). Deep-diving elephant seals have blue-shifted rod opsin pigments, which provide increased sensitivity to the blue-green wavelengths [$\lambda \sim 475$ nm (1, 5)]. This facilitates detecting bioluminescence prey, but how often does bioluminescence contribute to the foraging success of elephant seals under natural conditions?

We upgraded our previous feeding-event recorders [i.e., mandible accelerometers (3)] by including a highly sensitive light sensor to examine whether bioluminescence affects foraging success. By attaching these upgraded accelerometers on nine female seals (*SI Appendix*, Table S2), we obtained concurrent records of feeding signals, light intensity, and depth every 5 s throughout their 2-mo oceanic migrations (Fig. 3A). We defined a bioluminescence event as when the light intensity measurement was saturated (i.e., full-scale irradiance; Fig. 3A and *SI Appendix*, Fig. S4). The pattern of bioluminescence events reflected the diel vertical migration of mesopelagic prey [e.g., myctophid fish (3)] (Fig. 3B). The majority (approximately 90%) of bioluminescence events accompanied feeding signals at depth (Fig. 3C). In contrast, a maximum of only 20% of overall feeding signals cooccurred with bioluminescence (Fig. 3D). This pattern holds even when a lower light threshold level is used to define a bioluminescence event (*SI Appendix*, Fig. S4C). This suggests that while bioluminescence is important, it appears that the vibrissal system is the primary sensory modality for finding prey in the mesopelagic zone. The findings from the light sensors quantitatively match our video results, which showed that only $13.6 \pm 16.3\%$ of prey image included bioluminescence (Fig. 2A). A recent study on southern elephant seals (*Mirounga leonina*) reported similar results: only 1.7 to 26% of feeding was associated with bioluminescence (27). Also, the duration of whisker protraction did not differ significantly with the presence/absence of bioluminescence ($P = 0.95$; Fig. 2B), further supporting the importance of whisker-based prey sensing to foraging success.

Our results demonstrate that deep-diving elephant seals rely primarily on hydrodynamic prey sensing using their vibrissal system. Vision is important when occasional encounters with bioluminescence occur, shedding light on the sensory modality of pinnipeds that exploit the deep, dark ocean. This solves a decades-long mystery about how deep-diving seals locate prey in the darkness. Water disturbance is invariably caused by any organism moving underwater (e.g., prey and predators). Consequently, hydrodynamic sensory systems, such as lateral lines of fish, have evolved many times in the aquatic environment (28). Our study reveals a unique evolutionary adaptation of elephant

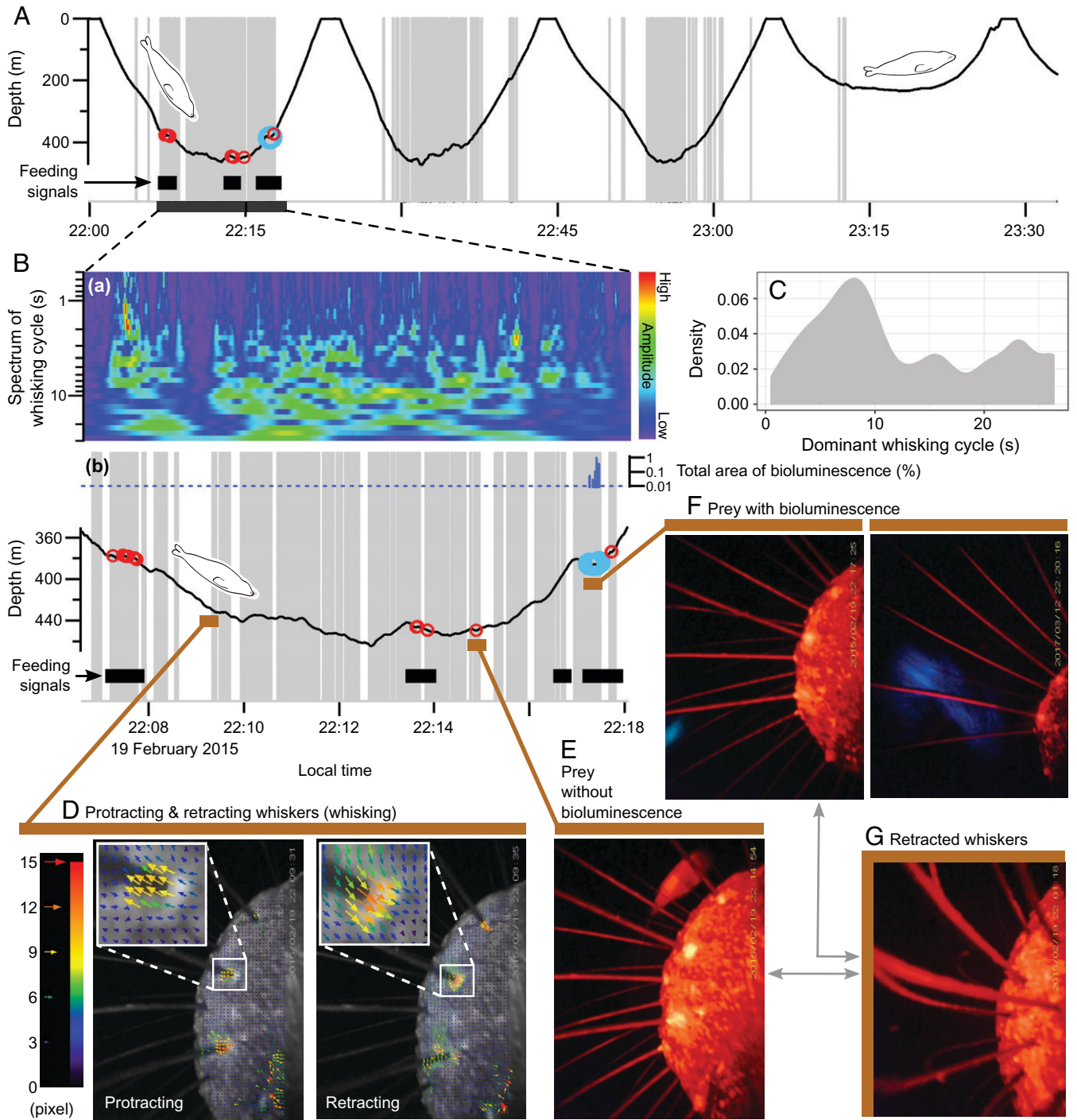


Fig. 1. Seals protracted whiskers at deep, dark depths to forage. (A) Time-series data of Seal ID 4441, showing periods when whiskers were protracted (gray vertical bars), depth profile (black solid lines), periods when feeding signals were recorded in mandible accelerometers (black squares), and the positions where prey without/with bioluminescence appeared in whisker video (red/blue open circles, respectively). (B) Zoomed time-series data of A, with additional information on (a) spectrum of whisking cycle and (b) total area of bioluminescence in each video frame. (C) Density distribution of dominant whisking cycle that summarizes results from spectrum analysis as in B and detailed in *SI Appendix, Fig. S2*. (D) Visualization of whiskers protracting/retracting by using PIV. (E and F) Whiskers protracted with prey appearance. (G) Whiskers retracted without prey appearance. Time-series data from all other seals are available in *SI Appendix, Fig. S1*.

seals to the utter darkness by primarily using their whiskers for foraging.

Whisker protraction is crucial to the high sensitivity of the vibrissal system but also poses energetic costs associated with muscle contraction (26) and excessive heat loss at the surface of whisker pads due to a separate blood circulation system (29). Therefore, the seals did not constantly protract whiskers but performed rhythmic whisker movement at foraging depths

(Figs. 1 B and C and 2 and *SI Appendix, Fig. S2*). Rhythmic whisker movement is likely a key sensory strategy to balance the benefits of prey sensing with the energetic costs associated with foraging in deep, cold water.

The mobility of ectothermic prey (e.g., fish) is limited in the mesopelagic ocean due to its cold temperature and low dissolved oxygen concentration. This makes the environment “quiet” in terms of hydrodynamic vibrations (3, 30–32). In this

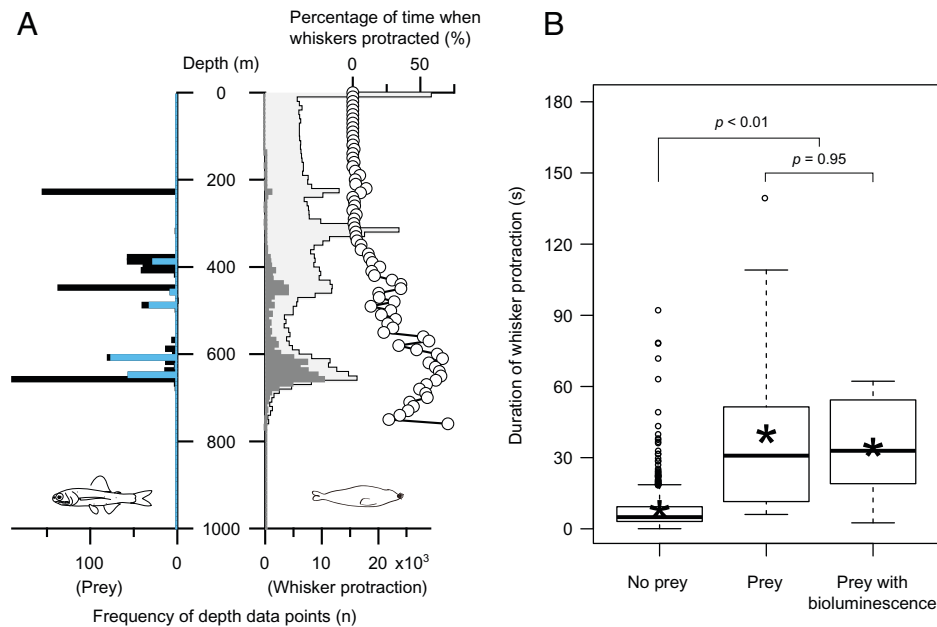


Fig. 2. Whisker protraction matched prey appearance. (A) Frequency distributions of a video frame that included prey (Left) and whisker protraction (Right) relative to depth with a bin size of 10 m. In the left panel, depths of all prey appearance (black) and prey with bioluminescence (blue) are shown. In the right panel, depth points where whiskers were protracted (dark gray bars) are divided by total depth points (light gray bars) to calculate the percentage of time when whiskers protracted (black open circles). (B) Duration of whisker protraction in response to prey appearance ($n = 554, 22,$ and 9 for the categories of No prey, Prey (without bioluminescence), and Prey with bioluminescence, respectively). The mean and median values are indicated by an asterisk and a horizontal thick black line, respectively. Outliers are shown as points beyond 1.5 times the interquartile range. P values from the Wilcoxon rank-sum test are shown above.

quiet environment, elephant seals constantly swim, covering broad spatial scales in search of prey rather than employing a sit-and-wait foraging strategy (3, 33). Persistent swimming is energetically expensive and propagates water disturbance that may signal the seals' presence to prey. However, this disturbance could elicit prey movement, which could be detected by the seal with the help of its whiskers. We show that seals can chase and capture fleeing nonbioluminescent prey even after they are no longer visible to the camera (Movie S3 and ref. 3). Further, protracted whiskers may also detect smaller water movements, such as the breathing currents of fish (24), enabling seals to capture immobile fish without bioluminescence (30). The elephant seal foraging strategy of persistent swimming is made possible by the adaptations seen in their vibrissal system: well-innervated, highly sensitive whiskers (14) with an undulated surface structure that suppresses self-generated flow noise (10–12). Such anatomical and morphological advantages are important factors, in addition to their extreme physiological diving ability (3), that enable elephant seals to forage in the deep, dark ocean.

Field Study Reveals How Sensory Abilities Shape Foraging.

Sensory abilities are crucial factors shaping a predator's hunting strategy in a given foraging environment (2). Our results reveal how sensory abilities lead to foraging niche segregation in deep-diving animals. Both toothed whales and elephant seals share deep mesopelagic water as their main foraging area. However, toothed whales are known to feed on large squids (e.g., sperm whales, with 50,000-kg body mass, foraging on jumbo squids), but female elephant seals (350 kg) specialize on highly abundant and small mesopelagic fish that dominate the world's total fish biomass (3). Our results suggest that elephant seal whisker sensing is essential for locating many small prey at a relatively short distance, compared to the echolocation of toothed whales foraging on single large prey at a distance. This demonstrates how sensory abilities are closely associated with prey selection in foraging marine animals.

Foraging is a complex behavior resulting from multimodal convergence, integrating information from different sensory sources. Our study is unique in investigating multimodality of natural foraging success compared to most experimental studies that restrict captive animals to performing tasks with only one sensory modality (6). Nevertheless, experimental studies have the advantage of accumulating basic knowledge of sensory capacity under controlled conditions. Under natural conditions, it is challenging to determine if the first prey cue during a dive is identified by rhythmic whisker movement or by vision with rapid dark adaptation rates (4). However, some reports show that free-ranging blind seals appeared to be well-nourished (34–36). Also, whiskers are known to function not only as hydrodynamic receptors but also as mechanoreceptors (i.e., haptic sense) (6), suggesting the importance of active touch at the final moment of prey capture (13, 37). Moreover, the protracted whiskers can function as a physical barrier, preventing prey from escaping to the side and leading them in a straight pathway into the seal's mouth. Each pinniped species has distinct whisker anatomy and morphology (26); therefore, comparative field studies on the association of whisker types with hunting strategies and prey selection would be informative. Since diving animals are taxonomically and ecologically diverse, the vibrissal system and other sensory systems (e.g., audition, chemoreception, electroreception, and magnetoreception) could play an essential role in shaping the sensory systems in different species (2). Consequently, an integrative approach will provide a better understanding of the multimodality in the sensory ecology of foraging, which forms a fundamental basis for the effective conservation of animals under various threats from sensory disturbance (38).

Materials and Methods

Field Experiments. Instruments were deployed on 10 adult female northern elephant seals at Año Nuevo State Park in California. This allowed us to study the 2-mo-postbreeding foraging migration (February to April) between 2015

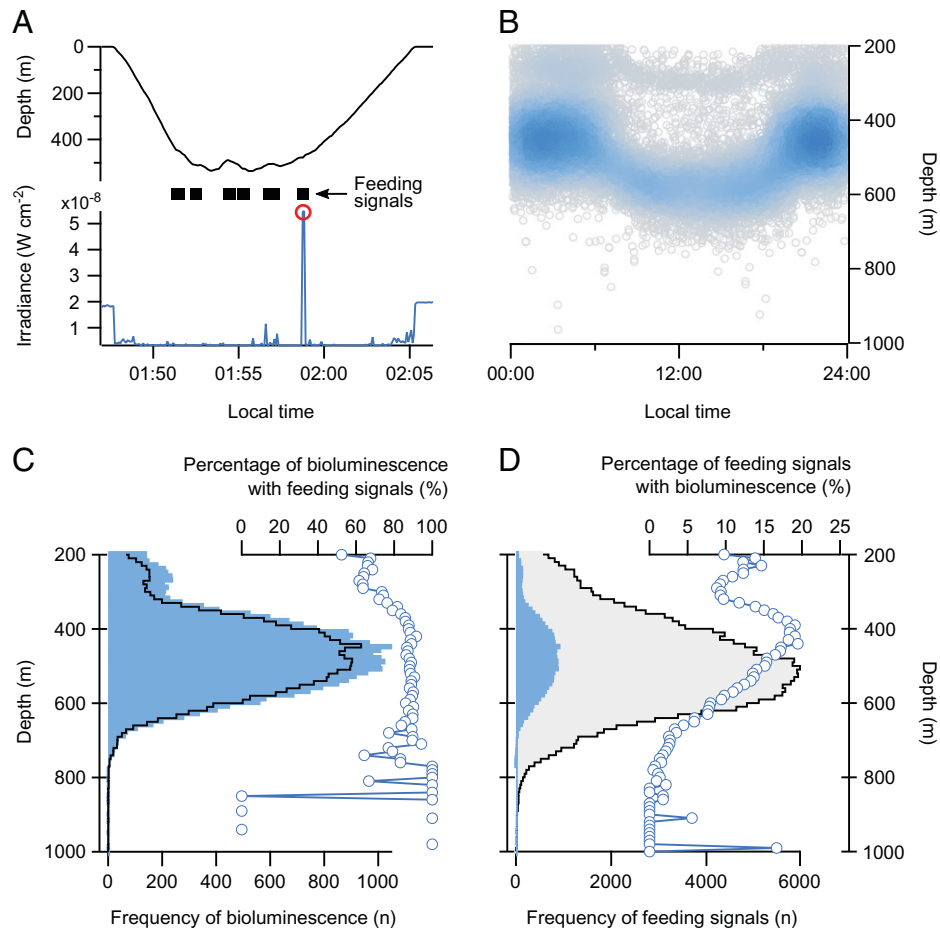


Fig. 3. Bioluminescence reliably and complementarily contributes to overall foraging success. (A) Example of the time-series data from mandible accelerometers with light sensor. (B) Diel changes of the depth of bioluminescence. (C and D) Depth distribution of the frequency and percentage of (C) bioluminescence and (D) feeding signals with a bin size of 10 m. In C, bioluminescence accompanied with feeding signals (black bars) is divided by all bioluminescence (blue bars) to calculate the percentage (blue circles). In D, feeding signals accompanied with bioluminescence (blue bars) are divided by all feeding signals (black-gray bars) to calculate the percentage (blue circles). The full-scale irradiance was used for the definition of bioluminescence (e.g., a red open circle in A; more details are available in *SI Appendix, Fig. S4*).

and 2018 (*SI Appendix, Table S2*). Each individual was chemically sedated with an intramuscular injection of Telazol (1 mg/kg, tiletamine hydrochloride and zolazepam hydrochloride; Fort Dodge Animal Health) using a standard protocol (39). During handling, data on body mass and morphometrics were collected. Upon return from their foraging migration, seals were sedated again to recover the loggers and collect postdeployment mass and morphometric measurements.

Each seal was equipped with either (or both) a “whisker video logger” (see the next section; $n = 5$ seals) or (and) a mandible accelerometer with a light sensor (see the next section; $n = 9$ seals) (*SI Appendix, Fig. S5*). All 10 seals were also equipped with a 0.5-W ARGOS transmitter (Wildlife Computers) and a very high frequency (VHF) transmitter (ATS). The data loggers were wrapped in rubber splicing tape and glued to the animal's left cheek (whisker video logger), lower jaw (mandible accelerometer), back (VHF transmitter), and head (ARGOS transmitter) using 5-min epoxy with high-tension mesh netting and cable ties.

Instruments to Record Whisker Movements and Bioluminescence.

Whisker video loggers (21 × 15 × 70 mm, 31 g in 2015 to 2017 and 23 × 21 × 72 mm, 53 g in 2018; Little Leonardo Co.) were designed to record video at 30 frames per second with a resolution of 1,280 × 960 pixels. To enhance the quality of video in dark water, red (in 2015 to 2017) or infrared (in 2018) LED lights were built into the video units (*SI Appendix, Fig. S5*). We chose long-wavelength LED light because it is not visible to northern elephant seals with short-wavelength sensitive rod opsin (5), allowing us to investigate noninvasively if seals move (i.e., protract) their whiskers actively in relation to prey appearance even in the deep, dark ocean. The whisker video logger had a delay timer (*SI Appendix, Table S2*); e.g., the delay timer was set as 30 d to target the middle of the foraging migration (3). Once the logger turned on after the delay, it

continued recording video until the battery was depleted, ranging from 1.0 to 4.0 h (*SI Appendix, Table S2*). The video logger in 2018 was upgraded to include a double-capacity battery, allowing the collection of longer-duration videos (*SI Appendix, Table S2*). To investigate the effect of day/nighttime on seals' behavior, we set delay timers to start either in the daytime (from 12:00 o'clock) or in the nighttime (from 22:00 o'clock) at local time (Pacific Standard Time). In total, we collected data from three and two seals during daytime and nighttime, respectively (*SI Appendix, Table S2*).

The occurrence of bioluminescence was quantified by upgrading the mandible accelerometers [i.e., feeding-event recorders (3)] to add a light sensor (Kami Light Logger, diameter 23 mm, length 87 mm, and mass 66 g; Little Leonardo Co.). The light sensor comprised a photodiode (S2386-8K; Hamamatsu Photonics KK) and a low-noise current-to-voltage converter. The light sensor was previously shown to detect bioluminescence in southern elephant seals (27, 40). These studies showed that the foraging intensity was positively related to the occurrence of bioluminescence, suggesting that bioluminescence provides elephant seals with visual cues of prey (27, 40). The mandible accelerometers with a light sensor record depth, number of feeding-related acceleration signals, and light intensity every 5 s. An on-board data processing algorithm counted the feeding-related acceleration signals that analyze 32-Hz single-axis longitudinal accelerometer as described in our previous studies (3, 41). The light intensity was sampled at 32 Hz, and the maximum value of every 5 s was recorded.

Analyzing Data from the Whisker Video Logger. Video analysis was conducted using Fiji (an open-source image processing package based on ImageJ; ImageJ version 1.52p and Java version 1.8.0_172) and IGOR Pro version 6.03

(WaveMetrics) with custom-written code, in addition to QuickTime Player version 7.7.9 (Apple Inc.) for visual inspection.

All video data were divided into 30-s video segments using Fiji to easily handle video data for further analysis. We scored whisker movements as either retracted (i.e., whiskers closed backward) or protracted (i.e., whiskers expanded forward) states (Fig. 1 *D–G* and *Movies S1* and *S2*). We visually scored the state of the whiskers for every frame of the 9.4 h of video. We found that the bimodal state frequently shifted (29 ± 13 times per dive) in response to depth and prey appearance during dives. We calculated the duration of whisker protraction as the continuous periods when seals protracted their whiskers underwater.

We quantified the dominant cycle of whisker protract–retract switching, the so-called whisking cycle, as often analyzed in rodents (26). The whisking cycle measures how long it takes to switch between whisker protraction and retraction (26). While other studies measured whisker angles (angle between the whisker and the midline of the head) (13, 26), we were unable to do this as this requires a view from above/below the head (dorsoventral view). We only had video images from a forward (craniocaudal) perspective from video loggers attached to the left cheek (*SI Appendix, Fig. S5*), so we took an alternative approach. We found that the size and brightness of whisker pads [i.e., mystacial pads (26)] in our images were useful; whisker pads were more visible (i.e., larger and brighter by reflecting the LED flash) in video frames when whiskers were protracted, suggesting steeper whisker angles (*SI Appendix, Fig. S2A* and *Movie S2*). Therefore, time-series data of the whisker pad area were used to calculate whisking cycles (*SI Appendix, Fig. S2*), allowing us to compare this important metric to previous studies.

We calculated the total whisker pad area in the image by using a custom-written code in Fiji with the following three steps applied on each video frame: 1) The full RGB image was converted to an 8-bit gray image; 2) we extracted the bright area by using the function `adaptiveThr` in an open-source plugin for ImageJ (42), where the local threshold was calculated by the mean with a minimum block size of 500 and subtraction value of -90 ; and 3) we calculated the total whisker pad area by using the built-in function `Analyze Particles`, where we set the minimum area of 200 pixels and minimum circularity of 0.5. This automated process was validated in three seals (Seal IDs: 4441, 5712, and U20; *SI Appendix, Table S3*) due to the field of view from the video loggers (due to the attachment angle). Then, time-series data of the total whisker pad area were analyzed using `Ethographer` (43) (an open-source plugin for IGOR Pro). The dominant whisking cycle was calculated in dives 1) which had a complete record and 2) in which the duration between the first to the last whisker protraction (visually inspected as in the last paragraph) was more than 5 min to remove resting dives from the analysis. Five complete dives met these criteria from the three seals in *SI Appendix, Table S3*. Data were summarized for each seal to visualize histograms and calculate medians of the dominant whisking cycle (9.2 ± 1.7 s; Fig. 1C and *SI Appendix, Fig. S2B*). Note that the calculated whisking cycle was not simply resulting from the swimming motion of seals (i.e., the whiskers are pushed back when the seal strokes to generate thrust) because the dominant stroke cycle is about 1.5 s (44), which is much faster than the whisking cycle. In addition, to visualize the motion of protracting and retracting phases of whiskers as shown in Fig. 1D, we introduced PIV (Particle Image Velocimetry) by using an open-source plugin `iterativePIV` for ImageJ (45).

We visually inspected the occurrence of prey in the video frames, categorizing prey type into “prey without bioluminescence” and “prey with bioluminescence.” To validate the visual inspection of the occurrence of bioluminescence, bioluminescence was also automatically detected from each video frame by a custom-written code in Fiji based on a sample code of ImageJ (available at https://imagej.nih.gov/ij/macros/Percent_Green.txt). To extract the object of blue color in the video frame, we used the HSB (hue, saturation, brightness; also known as HSV) color model, which is an alternative representation of the RGB color model. We set hue from 120 to 220, saturation from 128 to 255, and brightness from 51 to 255, representing the range of blue color along the HSV hexcone. Then, each video frame was investigated if it had at least one pixel within the set HSB range.

Because the whisker video logger did not include a depth sensor, we used depth data from mandible accelerometers to investigate whisker movements along with the dive profile. For the one seal in 2015 we attached our previous version of the mandible accelerometer (*SI Appendix, Table S2*) because the new version, which includes a light sensor, had not been developed yet. Still, both loggers have the same depth sensor. We summarized depth data points where whiskers were protracted as a frequency distribution. We calculated the

percentage of time when whiskers were protracted along with depth with a bin size of 10 m, ranging from 0 to 1,000 m (as shown in Fig. 2A and *SI Appendix, Fig. S3*).

All time-series data for each seal are available in Fig. 1 and *SI Appendix, Fig. S1*. Note that *SI Appendix, Fig. S1*, Seal ID U20 contains a resting/sleeping dive (3, 46) in which the seal did not protract its whiskers at all.

Analyzing Data from the Mandible Accelerometer with a Light Sensor.

Data from the mandible accelerometer with a light sensor was analyzed using IGOR Pro. We tested whether bioluminescence is used to locate prey by correlating the cooccurrence of feeding-related accelerations with bioluminescence events. We summarized the number of bioluminescence and feeding signals as frequency distributions along with depth with a bin size of 10 m, ranging from 200 m to 1,000 m (as shown in Fig. 3).

With these frequency distributions, we calculated two simple percentages. The first is the percentage of bioluminescence with feeding signals, which was calculated as

$$\frac{\text{No. of bioluminescence with feeding signals}}{\text{Total no. of bioluminescence}} \times 100, \quad [1]$$

where 100% indicates that all bioluminescence events occur together with feeding signals. Note that 1) each bioluminescence event was defined as the series of consecutive data points where light intensity exceeds the threshold as per the previous study (40) (see the next section for more details), 2) total number of bioluminescence was calculated as the sum of bioluminescence events, and 3) the bioluminescence event that contains at least one feeding-related acceleration signal is referred to as bioluminescence with feeding signals.

The second is the percentage of feeding signals with bioluminescence, which was calculated as

$$\frac{\text{No. of feeding signals with bioluminescence}}{\text{Total no. of feeding signals}} \times 100, \quad [2]$$

where 100% indicates that all feeding signals occur together with bioluminescence. Note that 1) each feeding signal was defined as the series of consecutive data points that contain feeding-related acceleration signals as per our previous study (41), 2) total number of feeding signals was calculated as the sum of the number of feeding signals, and 3) the feeding signal that contains at least one data point where light intensity exceeds the threshold is referred to as feeding signals with bioluminescence.

We quantitatively assessed how bioluminescence contributes to foraging success by combining these two percentages. We did this for all nine seals with the upgraded mandible accelerometers in 2016 to 2018 (*SI Appendix, Table S2*).

The Definition of Bioluminescence. To investigate the possible effect of the threshold of light intensity (irradiance) to detect bioluminescence events, we compared five different thresholds: full (saturated), 1/2, 1/5, 1/10, and 1/25 scale (*SI Appendix, Fig. S4A*). Note that the threshold value primarily affected the percentage of bioluminescence with feeding signals (*SI Appendix, Fig. S4B*). Still, the effect was much smaller in the percentage of feeding signals with bioluminescence (*SI Appendix, Fig. S4C*). Therefore, a full-scale threshold (similar to the 9/10 scale adopted by ref. 27) was used for the main result, as shown in Fig. 3.

Although we used highly sensitive light sensors, the elephant seal's vision may be more sensitive than the light sensors (27). However, our sensitivity analysis shows that weaker light levels accompanied fewer feeding signals (*SI Appendix, Fig. S4B*), suggesting that weaker bioluminescence is less likely to be a direct contributor to foraging success. Regardless of whether the elephant seal's vision is more sensitive than our light sensors, this pattern should hold.

Statistical Analyses. Statistical analyses were conducted using the open-source software R version 3.6.1. To test whether the duration of whisker protraction was affected by the occurrence of prey, we applied the Wilcoxon rank-sum test by using a function `wilcox.test` in the built-in package `stats` in R as our data were not normally distributed (e.g., “No prey” category shows positively skewed distribution; Fig. 2B). The median values of the duration of whisker protraction per category are 4.9, 30.8, and 32.9 s for “No prey” ($n = 554$), “Prey” ($n = 22$), and “Prey with bioluminescence” ($n = 9$), respectively. The original data are available at the ADS (Arctic Data archive System) of the National Institute of Polar Research (<https://ads.nipr.ac.jp/data/meta/A20220524-001>).

Data are presented as arithmetic mean \pm SD unless otherwise stated.

Data Availability. Data have been deposited in the ADS of the National Institute of Polar Research (<https://ads.nipr.ac.jp/data/meta/A20220524-001>).

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Author affiliations: ^aNational Institute of Polar Research, Tokyo 190-8518, Japan; ^bDepartment of Biological Sciences, Graduate School of Science, The University of Tokyo, Tokyo 113-0032, Japan; ^cSchool of Biology, University of St Andrews, Fife KY16 9SY, United Kingdom; ^dDepartment of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95060; ^eInstitute of Marine Sciences, University of California, Santa Cruz, CA 95060; ^fCentre for Ecology and Conservation, University of Exeter, Penryn TR10 9FE, United Kingdom; ^gDepartment of Integrated Biosciences, Graduate School of Frontier Sciences, The University of Tokyo, Chiba 277-0882, Japan; and ^hDepartment of Polar Science, The Graduate University for Advanced Studies, Tokyo 190-8518, Japan

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