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Visual and behavioral evidence indicates active hunting by sperm whales

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ABSTRACT: It is hypothesized that sperm whales employ active pursuit strategies for hunting prey, mainly deep-sea squid at great depths, but no visual evidence has been obtained to confirm this. We recorded the hunting behavior of sperm whales using animal-borne cameras and accelerometers simultaneously deployed on 17 whales, and obtained 42.8 h of diving data, including 17 715 images. A statistical comparison indicated no clear effect of light (with or without flashing white lights from cameras) on diving behavior of tagged whales. Although 98.5 % of the still images were of empty water and uninformative, 5 classes of images with visible material were identified: (1) suspended material, possibly squid ink (n = 17), (2) unidentified particles (n = 4), (3) possible animal body parts (n = 2), (4) other sperm whales (n = 221), and (5) the seafloor (n = 8). All image classes were recorded at deeper depths (mean ± SD = 785 ± 140 m), except Class 4 images, which were recorded only at depths <339 m, suggesting that tagged whales swam alone while foraging at great depths. Simultaneous use of speed and image sensors revealed that Class 1 images were associated with bursts of speed up to approximately twice (3.3 ± 1.0 m s^{-1}, max. 6 m s^{-1}) the mean swim speed (1.8 ± 0.4 m s^{-1}). These images, likely derived during chasing prey, support the hypothesis that sperm whales actively hunt to capture prey.

KEY WORDS: Animal-borne camera · Cetacean · Data logger · Diving behavior · Hunting · Swim speed · *Physeter macrocephalus*

INTRODUCTION

The sperm whale *Physeter macrocephalus* is one of the deepest- and longest-diving mammals, with foraging dives routinely deeper than 400 m (Watkins et al. 2002, Watwood et al. 2006). Based on studies that investigated the stomach contents of the species, sperm whales feed principally on cephalopods (e.g. Clarke 1980). Early hypotheses that attempted to explain their hunting strategy were based on the sit-and-wait strategy, which would be energetically less costly than active pursuit (Beale 1839, Clarke 1970). An alternative hypothesis is that sperm whales actively search for and approach prey using echolocation clicks (e.g. Norris & Harvey 1972, Møhl et al. 2000).

Using a sound recording tag and accelerometer (Dtag; Johnson & Tyack 2003), it has been shown that a rapid decline in click interval (buzzes) is accompanied by changes in body posture, suggesting that whales actively approach and capture their prey

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(Miller et al. 2004). The use of a speed sensor with an accelerometer has revealed that tagged sperm whales occasionally accelerate up to approximately 7.0 m s^{-1}, with rapid changes in body posture and sharp turns (Amano & Yoshioka 2003, Aoki et al. 2012). These events, termed bursts of speed, have been suggested to occur only when whales capture large and/or muscular prey. However, there has been no visual evidence associating these recorded active movements with hunting. In this study, we present evidence from concurrent recordings of still images, acceleration, and swim speed showing active hunting by sperm whales. We also provide visual evidence that sperm whales interact with each other underwater.

MATERIALS AND METHODS

Tagging was conducted off the Ogasawara Islands of Japan, in the northwest Pacific (26° 40′ N, 141° 40′ E to 27° 40′ N, 142° 40′ E), from 2010 to 2012. Groups of female and immature sperm whales are found throughout the year in this area (Mori et al. 1995). We approached sperm whales with a fishing boat (length: 20 or 6 m), and used a 5 m or 10 to 13 m pole to deploy a single suction-cup-attached tag, which included camera and accelerometer, with or without a speed sensor. The mass of the whole tag was 710 to 1300 g (for tag details, see the Type B tag in Aoki et al. 2012). After tag deployment, we stayed more than 100 m from the whale (attempting to avoid any type of disturbance) and tried to follow it to observe its behavior until its next surfacing.

Three types of animal-borne devices, made by Little Leonardo, were used: a DSL2000-VDT II (30 × 150 mm, 183 g in air) camera with LED modules (30 × 135 mm, 150 g in air); a W2000-PD3GT 3-axis accelerometer with speed sensor (23 × 123 mm, 90 g in air); and a W2000-D2GT 2-axis accelerometer (17 × 65 mm, 31 g in air). We used cameras with 1 LED module in 2010 and cameras with 3 LED modules in 2011 and 2012. The visible area of the cameras was restricted because of the narrow angle of view (52°) and the short range of object visibility (2 m for 1 LED module and 4 m for 3 LED modules in deep water). The cameras were set to record depth at 1 s intervals, and a still image with a LED flash at 4 s intervals. High-sensitivity shooting was used, which allowed a maximum number of 1500 to 3000 images to be recorded per deployment. The cameras were set to record still images once they had submerged below depth criteria that were set at each deployment (1–100 m; Table 1). Flashing white lights were activated at the same depth criteria in 2010 and 2011 (Table 1) and at depths deeper than 100–200 m in 2012. The accelerometers were set to record depth at 1 s intervals, and 2- or 3-axis acceleration at 1/16 s intervals. Additionally, 3-axis accelerometers were set to record swim speed at 1 s intervals. The measurement range of the pressure sensors of both animal-borne devices was from 0 to 2000 m, with a resolution of 0.5 m. Prior to deployment, the time on the devices was synchronized to GPS time. In addition, time synchronization on the camera and accelerometer was verified by comparing the depth data recorded by each device.

The start and end of dives were defined as the time when the whales descended below and ascended above a depth of 4 m, respectively. All deep dives (>400 m) were divided into 3 phases: (1) the descent phase (from the start of a dive to the first time at which the depth change rate was negative); (2) the ascent phase (from the last time at which the depth change rate was positive to the end of the dive); and (3) the bottom phase (the time between the end of the descent phase and the beginning of the ascent phase) (see Aoki et al. 2007 for details). Dive depth was defined as the maximum depth of the dive. Speed through the water was measured using an external propeller on the PD3GT accelerometer, and the propeller rotation count was converted to the actual swimming speed (m s^{-1}) using a calibration method (Blackwell et al. 1999, Amano & Yoshioka 2003). Swim speed was calculated based on the number of rotations of the data logger's propeller, according to a linear relationship with the vertical depth change rate. For each whale, we regressed 3, 5, and 10 percentile points of velocity data to their corresponding vertical depth change rates, and used the line with the highest regression coefficient value. High-frequency specific acceleration (>0.10 Hz) of the dorso-ventral or longitudinal axis was used to identify thrusting using fluking (Sato et al. 2003, Aoki et al. 2012). Bursts of speed were identified in the same manner, as described in Aoki et al. (2012). A burst was identified according to the following 2 criteria: (1) a forward acceleration of >0.15 m s^{-2}, calculated from the swim speed at 5 s intervals; and (2) a swim speed greater than the mean + 1.5 SD during the bottom phase of each dive (for details, see Figs. 2 & S4 in Aoki et al. 2012).

Since white light is visible to mammals, tagged sperm whales were likely to see the flashing white lights produced by the tag, which might have affected their behavior. To investigate whether this

Table 1. Summary of tag deployment and 5 classes of still images for 17 sperm whales off the Ogasawara Islands of Japan. We used a camera (DSL2000-VDTII) with 1 LED module in 2010 and a camera with 3 LED modules in 2011 and 2012. Three LED modules yield a longer range of object visibility (ca. 4 m) than 1 LED module (ca. 2 m), but the deployment duration was reduced by increasing frontal area of the whole device. Flashing lights were activated at the same depth criteria in 2010 and 2011, and at depths >100–200 m in 2012. In 2012, the cameras were set to start recording from just under the water surface because the data storage capacity of the cameras was enough to record for the whole attachment duration. For duration of attachment, parentheses show the recording duration of the cameras if it was shorter than the deployment duration, e.g. when the camera stopped recording images mid-deployment because the memory was full. See Fig. 2 for examples of each class of still image

Individual ID	Deployment date	Depth criteria for starting records of still images (m)	Duration of attachment (h)	No. total still images	Class of still image				
					Suspended materials	Unidentified particle	Possible animal body parts	Other sperm whales	Near sea floor
O10c	17 Sep 2010	30	6.2 (2.3)	2094	5	0	0	0	0
O10d	20 Sep 2010	50	13.8 (1.9)	1753	0	0	1	0	8
O11b	30 Jun 2011	30	3.4	2497	0	1	0	7	0
O11d	6 Jul 2011	100	1.3	940	0	0	1	0	0
O11g	29 Sep 2011	50	4.1	2203	1	2	0	0	0
O12c	2 Jun 2012	5	0.9	556	1	0	0	0	0
O12d	8 Jun 2012	10	0.5	455	7	0	0	0	0
O12f	15 Jun 2012	5	5.7 (4.6)	2609	2	0	0	0	0
O12g	17 Jun 2012	15	0.5	287	0	0	0	0	0
O12k	13 Sep 2012	10	1.4	793	0	0	0	0	0
O12n	14 Sep 2012	5	0.6	240	0	0	0	4	0
O12o-1	20 Sep 2012	1	0.2	172	0	0	0	39	0
O12o-2	20 Sep 2012	1	2.3	1595	1	1	0	1	0
O12p	21 Sep 2012	1	1.0	748	0	0	0	0	0
O12t	9 Nov 2012	10	0.2	215	0	0	0	0	0
O12s	9 Nov 2012	1	0.3	224	0	0	0	41	0
O12v	9 Nov 2012	1	0.4	334	0	0	0	129	0

occurred, we used linear mixed effect models (lmer function with a Gaussian error distribution and an identity link function in the R package of the R Project for Statistical Computing) to compare diving parameters among conditions (with flashing lights, without flashing lights, and no camera). This statistical model included any 1 of 5 diving parameters (dive depth, dive duration, bottom duration, overall vertical descent speed during descent phase, and overall vertical ascent speed during ascent phase) as a dependent factor, conditions as fixed independent factors, and individual ID as a random factor. We used complete deep dives (>400 m) obtained from 7 individuals with flashing lights and from 3 individuals for both conditions (i.e. with flashing lights and without flashing lights). The attachment duration for the tags on these 3 individuals was relatively long (ID O10c, O10d, and O12f; Table 1). As a consequence, the camera stopped recording images during mid-deployment since the memory was full. However, this provided scope to measure conditions both with and without flashing lights. It is conceivable that the behaviors of tagged whales were affected by light conditions after the camera stopped recording; however, our data did not provide enough coverage to compare diving behaviors under conditions before activating the light with those after activating the light. We therefore added diving data of female or immature sperm whales obtained from a previous study conducted off the Ogasawara Islands (for details, see Aoki et al. 2012) as 'no camera' conditions for these comparisons of the 5 diving parameters. All statistical analyses were performed using R version 3.0.2 (R Development Core Team 2008). Means ± SD are presented unless otherwise indicated.

RESULTS AND DISCUSSION

A total of 42.8 h of diving data, including 35 complete and 12 incomplete deep dives (>400 m) and 17 715 still images, was obtained from 17 sperm whales (Table 1; examples of images are shown in Movie A in the Supplement at www.int-res.com/articles/suppl/m523p233_supp/). The mean dive duration and depth of complete dives were 42 ± 10 min and 793 ± 248 m, respectively. The maximum dive duration and depth of complete dives were 57 min and 1354 m, respectively. Diurnal patterns of dive depth were as previously reported off the Ogasawara Islands (Aoki et al. 2007): the whales dived deeper during the day than during the night (day: 889 ± 187 m, n = 24 dives from 10 individuals; night: 560 ± 220 m, n = 11 dives from 3 individuals).

Effects of the flashing white light of the camera on the diving behavior of tagged sperm whales

To investigate whether the flashing white light of the camera affected the behavior of tagged whales, likelihood ratio testing was used to test for differences among the conditions with flashing lights, without flashing lights, and with no camera in mean values for 5 parameters (dive depth, dive duration, overall vertical descent speed during descent phase, and overall ascent speed during ascent phase) (Table 2). There was no significant effect on the diving behavior of tagged whales. It is possible that the flashing white light emitted by the camera surprised the whales, thus affecting acceleration or deceleration. However, there was no clear change in either acceleration or swim speed when the light flashed in 4 s cycles (Fig. 1). The flashing light was not sufficiently bright to cover the large body of sperm whales (the range of the object visibility is 2 m for the 1 LED module and 4 m for the 3 LED modules in deep water). Therefore, tagged whales did not appear to react strongly to flashing lights. Of course, because white light is visible to mammals, it remains possible that the flashing white lights had other effects. We could not test the possibility that the white light from the LED affected the behavior of other whales or prey around the tagged individuals.

Five classes of still images obtained from animal-borne cameras in relation to sperm whale behavior

The majority of still images were relatively dark because nothing reflected the light emitted from the LED modules (Fig. 2a). Five classes of images with visible material were identified (Table 1): (1) suspended material in 17 images from 6 individuals (Fig. 2b, Movie A in the Supplement); (2) unidentified particles in 4 images from 3 individuals (Fig. 2c); (3) possible animal body parts in 2 images from 2 individuals (Fig. 2d); (4) other sperm whales in 221 images from 6 individuals (Fig. 2e,f, Movie A in the Supplement); and (5) the seafloor in 8 images from 1 individual (Fig. 2g). The images recorded near the seafloor were distinguished from images of suspended materials based on their uniform, bright reflection of LEDs (Fig. 2g) and their coincidence with the flat bottom phase of the depth profile.

The images of other sperm whales were recorded in the depth range of 0–339 m: 4 images near the surface during post-dive surface time, and 210 images in 4 possible non-foraging dives (maximum depths: 111, 186, 160, and 359 m). Body contact between the tagged whales and other sperm whales was identified in 14 of these images (Fig. 2f). In addition, 7 images of another individual whale were continuously recorded during the beginning of the descent (121–152 m depth) of a possible foraging dive (maxi-

Table 2. Linear mixed models examining significant differences among conditions (with flashing lights, without flashing lights and no camera; mean ± SE) on 5 diving parameters of sperm whales. This statistical model included any 1 of 5 diving parameters as a dependent factor, conditions as fixed independent factors, and individual ID as a random factor (for details, see 'Materials and methods'). A total of 165 complete deep dives (>400 m) was used for this comparison: 22 dives with flashing lights from 10 ind., 13 dives without flashing lights from 3 ind., and 130 dives without cameras from 12 ind. obtained from a previous study conducted off the Ogasawara Islands (females or immature sperm whales tagged with a data logger in 2004 to 2008; Aoki et al. 2012). Likelihood ratio tests were used to assess the significance of the term 'conditions'. There were no significant differences among conditions in mean values for all parameters, indicating no clear effects of the lights on the diving behavior of tagged whales

Diving parameter	No. of dives	Dive depth (m)	Dive duration (min)	Bottom duration (min)	Vertical descent speed (m s^{-1})	Vertical ascent speed (m s^{-1})
With flashing lights	22	767 ± 100	37.6 ± 2.2	19.5 ± 2.5	1.2 ± 0.1	1.2 ± 0.1
Without flashing lights	13	762 ± 99	38.5 ± 3.6	22.1 ± 2.7	1.2 ± 0.1	1.2 ± 0.1
No camera	130	711 ± 108	33.5 ± 6.6	16.6 ± 3.1	1.4 ± 0.1	1.3 ± 0.1
χ^2		0.59	2.28	2.91	1.53	2.19
df		2	2	2	2	2
p		0.75	0.32	0.23	0.47	0.34

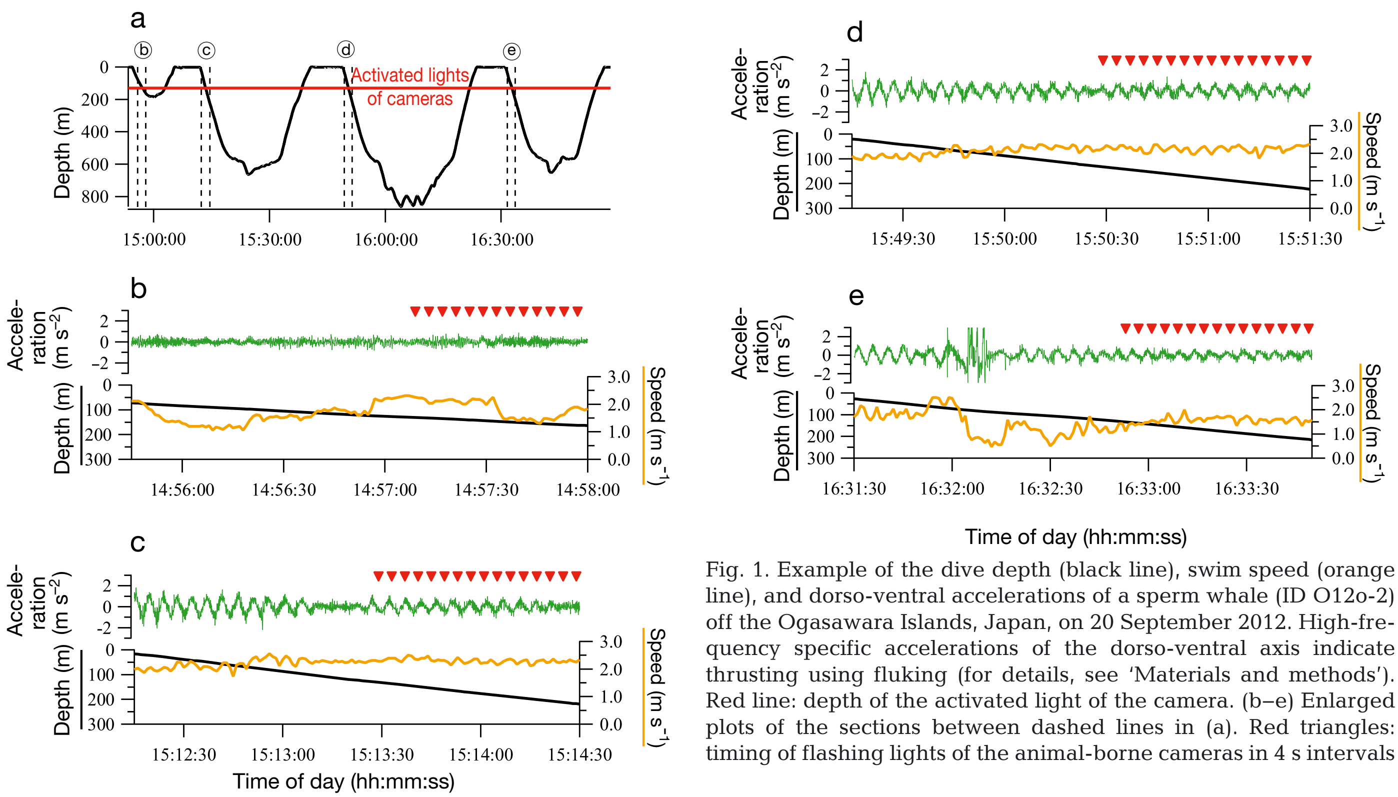

Fig. 1. Example of the dive depth (black line), swim speed (orange line), and dorso-ventral accelerations of a sperm whale (ID O12o-2) off the Ogasawara Islands, Japan, on 20 September 2012. High-frequency specific accelerations of the dorso-ventral axis indicate thrusting using fluking (for details, see 'Materials and methods'). Red line: depth of the activated light of the camera. (b–e) Enlarged plots of the sections between dashed lines in (a). Red triangles: timing of flashing lights of the animal-borne cameras in 4 s intervals

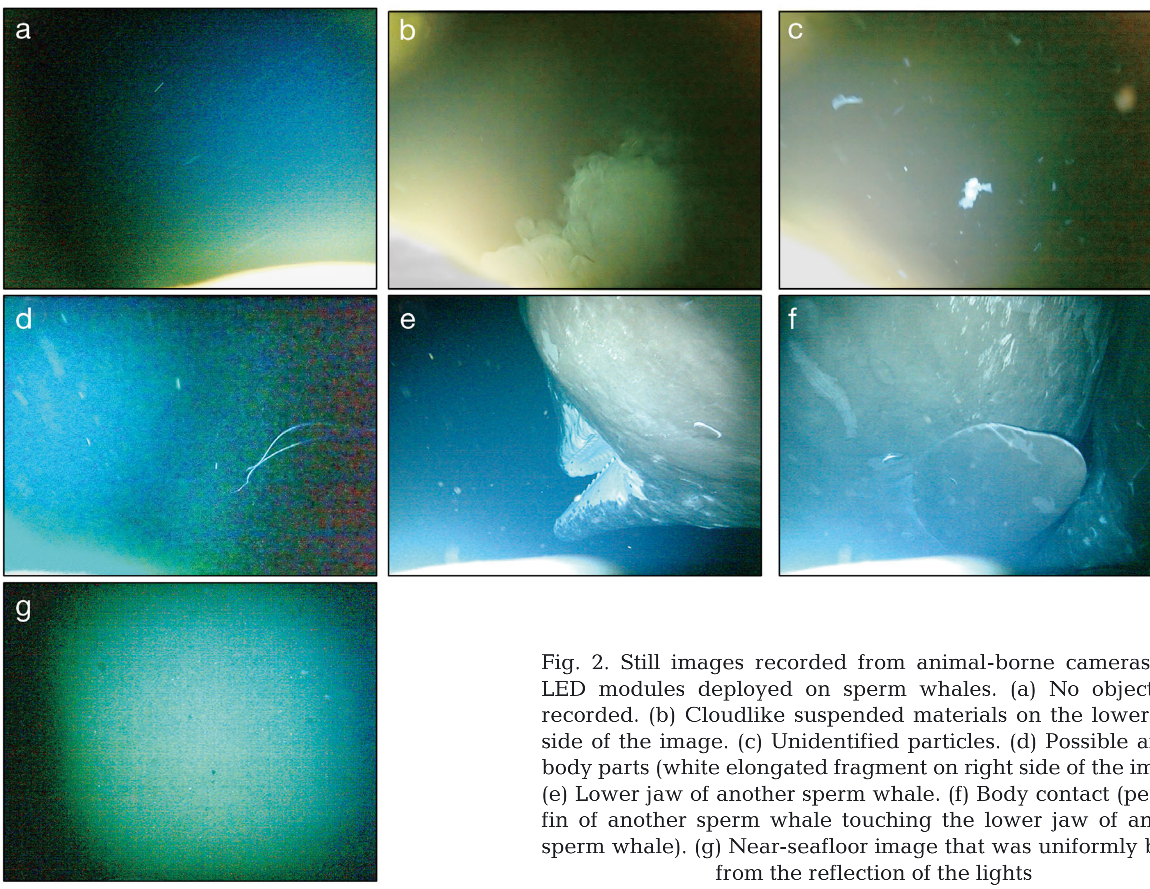

Fig. 2. Still images recorded from animal-borne cameras with LED modules deployed on sperm whales. (a) No object was recorded. (b) Cloudlike suspended materials on the lower right side of the image. (c) Unidentified particles. (d) Possible animal body parts (white elongated fragment on right side of the image). (e) Lower jaw of another sperm whale. (f) Body contact (pectoral fin of another sperm whale touching the lower jaw of another sperm whale). (g) Near-seafloor image that was uniformly bright from the reflection of the lights

mum depth: 514 m), indicating that the 2 whales descended together for 25 s and then separated. These results suggest that the tagged whales swam alone while foraging at deeper depths. Six tagged whales were associated with the underwater images of other individuals, and 5 of the 6 whales were also sighted with another 1 to 8 individuals at the surface (i.e. the one remaining whale was alone at the surface). In contrast, 11 tagged whales had no underwater record of other individuals, and 9 of the 11 whales were also alone at the surface (i.e. the remaining 2 stayed together with 1 or 2 other individuals). This indicates that the whales that stayed close to each other at the surface also swam in close proximity underwater. We cannot ascertain the meaning of this behavior based on a few observations; however, similar behavior has been observed in other deep-diving Odontoceti, and it has been suggested to have a social function (Aoki et al. 2013). Alternatively, other sperm whales might have been attracted to the flashing LED of the cameras because they were likely to see the lights being produced by the suction-cup-attached tag if they stayed close to the tagged whale. Unfortunately, however, it is difficult to investigate the impacts of the lights on other sperm whales with our data.

The images of suspended material, unidentified particles, and possible animal body parts were recorded at 810 ± 88 m (n = 17 images), 504 ± 57 m (n = 4 images), and 754 m and 884 m (n = 2 images), respectively, and were not obtained at shallow depths (less than ca. 400 m). The simultaneous use of an accelerometer with a speed sensor (the PD3GT) and an animal-borne camera on 6 tagged whales revealed that the suspended material was related to bursts of speed up to approximately twice (3.3 ± 1.0 m s^{-1}, max. 6 m s^{-1}) the mean speed observed during dives (1.8 ± 0.4 m s^{-1}; n = 10 dives from 6 individuals; Fig. 3). Suspended material occurred in only 9 of a total of 4362 images obtained from 6 tagged whales (0.03 images min^{-1}), but 7 of the 9 images of suspended material were taken during bursts (0.3 images min^{-1}). The occurrence of images of suspended material was significantly higher during bursts than at other times (7 of 306 images during bursts, 2 of 4056 images during other times; Fisher's exact test, $p < 0.0001$, odds ratio = 47). The bursts occurred at a mean depth of 729 ± 106 m (n = 38 bursts). Six of the 38 bursts were accompanied by images of suspended material. The images of suspended material were taken 7 s before and 17 s after the maximum speed of the bursts. Additionally, there was a concomitant strong signal of acceleration for 8 of these 9 images of suspended material (Fig. 3b), indicating rapid movements of the tagged whales.

Since the images of suspended material were recorded only at depth, and most were taken during burst events, we suggest that the material was related to the feeding activity of sperm whales, and was possibly squid ink. Indeed, underwater camera systems have previously observed the ink spurted by flying squids *Ommastrephes bartrami* (see Movie B in the Supplement at www.int-res.com/articles/suppl/m523p233_supp/; T. Kubodera unpubl. data) in mesopelagic waters of this area (Kubodera & Mori 2003). Unfortunately, without images of prey, we cannot verify this hypothesis; however, it is unlikely that these materials were sediments blown up by the whales because they occurred midway through the ascent or descent (e.g. Fig. 3f; difference from maximum depth: 144 ± 59 m, n = 17). Our study provides images of suspended material that are associated with bursts of speed, which give collateral evidence of prey capture by actively hunting sperm whales.

Considerations for future improvement of suction-cup-attached tags

Despite the fact that similar animal-borne cameras or videos have succeeded in capturing images of prey for many other taxa (e.g. Davis et al. 1999, Ponganis et al. 2000, Watanabe et al. 2004, Watanuki et al. 2008, Kokubun et al. 2013, Naito et al. 2013, Narazaki et al. 2013, Watanabe & Takahashi 2013, Nakamura & Sato 2014, Heaslip et al. 2014), our systems did not allow us to observe direct feeding events of sperm whales, owing to 3 possible factors. (1) The narrow angle of view (52°) and the short range of object visibility (2 m for 1 LED module and 4 m for 3 LED modules in deep water) compared to the larger bodies of sperm whales than other taxa (Fig. 4). (2) Difficulty in deploying the suction-cup-attached tag to capture images around the mouth within the visible range of the camera. Since the protruding forehead of the sperm whales was likely to block the view of the camera, it prevented the capture of images around the mouth of the sperm whale even if we attached the tag to the upper parts of the head (Fig. 4). To solve this, we tried a new system in which a suction cup towed the camera tag, but a tagged whale reacted to this system (the whale started rolling just after the deployment and continued rolling until the tag detached; K. Aoki unpubl. data). (3) The combination of longer sampling intervals and quick movements of possible prey. The sam-

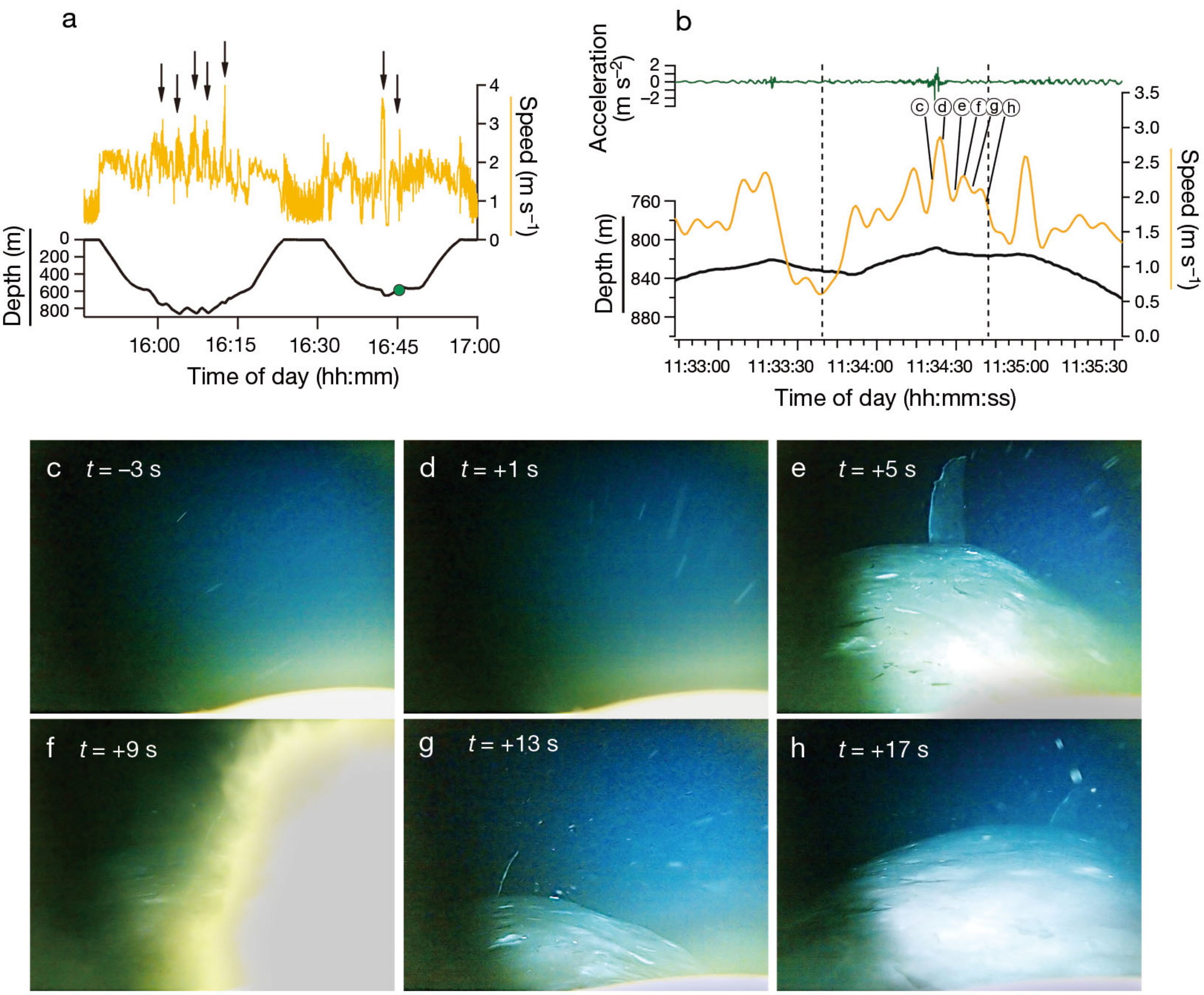

Fig. 3. Still images of suspended material associated with bursts of speed. (a) Depth and swim speed of a tagged whale, ID O12o-2. Arrows highlight bursts of speed. Green circle: image of suspended material was obtained. (b) Dorsal-ventral acceleration, depth and swim speed of sperm whale O12d. Images (c–h) of suspended material were obtained during a burst in (b), (shown between dashed lines; letters show the timing of images). Time (*t*) was calculated from the moment of maximum speed. Suspended material strongly reflected light emitted from the LED module (f)

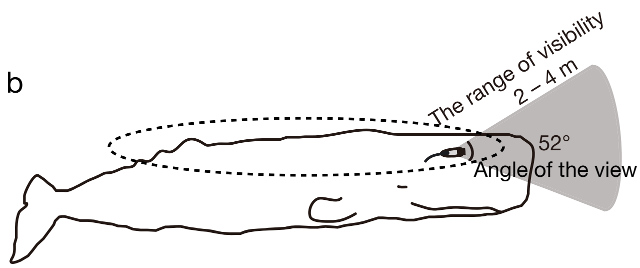

Fig. 4. Suction-cup-attached tag deployed on a sperm whale. (a) Tagged sperm whale (ID O10d). A white circle highlights the tag. (b) Visible area (gray shading) seen through the animal-borne camera deployed on a tagged sperm whale. The narrow angle of the view and the short range of visibility restricted the visible area. Dashed oval shows the possible deployment area of the tag

pling rate of our camera and LED light was 4 s. On the basis of the mean swimming speed of tagged whales (1.8 m s^{-1}), the distance that a whale swam between still images was approximately 7.2 m. Since this distance was longer than the range of object visibility (2–4 m), the sampling covered only a part of the foraging paths of the whales.

The present versions of animal-borne cameras have succeeded in providing new insights not only into a predator's prey type, but also into the foraging habitats of several other taxa, including pinnipeds (Watanabe et al. 2004, 2006, Naito et al. 2013), penguins (Kokubun et al. 2011, 2013), shags (Watanuki et al. 2008), and sunfishes (Nakamura & Sato 2014). However, we found it was difficult to obtain images of prey from sperm whales using the present systems. To capture images of sperm whale prey, we need to solve the difficulty of the camera deployment around the mouth (Factor 2). Alternatively, smaller, more powerful infrared lights, high sampling cameras with higher sensitivity and wider visible areas, and video would also contribute to the direct measurement of feeding events of sperm whales (possible solutions to Factors 1 and 3).

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