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RESEARCH ARTICLE

Acceleration-triggered animal-borne videos show a dominance of fish in the diet of female northern elephant seals

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ABSTRACT

Knowledge of the diet of marine mammals is fundamental to understanding their role in marine ecosystems and response to environmental change. Recently, animal-borne video cameras have revealed the diet of marine mammals that make short foraging trips. However, novel approaches that allocate video time to target prey capture events is required to obtain diet information for species that make long foraging trips over great distances. We combined satellite telemetry and depth recorders with newly developed date-/time-, depth- and acceleration-triggered animal-borne video cameras to examine the diet of female northern elephant seals during their foraging migrations across the eastern North Pacific. We obtained 48.2 h of underwater video, from cameras mounted on the head (n=12) and jaw (n=3) of seals. Fish dominated the diet (78% of 697 prey items recorded) across all foraging locations (range: 37–55°N, 122–152°W), diving depths (range: 238–1167 m) and water temperatures (range: 3.2–7.4°C), while squid comprised only 7% of the diet. Identified prey included fish such as myctophids, *Merluccius* sp. and *Icosteus aenigmaticus*, and squid such as *Histioteuthis* sp., *Octopoteuthis* sp. and *Taningia danae*. Our results corroborate fatty acid analysis, which also found that fish are more important in the diet, and are in contrast to stomach content analyses that found cephalopods to be the most important component of the diet. Our work shows that *in situ* video observation is a useful method for studying the at-sea diet of long-ranging marine predators.

KEY WORDS: Bio-logging, Diving behavior, Foraging, Marine mammal, Mesopelagic zone

INTRODUCTION

Marine mammals play an important role in marine ecosystems as major consumers of a wide variety of prey (Estes et al., 2016). Knowledge regarding when, where and on what type of prey marine mammals feed is fundamental to understand their roles in marine ecosystems and their responses to marine environmental changes (Costa et al., 2012; Miloslavich et al., 2018; Bax et al., 2019). Recent developments in bio-logging technologies have allowed us to obtain information about when and where marine mammals feed on their prey. For example, animal-borne satellite transmitters or GPS loggers are routinely used to identify hotspots where marine mammals focus their foraging (Block et al., 2011; Costa et al., 2012; Hussey et al., 2015). In addition, instruments such as stomach temperature loggers or accelerometers attached to the head or jaw of animals identify when animals capture and consume prey, at a fine temporal scale (Kuhn et al., 2009; Naito et al., 2013; Guinet et al., 2014). However, these technologies are not able to identify what type of prey marine mammals consume in the open ocean.

Marine mammal diet has been studied by various techniques, such as stomach content analysis, scat content or scat DNA analysis, stable isotopes and fatty acid analyses (reviewed in Tollit et al., 2010). Stomach content analysis allows the direct assessment of prey that was consumed by marine mammals (Antonelis et al., 1987, 1994; Field et al., 2007). However, this method has inherent biases toward prey with hard parts and recently consumed items (Harvey and Antonelis, 1994). Similarly, scat content analysis has been widely used but also presents challenges to identify prey items that are highly digested as well as inherent biases toward prey items with hard parts (Gales and Cheal, 1992; Tollit et al., 2010). More recently, scat DNA analysis has been developed to help address the identification and bias issues, but there are still unavoidable limitations as only recently consumed items will be present in scat. Stable isotope (Cherel et al., 2008; Hückstädt et al., 2012) and fatty acid analyses (Bradshaw et al., 2003) allow us to estimate the diet that is consumed (and incorporated) over a relatively long period, though some necessary information such as isotopic and fatty acid signatures of prey are often difficult to obtain, limiting the ability to precisely estimate the diet composition (but see Goetsch et al., 2018). Hence, new developments are still necessary to identify the types of prey that marine mammals feed on at sea, and these should operate at a temporal resolution that matches the behavioral data on where and when they feed.

Recently, animal-borne videos have been used successfully to quantify at-sea diet compositions of relatively short-ranging pinnipeds, such as Weddell seals, *Leptonychotes weddellii* (Davis et al., 1999), harbor seals, *Phoca vitulina* (Bowen et al., 2002), Antarctic fur seals, *Arctocephalus gazella* (Hooker et al., 2002), and Australian fur seals, *Arctocephalus pusillus doriferus* (Kernaléguen et al., 2016). This approach has allowed us to examine detailed at-sea diet at a fine temporal scale. However, the duration of the video recordings is limited to several hours or days by battery/memory capacity, unlike the behavioral data obtained from satellite transmitters or time–depth recorders that can last for several months. Moreover, successful video recordings of prey captures are often limited, because animal-borne cameras do not target areas where prey capture events occur (e.g. depth), especially in situations where rates of prey encounters are relatively low. Hence, use of video to estimate diet has largely been confined to breeding seasons,

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when it is possible to recover videos after a few days. It has not been applied, however, to study the diet of the wide-ranging species that spend prolonged periods of time (weeks to months) feeding at sea.

Northern elephant seals, *Mirounga angustirostris* (Gill 1866) are upper-trophic level predators of the North Pacific, and their colonies extend from California (USA) to Mexico. Female northern elephant seals feed primarily at depths between 400 and 800 m (Le Boeuf et al., 2000; Robinson et al., 2012), with maximum dive depths over 1000 m (Robinson et al., 2012; Naito et al., 2013). They move over long distances during biannual foraging migrations that last approximately 75 or 220 days (Le Boeuf et al., 2000; Robinson et al., 2012). Their migration routes and diving behaviors have been widely studied using satellite transmitters or time–depth recorders (Simmons et al., 2010; Robinson et al., 2012). However, relatively few studies have examined the diet of northern elephant seals while they are at sea. Previous studies using stomach content analysis (Antonelis et al., 1987, 1994) suggested that seals fed more on squid than on fish. Yet, more recently, Naito et al. (2013, 2017) proposed that northern elephant seals feed on myctophids and ragfish in the mesopelagic zone, based on several images and videos obtained from animal-borne still and video cameras. Similarly, Goetsch et al. (2018) reported that energy-rich mesopelagic fish, such as myctophids, are more important in the diet than squid, based on quantitative fatty acid signature analyses.

The present study examined the at-sea diet of female northern elephant seals using digital video, obtained from recently developed video loggers with a feeding-triggered (acceleration) system (Naito et al., 2017). As described in Naito et al. (2017), the video camera remains in a power-saving mode until a predetermined date, at which time individual video recordings are then triggered when a predetermined depth and acceleration threshold are reached. This allows for the efficient video recording of prey capture events. Studies on the congeneric southern elephant seals (*M. leonina*) suggested that their diet varies spatially (Daneri et al., 2000). Therefore, we hypothesized that the diet of female northern elephant seals differs among foraging areas, foraging depths or water temperatures, and we tested these hypotheses using information obtained from satellite transmitters and time–depth/temperature recorders that were attached to elephant seals outfitted with video cameras.

MATERIALS AND METHODS

Field experiments and instruments

Fieldwork was conducted at Año Nuevo State Park, California, USA (37.12°N, 122.33°W). We used an intramuscular injection of Telazol (Tiletamine hydrochloride and Zolazepam hydrochloride, Fort Dodge Animal Health, Fort Dodge, IA, USA) at an estimated dose of 1 mg kg^{-1} to chemically immobilize seals for the attachment of instruments. To investigate the at-sea diet, we attached depth- and acceleration-triggered video cameras (Little Leonardo Co., Tokyo, Japan; Naito et al., 2017) on the head or jaw of post-breeding female northern elephant seals, in February of each study year (Tables 1 and 2). The head- and jaw-mounted video instruments were designed to record surge acceleration signals at 32 Hz, depth at 0.2 Hz and video at 30 frames s^{-1}, except two jaw-mounted video cameras used in 2016, which recorded three axes of acceleration at 100 Hz, depth at 1 Hz and video at 30 frames s^{-1}. To start recording when elephant seals feed, all except two instruments (Table 1) used a three-step trigger. First, we implemented a start delay timer, which caused the loggers to start recording videos at a designated date/time after deployment of the instruments, presumably when seals were well into their foraging migration. Second was a depth trigger; because elephant seals usually feed at 400–800 m depths (Naito et al., 2013), we set the trigger depths at either 300, 400 or 800 m. The instrument would only respond to feeding events on dives below those depths. The third trigger was a feeding signal based on acceleration. The camera would start recording only when the signal from the built-in acceleration sensor suggested signals consistent with foraging (within 10 s from receiving the acceleration signal, because of the inherent delay in starting video records). Feeding attempts were identified as head or jaw motions with a surge acceleration amplitude threshold of 0.3 ***g***, based on Naito et al. (2013, 2017). In 2013, the first study year, we set video cameras to record for a duration of 9.7 and 4.7 min for the depth triggers of 300 and 800 m, respectively (Table 1). In 2015 and 2017, we set the camera to record for a duration of 1 and 4 min for the depth triggers of 400 and 800 m, respectively (Table 1), as we found that these recording durations would allow us to record video clips of feeding attempts more frequently, based on the analysis of depth and jaw motion events obtained prior to this study (Naito et al., 2013). After recording video for a predetermined duration, the video cameras stopped recording until the initiation of the next dive,

Table 1. Summary of video recordings from adult female northern elephant seals from Año Nuevo, California, USA

Seal ID	Year	Position of video	Flash type	Delay timer duration (days)	Trigger depth (m)	Scheduled duration of one video (h:min:s)	Total video duration (h:min:s)	Total no. of prey items recorded	No. of prey items per hour
X387	2013	Head	Infrared	18	300	0:09:40	3:41:17	51	13.8
2161	2013	Head	Infrared	15	800	0:04:40	1:05:23	19	17.4
5061	2015	Head	Infrared	36	400	0:01:00	3:35:00	41	11.4
U549	2015	Head	Infrared	36	400	0:01:00	3:35:25	54	15
4176	2015	Head	Infrared	0	800	0:04:00	2:42:16	8	3
6037	2015	Head	Infrared	21	800	0:04:00	3:31:04	58	16.5
6651	2015	Head	Infrared	21	800	0:04:00	3:25:28	39	11.4
6762*	2015	Head	Infrared	21	800	0:04:00	0:51:46	6	7
YN371	2015	Head	Infrared	36	400	0:01:00	3:17:13	117	35.6
VX372	2015	Jaw	Near-red	21	800	0:04:00	2:31:31	88	34.8
6762*	2016	Jaw	Near-red	21	0	Continuous‡	5:05:01	42	8.3
T28	2016	Jaw	Near-red	21	0	Continuous‡	5:40:28	5	0.9
5712	2017	Head	Infrared	36	400	0:01:00	2:09:47	35	16.2
6108	2017	Head	Infrared	36	400	0:01:00	3:29:10	54	15.5
U20	2017	Head	Infrared	36	400	0:01:00	3:29:47	80	22.9

*Video attached on the same seal.
‡Continuous recording once video recording started.

Table 2. Summary of video instruments deployed on female elephant seals from Año Nuevo, California, USA

Type	Size and mass	Resolution (pixels)	Start tiggers
Head-mounted videos	30 mm (diameter)×151 mm (length), 158 g	640×480	Delay timer, depth, acceleration
Infrared flash unit for head-mount video	30 mm (diameter)×130 mm (length), 187 g		
Jaw-mounted video (2015)	28 mm (diameter)×106 mm (length), 118 g	640×480	Delay timer, depth, acceleration
Near-red flash unit for jaw-mount video (2015)	28 mm (diameter)×93 mm (length), 117 g		
Jaw-mounted video (2016)*	23×21×72 mm, 53.2 g	1280×960	Delay timer only

*Near-red flash was built in with video.

the next depth threshold and feeding signal. This allowed us to obtain relatively short video clips for each dive across many dives. To examine the efficiency of this three-step trigger, we also deployed two jaw video cameras that recorded continuously after an initial delay, with no depth or acceleration triggers (Tables 1 and 2). The visibility range of the video is approximately 60 cm from the mouth of a seal (Naito et al., 2017).

The at-sea locations of seals were recorded using satellite transmitters (Wildlife Computers, Redmond, WA, USA, or Sea Mammal Research Unit, St Andrews, Scotland; Robinson et al., 2010). We recorded depth profiles using jaw-mounted accelerometers (KamiKami Logger, Little Leonardo Co., Tokyo, Japan; Naito et al., 2013). Water temperature was obtained every 4 s from time-depth recorders (MK9, Wildlife Computers; Robinson et al., 2012) that were affixed to the back of the seals. All instruments were wrapped in rubber splicing tape and attached to high-tension mesh with cable ties. These packages were adhered to the seals' pelage using Loctite Quickset™ epoxy (Henkel Corp., Düsseldorf, Germany).

This study was conducted under the National Marine Fisheries Service permit numbers 14636 and 19108 issued to D.P.C., and was approved by the Institutional Animal Care and Use Committee at the University of California, Santa Cruz.

Data analysis

All video data were analyzed using QuickTime Player (Ver.10.2, Apple Inc., Cupertino, CA, USA) to visually determine prey capture events. Prey items that were consumed by the seals were classified as fish, cephalopods or unidentified prey items. We identified prey items to the lowest possible taxonomic level based on available literature and expert opinion.

Satellite data were processed using the R package crawl (Johnson et al., 2008) to eliminate erroneous location estimates and interpolate between locations (see also Robinson et al., 2010, 2012). To test possible regional differences in the proportion of prey types (fish versus squid), we categorized daily locations where seals captured prey into three regional categories (California Current, Gulf of Alaska and Eastern North Pacific offshore), based on boundaries of Large Marine Ecosystems of the Worlds (http://lme.edc.uri.edu/index.php/digital-data) (Fig. S1). To examine possible differences in prey types between day and night, we assigned prey capture events to day or night, based on solar zenith angle calculated from the time and location, using the R package GeoLight (Lisovski and Hahn, 2012). Regional and day–night differences in the proportion of prey types (fish versus squid) were examined with *G*-tests by pooling the data from all seals, using the R package DescTools (https://cran.r-project.org/package=DescTools). Depth and water temperature data for where seals fed on prey were extracted using IGOR Pro software (Ver. 6.22J; WaveMetrics, Inc., Lake Oswego, OR, USA). Water temperature data were unavailable for three of the 15 seals studied, owing to temperature sensor malfunction of time-depth recorders. We tested the effect of prey types (fish versus squid) on depth and water temperature where seals fed on prey with linear mixed-effect models (LMM) with seal ID included as a random effect, using the R packages lme4 (http://cran.r-project.org/web/packages/lme4) and multcomp (Hothorn et al., 2008).

RESULTS

Video observations

Seals in our study (n=15) ranged widely over the eastern North Pacific (Fig. 1). From these seals, a total of 48.2 h of video records from 1467 dives were obtained from head-mounted (n=12) and jaw-mounted cameras (n=3) (Table 1). A total number of 697 prey items were observed (Movies 1 and 2) across a total of 77 days during the foraging trips of the 15 seals. Out of all prey captured, 543 (78%) were identified as fish, whereas 49 (7%) were identified as cephalopods. The remaining 105 items (15%) could not be identified. Unidentified prey items (referred to as unknown prey) likely included both fish and cephalopods.

Fish dominated the diet in most seals, across all sampling years and trigger depths (Fig. 2). The proportion of fish in the diet was >50% for all seals that had video records that included more than 19 prey items (n=12). Fish and cephalopod captures were recorded on 72 and 24 days, respectively, of the 77 total days of foraging for which we had video records. Fish dominated the prey items both during the day and night (92.4% and 90.6% of 380 and 212 identified items, respectively), with no significant differences in prey type composition between day and night (*G*-test, G=0.57, d.f.=1, P=0.45).

Consistency of diet across regions, depths and water temperature

Prey items were recorded in videos captured at a wide range of locations across the eastern North Pacific (Fig. 1). Because the start of video recordings was delayed up to 36 days and triggered by depth (Table 1), video clips encompassed the portion of the post-breeding migration ranging from 122°W to 152°W in longitude and from 36°N to 56°N in latitude (Fig. 1). Both prey types were recorded across coastal and pelagic regions of the eastern North Pacific. Cephalopods occurred more frequently in the Eastern North Pacific offshore (12.7% of 245 prey items of which prey type was identified) than in the California Current and Gulf of Alaska (4.3% and 6.0% of 164 and 183 prey items, respectively) (*G*-test, G=10.909, d.f.=2, P<0.01). Fish were recorded across all longitudinal and latitudinal ranges. Cephalopods were not seen in the records from the seals that moved north of 50°N, along the west coast of Canada (Fig. 1).

Prey items were recorded across a range of depths between 238 and 1167 m (Fig. 3). Prey captures were recorded most frequently at 400–500 m depths (33% of all captures recorded) because six out of 15 videos were set to start recording when the seal reached 400 m. Fish dominated the diet across depth ranges deeper than 400 m (Fig. 3). Within the depth range of 238–400 m, a total of 17

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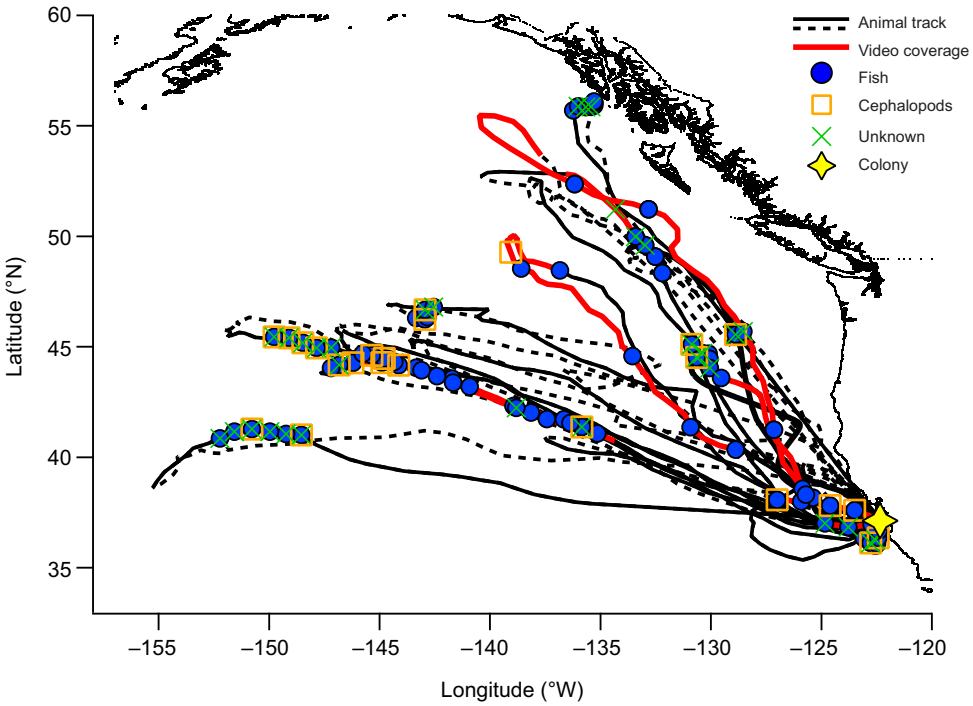

Fig. 1. At-sea movements of 15 female northern elephant seals from Año Nuevo, California, during 2013–2017. Black lines indicate animal tracks (solid and dashed lines represent the outbound and inbound part of each track, respectively). Red line sections indicate where video data were recorded. Blue circles indicate daily locations where video cameras recorded the seals catching fish. Orange squares indicate daily locations where cephalopods were caught, and green crosses indicate unknown prey items.

prey items were recorded, 53% of which were cephalopods. Depths where seals captured prey items did not differ significantly between fish and squid prey (LMM, effect of prey type on depth; estimate±s.e.=−11.62±11.64, z=−0.99, P=0.54).

Seals captured prey across temperatures that varied between 3.2 and 7.35°C, although prey captures occurred more frequently between 3.5 and 4.0°C (Fig. 4), possibly reflecting the spatial distribution of video recordings (Fig. 1). Fish dominated the diet across all water temperature ranges (Fig. 4). Water temperatures where seals captured cephalopod prey were slightly (0.26°C) higher than that for fish prey (LMM, effect of prey type on water temperature; estimate±s.e.=0.26±0.06, z=4.26, P<0.01).

Prey identification and prey behavior

In most cases, it was not possible to identify the species or genus of all prey items. However, three fish (Fig. 5) and six squid (Fig. 6) were identified to the species or genus level, based on the shape and appearance of the overall body, fins or tentacles.

Behavior of fish and squid, just before being captured, was highly variable among capture events. For example, some fish were motionless and appeared to be not responding to seals' approaches (clips 1–3 of Movie 1), but other fish swam vigorously to escape from the seal (clip 4). Some squid were motionless (clip 1 of Movie 2), but others showed escape movements (clips 2 and 3), occasionally emitting bioluminescence, to which the seal appeared to respond (clip 3).

DISCUSSION

Diet of northern elephant seals

Our results indicate that fish largely dominate the diet of post-breeding female northern elephant seals (Fig. 2). Our data offer a contrasting view to previous studies that, based on stomach

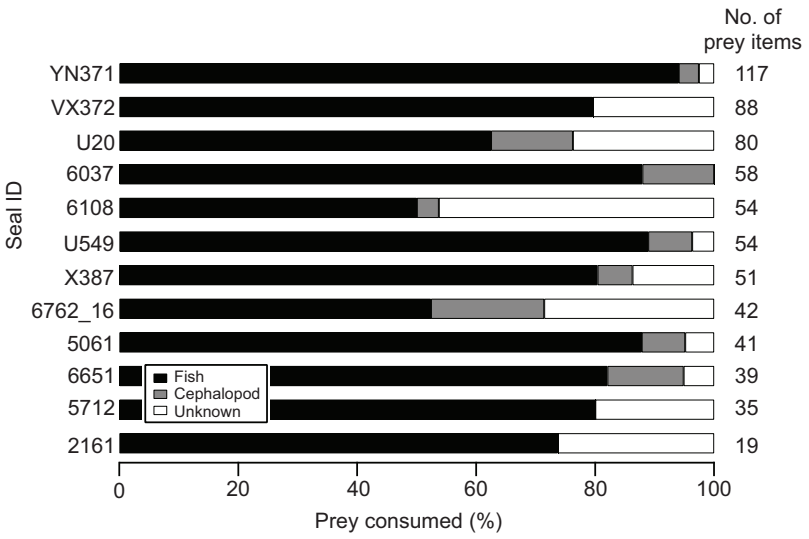

Fig. 2. Percentage of prey types consumed by adult female northern elephant seals from Año Nuevo, California, determined from animal-borne video records. Data from 12 seals with >19 observed prey capture events are shown. The shade of the bar indicates the percent of fish (black), cephalopod (grey) or unknown prey items (white).

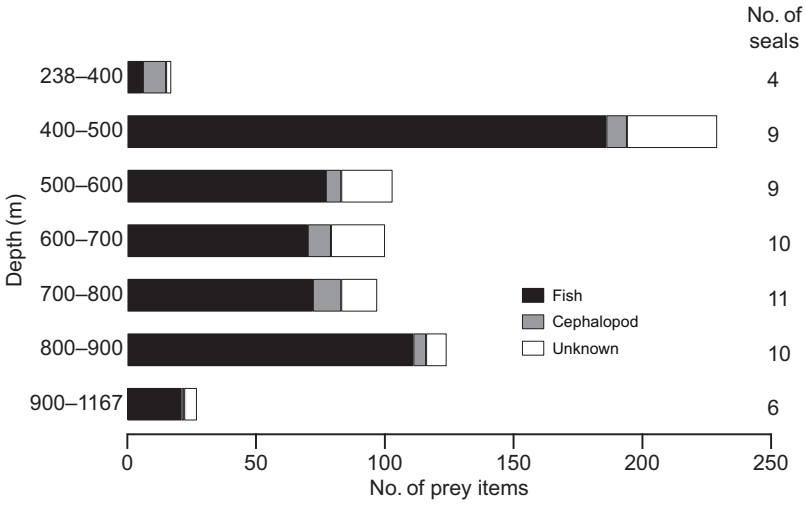

Fig. 3. Composition of prey types of adult female northern elephant seals from Año Nuevo, California, in relation to feeding depth, observed using animal-borne video cameras. Color codes indicate fish (black), cephalopod (grey) and unknown prey items (white).

contents, reported a higher occurrence of cephalopods than fish (cephalopods and teleosts found in 112 and 75 out of 193 stomach contents, respectively; Antonelis et al., 1987, 1994). Stomach contents analysis has an inherent bias toward hard parts such as squid beaks that tend to be retained in the stomach, which likely explains the discrepancy (Harvey and Antonelis, 1994). More recently, Goetsch et al. (2018), based on quantitative fatty acid signature analysis, reported that fish and squid comprised 63.7% and 36.3% of population level diet of female northern elephant seals, respectively, and that energy-rich mesopelagic fish are important in the diet. This finding is consistent with our results.

Mesopelagic fish, such as myctophids, would be preferable prey for northern elephant seals, as they are energy-rich and highly abundant in the mesopelagic depth zone (200–1000 m) (Brodeur and Yamamura, 2005; Catul et al., 2011). New estimates suggest that the biomass of mesopelagic fish is one order of magnitude higher than previously thought, based on acoustic observations (Irigoien et al., 2014). High mesopelagic fish biomass (consisting mainly of myctophid fishes) was also reported using ship-based net sampling in the Transition Zone of the eastern North Pacific (Saijo et al., 2017), the primary foraging area of female northern elephant seals (Robinson et al., 2012). Female northern elephant seals generally show a large number of feeding-associated jaw motion events (around 2000 times per day) (Naito et al., 2013), which agrees with the hypothesized abundance of myctophids. Myctophidae fish often form dense aggregations (Catul et al., 2011), which would make them easier to detect by predators, and generally have high energy density (7–13 kJ g^{-1} wet mass; Lea et al., 2002; Sinclair et al., 2015; Goetsch et al., 2018), and therefore should be preferentially targeted by northern elephant seals.

Our results confirm that post-breeding female northern elephant seals feed on fish across their foraging range (Fig. 1) and main foraging depths (Fig. 3) in the eastern North Pacific. Slightly higher occurrence of cephalopod in the Eastern North Pacific offshore region might reflect regional differences in the distribution and abundance of mesopelagic squid (Brodeur and Yamamura, 2005). Although our depth-trigger system biased our records to 400 and 800 m depths, our previous work using jaw motion event recorders shows these depths to be the primary foraging depths of female northern elephant seals (Naito et al., 2013, 2017; Adachi et al., 2019).

Comparison with other marine mammals

Previous studies suggested that southern elephant seals, the congeneric species of northern elephant seals in the southern hemisphere, feed on both fish and cephalopods (Daneri et al., 2000; Daneri and Carlini, 2002; Bradshaw et al., 2003; Field et al., 2007; Cherel et al., 2008). Daneri and Carlini (2002) found more cephalopods than fish in stomach content samples (98.1% and 14.8%, respectively) at King George Island, with myctophids as the most dominant (76.6%) fish group. Similarly, Field et al. (2007) reported a higher occurrence of squid than fish remains in the

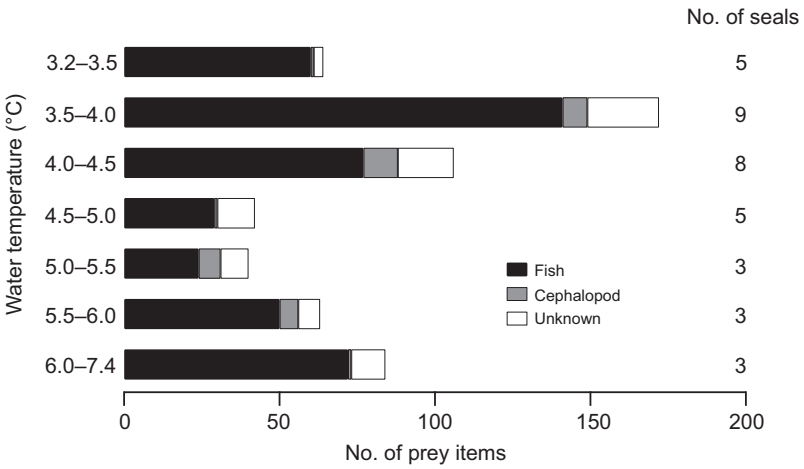

Fig. 4. Composition of prey types of adult female northern elephant seals from Año Nuevo, California, in relation to *in situ* water temperature, observed using animal-borne video cameras. Color codes indicate fish (black), cephalopod (grey) and unknown prey items (white).

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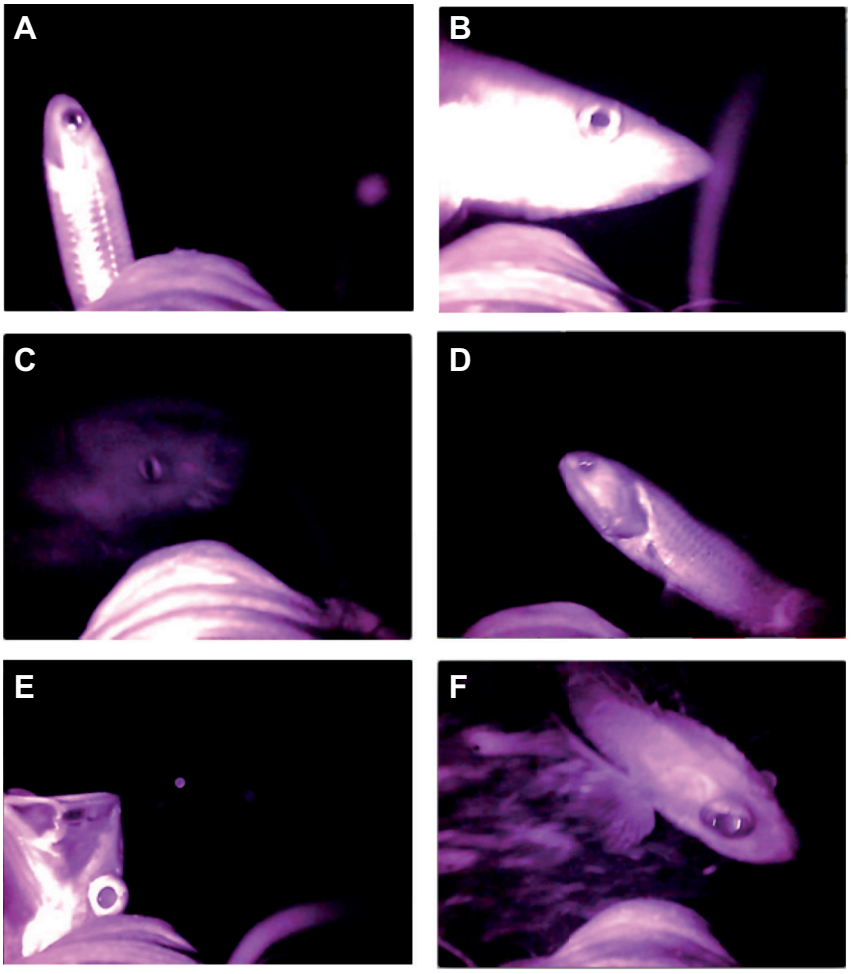

Fig. 5. Fish prey images from head-mounted video cameras on adult female northern elephant seals. (A) Myctophidae, (B) *Merluccius* sp., (C) *Icosteus aenigmaticus* and (D–F) unidentified fishes. The seal's snout is visible at the bottom of the images. The seal's supraorbital vibrissae are also visible in B and E.

stomach content samples (100% and 75.9%, respectively) at Macquarie Island. However, Cherel et al. (2008) concluded that southern elephant seals in the Kerguelen Islands fed mainly on mesopelagic fish, especially myctophids, based on stable isotope analysis of blood samples. Similarly, northern elephant seals had a higher occurrence of cephalopods reported from stomach content analyses (Antonelis et al., 1987, 1994), in contrast to a higher occurrence of fish as determined by quantitative fatty acid (Goetsch et al., 2018) and video analyses (present study). Recently, McGovern et al. (2019) obtained head-mounted video records from five female southern elephant seals at Peninsula Valdes, Argentina, and reported a few fish species (myctophids, smelt, dragonfish), but no squid, in the video records. However, no quantitative descriptions on the composition of fish species were available in McGovern et al. (2019). These results suggest that the diet of northern and southern elephant seals is broadly similar. It appears that there may be some geographical variation in the relative importance of fish versus squid in the diet of southern elephant seals, though methodological differences between studies make quantitative assessments difficult.

In the North Pacific, mesopelagic fish, such as myctophids, have been important in the diet of other marine mammals, such as dolphins and fur seals (Springer et al., 1999; Ohizumi et al., 2003; Brodeur and Yamamura, 2005). However, dolphins and fur seals are considered to feed on myctophids when the fish migrate to the surface during the night (Ohizumi et al., 2003), whereas northern elephant seals are feeding on myctophids much deeper in the water column. The density of myctophids was reported to be higher in deeper depths (250–550 m) than near the surface during the night, which may explain why northern elephant seals feed at deep depths despite increased diving costs (Saijo et al., 2017). Also, the size of individual fish tends to be larger in deeper depths (Frost and McCrone, 1979), which may bring further benefit to deep-diving seals. Mesopelagic fish are also consumed worldwide by beaked whales (~30% frequency of occurrence in stomach contents; MacLeod et al., 2003), with foraging presumed to occur at deep depths that have not been quantified. Northern elephant seals appear to occupy a unique trophic niche, foraging mainly on mesopelagic fish at deep depths, by having a deep diving ability. Their relatively small body size (compared with beaked whales that dive to similar depth zones) and relatively low metabolic rates (Maresh et al., 2015) might allow them to fulfill energy requirements by feeding on relatively small fish prey rather than on large squid (Naito et al., 2013). However, mesopelagic squid constitute an important component of the diet of toothed whales. Squid species including *Berryteuthis* sp., *Octopoteuthis* sp. and *Histioteuthis* sp. are reported in the diet of sperm whales (*Physeter macrocephalus*) and short-finned pilot whales (*Globicephala macrorhynchus*) (Kawakami, 1980; Sinclair, 1992), and are also found in the diet of northern elephant seals (Antonelis et al., 1987, 1994; Goetsch et al., 2018; present study). Northern elephant seals might feed opportunistically on mesopelagic squid species, complementing their feeding on mesopelagic fish. Given that substantial interannual variability and decadal-scale trends were reported on the relative abundance of

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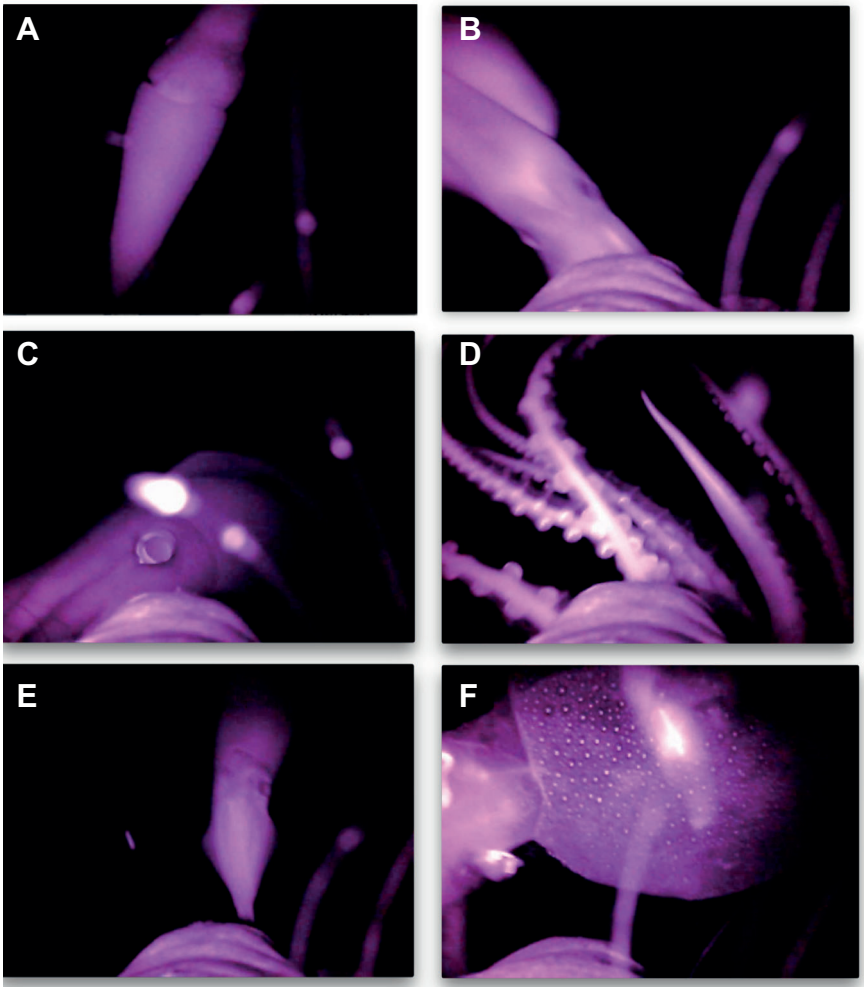

Fig. 6. Squid prey images from head-mounted video cameras on adult female northern elephant seals. (A) *Histioteuthis* sp., (B) *Octopoteuthis* sp., (C) *Taningia danae*, (D) *Belonella* sp., (E) *Berryteuthis* sp. and (F) *Japetella* sp. The seal's snout is visible at the bottom of the images. The seal's supraorbital vibrissae are also visible in A–C, E and F.

myctophid fish (Springer et al., 1999; Brodeur and Yamamura, 2005), the foraging and reproductive success of northern elephant seals can potentially serve as a sentinel of the mesopelagic fish and squid abundance in the eastern North Pacific (Le Boeuf and Crocker, 2005; Crocker et al., 2006).

Advantages and limitations of animal-borne video cameras

Animal-borne video cameras can provide insight into what animals feed on in the open ocean. By combining video cameras with satellite tags and time-depth recorders, we were able to identify prey items in the diet of northern elephant seals in relation to foraging location and depth. We have shown that animal-borne video cameras are a useful tool for studying the at-sea diet of marine predators. Video cameras with depth and acceleration triggers are more efficient in recording prey encounters, as those loggers with such triggers recorded 17 items per hour on average, while those that only used a delay timer recorded 4.6 prey items per hour on average (Table 1). Previous studies reported acceleration signals of prey encounters in a range of marine predators (Kokubun et al., 2011; Guinet et al., 2014; Nakamura et al., 2015; Sato et al., 2015; Foo et al., 2016), and these signals could be used to trigger the start of videos for efficient video recordings. There are still some limitations that need to be considered. The duration of video recordings was limited by the battery capacity (4–5 h per device), and the video resolution and sensitivity made prey identification difficult. Furthermore, our feeding-signal triggers may have biased our sample toward prey found in schools rather than solitary prey, as our cameras might not be able to record solitary prey items that induced the first feeding signal owing to the delay (<10 s) in starting video recording after the trigger was reached. Further developments and adjustments will improve the utility of animal-borne cameras, making them more widely applicable to diet studies of marine predators.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.T., D.P.C., Y.N.; Methodology: K.Y., A.T., T.A., Y.N.; Formal analysis: K.Y., A.T.; Investigation: K.Y., A.T., T.A., D.P.C., P.W.R., S.H.P., L.A.H., R.R.H., Y.N.; Writing - original draft: K.Y., A.T.; Writing - review & editing: T.A., D.P.C., P.W.R., S.H.P., L.A.H., R.R.H., Y.N.; Project administration: A.T., D.P.C., P.W.R., Y.N.; Funding acquisition: A.T., D.P.C., Y.N.

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Data availability

Data associated with this article are available at the ADS (Arctic Data archive System) of the National Institute of Polar Research (https://ads.nipr.ac.jp/dataset/A20191218-001).

Supplementary information

Supplementary information available online at
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