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Animal-borne video cameras reveal differences in northern fur seal foraging behavior related to prey size selection

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A key aspect of foraging ecology research is understanding how predator foraging behavior and success are influenced by variation in prey resources. For northern fur seals (*Callorhinus ursinus*), an understanding of predator-prey relationships is critical to help identify potential causes for the unexplained population decline in Alaska. To examine how foraging behavior differs based on prey size selection, we equipped northern fur seals on St. Paul and St. George islands (Alaska, USA) in September (2017, n=6) and August (2018, n=4, and 2019, n=3) with satellite-linked dive recorders and animal-borne video cameras. We categorized prey capture attempts based on relative prey size (small vs. large) and examined differences in capture depth, time of day, water temperature, and depth relative to the mixed-layer. Successful prey captures (n= 2224) primarily occurred at night ($89.7 \pm 3.1\%$) and small prey accounted for the majority of captures ($70.5 \pm 13.2\%$), but there was significant variation among individuals. Large prey were captured at nearly twice the depth of small prey (42.9 ± 3.7 m and 23.1 ± 1.8 m, respectively) and the proportion of large prey caught during the day was 3 times higher than at night (0.77 ± 0.1 vs. 0.25 ± 0.1). There was no relationship between prey size and water temperature after we accounted for temperature changes with depth. The highest proportion of prey captures occurred below the mixed-layer depth regardless of prey size, but the proportion of small prey captures above mixed-layer depth was double that of large prey. This enhanced understanding of northern fur seal prey capture behavior will be pivotal for better interpretation of decades of historical dive and diet data and can provide insight into how northern fur seals may respond to future variation in prey resources, which is essential to develop ecosystem-based approaches for northern fur seal conservation.

KEYWORDS

northern fur seal, *Callorhinus ursinus*, Bering Sea, foraging behavior, video, prey capture, walleye pollock, dive behavior

Introduction

Advances in biologging technology, such as dive recorders and satellite tracking instruments, have greatly expanded our ability to understand the at-sea behavior of marine predators (Kooyman, 2004; Rutz and Hays, 2009; Cooke et al., 2012). These instruments, which can be used to track habitat use and underwater movements, have provided insight into the foraging behavior of numerous species including the ability to identify how physiology, environmental conditions, and prey availability shape behavior (Butler et al., 1995; Block, 2005; Evans et al., 2013). Yet, for many species, collecting data on when and where successful foraging occurs has been challenging. Recent improvements to animal-borne video technology, specifically a reduction in size and increased recording duration, have made it possible to address this challenge and get a direct view into the foraging behavior of marine predators (e.g., Kernaléguen et al., 2016; Handley et al., 2018; Sutton et al., 2020; Yoshino et al., 2020). In addition, unlike other techniques used to quantify prey capture, such as jaw sensors or stomach temperature recorders (Austin et al., 2006; Liebsch et al., 2007; Iwata et al., 2011), video cameras can often provide more detail about the specific prey being targeted (e.g., species, age-class, or size) (Watanabe and Takahashi, 2013; Heaslip et al., 2014; Volpov et al., 2015; Yoshino et al., 2020). This detailed information about predator-prey interactions and foraging success obtained from animal-borne video can be used to link fine-scale behavior and habitat use with prey availability, which is essential for developing ecosystem-based conservation approaches for marine predators.

Understanding predator-prey relationships for the northern fur seal (*Callorhinus ursinus*) is critical to help identify potential causes for the unexplained population decline. The Eastern Pacific stock of northern fur seals, which includes animals that breed on St. Paul, St. George, and Bogoslof islands (Alaska, USA), once comprised over three-quarters of the world's population (Loughlin et al., 1994; Gentry, 1998; NMFS, 2007). The Eastern Pacific stock was designated as depleted under the Marine Mammal Protection Act in 1988 and continued declines since the 1970s have resulted in pup production on St. Paul Island surpassing a 100-year low in 2018 (Towell et al., 2006; NMFS, 2007; Towell et al., 2018). The northern fur seal conservation plan identifies possible reasons for the decline including natural factors (e.g., predation, disease, and environmental change), human-related factors (e.g., effects of commercial fishing, pollution, and poaching), or a combination of multiple factors (NMFS, 2007). Obtaining more information about relationships between fur seals and fish resources in the Bering Sea has been identified as an important research priority to recover and protect this stock (NMFS, 2007).

On the Pribilof Islands (St. Paul and St. George), variability in northern fur seal diet during the summer reproductive season is

correlated with rookery location and the use of distinct foraging habitats within the Bering Sea (Zeppelin and Ream, 2006). For adult female fur seals, a long-term diet study found twenty-three fish and four squid species are consumed, with the frequency of occurrence (FO) varying based on rookery location and whether an animal forages in the deep Bering Sea basin (> 200 m) or on the Bering shelf (Zeppelin and Ream, 2006). Nevertheless, regardless of rookery location, the fur seals' primary prey species is walleye pollock (*Gadus chalcogrammus*, hereafter "pollock", FO 42.7% - 91.4%, Zeppelin and Ream, 2006; Jeanniard-du-Dot et al., 2017), which is also the target of the largest commercial fishery by volume in the United States (NMFS, 2020). Patterns of annual variation in fur seal diet at the population level suggest that although both young and adult pollock are consumed, pollock age-classes are differentially targeted each year (Sinclair and Loughlin, 1994; Gudmundson et al., 2006; McHuron et al., 2020). These age-related consumption patterns coincide with annual variations in pollock recruitment with a high prevalence of age-0 pollock in the fur seal diet during years of strong recruitment and larger pollock identified in years with lower age-0 availability (Sinclair et al., 1996; McHuron et al., 2020). Studies of fur seal dive behavior suggest that there may also be variation among individuals within a year for the age-class of pollock being consumed (Kooyman and Goebel, 1986; Kuhn et al., 2010; Nordstrom et al., 2012).

To understand how foraging behavior varies when fur seals target different sizes or age-classes of prey, it is necessary to identify feeding events and the prey being consumed. By equipping northern fur seals with video cameras, we were able to characterize prey capture behavior, specifically examining the size of the targeted prey in relation to dive depth, time of day, and water temperature. Based on the biology and behavior of pollock and historic data on northern fur seal dive behavior, we hypothesized that 1) large fish will be captured at deeper depths and closer to the sea floor (Bailey, 1989; Sogard and Olla, 1993; Boldt et al., 2012); 2) large fish will be captured more often during the day (Kooyman and Goebel, 1986; Goebel et al., 1991; Kuhn et al., 2010); and 3) large fish will be captured at colder water temperatures, below the mixed-layer depth (Francis and Bailey, 1983; Olla and Davis, 1990; Boldt et al., 2012).

Materials and methods

Fur seal instrumentation

This research was conducted as part of a larger study examining the summer foraging behavior of northern fur seals on St. Paul and St. George islands, Alaska (Figure 1). We tracked adult female fur seals from July to September (2017) and August to September (2018 and 2019). Females observed with a dependent pup were captured, weighed using a digital scale (\pm

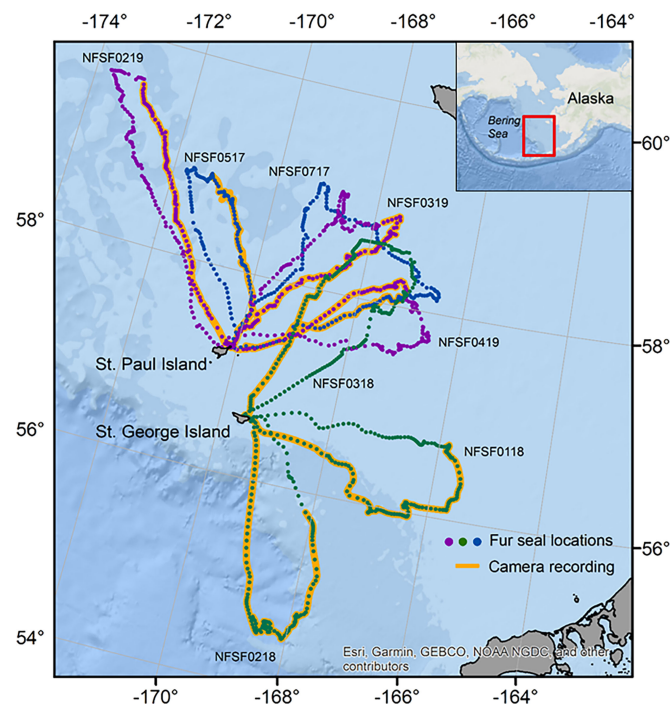


FIGURE 1

Hourly locations for eight northern fur seals (2017: blue, 2018: green, and 2019: purple points) equipped with animal-borne video cameras. The portion of the foraging trip with video data is highlighted in orange. Northern fur seals were instrumented on St. Paul Island and St. George Islands in the Bering Sea, Alaska (inset).

0.2 kg), and physically restrained to attach tracking instruments. Fur seals were equipped with a SPLASH10-X instrument (105 × 56 × 34 mm, 218 g, Wildlife Computers) and VHF tag (18 × 44 × 8 mm, 17 g, Advanced Telemetry Solutions) for the duration of the tracking period (July/August–September), and a CATS cam instrument (110 × 80 × 40 mm, 390 g, Customized Animal Tracking Solutions) for 1 to 3 foraging trips (2017: n=6, 2018: n=4, and 2019: n=3 fur seals). Instruments were attached directly to the dorsal fur using a combination of Loctite 422 and Devcon quick-set epoxy. The total mass of instruments was on average $1.7 \pm 0.05\%$ of body mass (max < 2.1%). The results presented only include data collected when the fur seals were equipped with all tracking equipment (SPLASH10-X, VHF tag, and CATS cam).

SPLASH10-X tags sampled depth and external temperature (fast-response thermistor) at 1-s intervals, triaxial acceleration at 1/16-s intervals, and provided satellite locations *via* the Argos satellite system. To conserve battery power, satellite transmissions were shut off between 0:00 and 01:59 GMT and 10:00 and 11:59 GMT, which are periods of reduced satellite coverage. The CATS cams were programmed to record depth and temperature at 1-s intervals and HD video when the fur seals' depth exceeded 10 m. A depth trigger of 10 m was chosen to extend video recording duration over a longer proportion of

the foraging trip by reducing the chance video was recorded during shallow dives used during transit periods. The cameras were equipped with two IR LEDs on either side of the lens that turned on in low light conditions, such as during deep dives or at night. Video was recorded at 30 frames per second and 1280 × 720 p resolution. The CATS cams recorded for a minimum duration of 1 min once triggered by depth and stopped recording when the fur seal was < 10 m deep or at a maximum duration of 5 min. The VHF tag was used to locate the fur seals on land for recapture. Fur seals were physically restrained for instrument removal and reweighed prior to release.

Data analysis

SPLASH10-X and CATS cam dive data were processed using Instrument Helper (Wildlife Computers) after converting the CATS file to a format that could be read by the software. Dives were defined as a minimum depth of 3 m. Videos were analyzed using BORIS (Behavioral Observation Research Interactive Software) (Friard and Gamba, 2016). For successful prey captures, we attempted to identify the prey to class or family using distinguishing characteristics and a dichotomous key created specifically for fish encountered in the Northeast

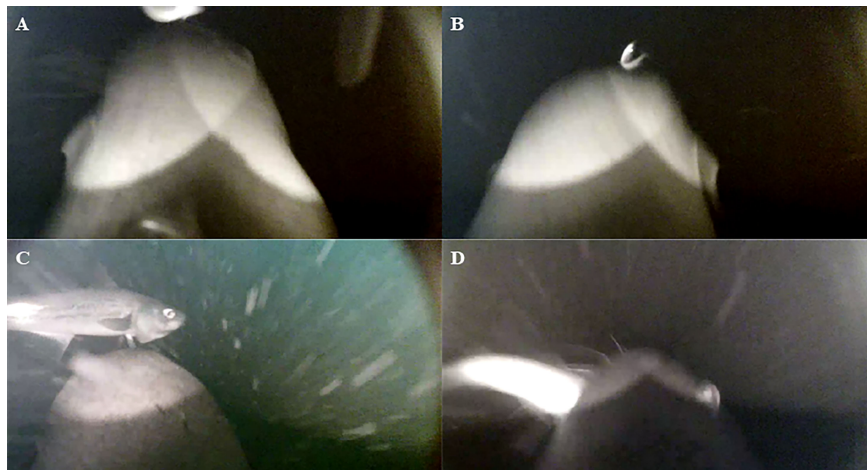


FIGURE 2

Still images collected from video files recorded from cameras mounted on northern fur seals. Cameras were placed in the upper back/shoulder region, so the fur seal's head is visible. Images show examples of small prey prior to capture (A, B), and large prey prior to capture (C) and during handling (D). Illumination from the two IR LEDs is visible in night images (A, B, D) and at depth (C).

Pacific groundfish fishery (Alaska Fisheries Science Center, North Pacific Observer Program, unpublished). Due to rapid movements during prey capture events and because most captures occurred in low light, we were unable to identify many preys except when large fish were targeted (Figure 2). Based on historic northern fur seal food habits information, if a prey item was identified as a fish, we assumed it belonged to the most abundant class in the diet, Actinopterygii (Sinclair and Loughlin, 1994; Antonelis et al., 1997; Zeppelin and Ream, 2006).

Northern fur seal diet in this region is dominated by a single species, walleye pollock, which suggests that prey size differences were related to fur seals targeting different pollock age classes. When fur seals foraged on the Bering Sea shelf (< 200 m), we are confident that in most cases the species being targeted was pollock (66.2% FO vs. the next highest prey species < 18% at all study locations) (Zeppelin and Ream, 2006). For fur seals that forage off the Bering Sea shelf, frequently targeted prey includes pollock (FO > 45%), northern smoothtongue (*Leuroglossus schmidti*) (maximum FO < 16%), and numerous squid species (FO up to 38%) (Zeppelin and Ream, 2006).

Each video was reviewed by two people to identify prey capture attempts (PCAs) and discrepancies were re-examined when the results were compiled. PCAs were characterized by a striking behavior and distinguished from other head movements by the presence of prey. For each PCA, reviewers determined if the prey was successfully captured (categories: captured or missed) and the size of the prey relative to the width of the fur seal's head just prior to capture or during handling. Prey which were equal to or smaller than the fur seal's head were classified as small and estimated to be approximately 150 mm or less, which

would include age-0 and age-1 pollock (Figures 2A, B; Smith, 1979; Ianelli et al., 2019; McCarthy et al., 2020). Large fish, estimated to be larger than 150 mm, were often seen hanging out of the fur seal's mouth when caught (Figures 2C, D). This cutoff was determined based on the pollock age-class distribution within the Bering Sea during the three study years, which generally followed a bimodal distribution with fewer pollock within the 200 to 350 mm length range (Ianelli et al., 2019; McCarthy et al., 2020).

In a few cases, fur seals displayed a stereotypical behavior that appeared to be chewing or repositioning prey after a clear head strike when no prey were visible; for example, when a strike occurred off camera or the fur seal's head blocked the view. These were classified as successful PCAs but the prey size was marked as unknown. Given the lack of visible prey and the short duration of the handling movements, it is highly likely that these were small prey. As a result, they were included in the small prey category for analysis. We chose to not include missed PCAs in our analysis because we were unable to determine if subsequent capture attempts within a single dive were targeting the same or a different prey and did not want to overestimate prey interactions.

Factors related to prey capture

We examined prey size category in relation to three factors: capture depth, water temperature, and time of day. The SPLASH10-X and CATS cam data were synced by time using the dive analysis files, and capture depth and temperature were extracted from the raw SPLASH10-X data. Satellite locations

were filtered based on a maximum transit rate of 3 m s^{-1} (R package “argosfilter”) after class Z locations were removed (Freitas et al., 2008). Foraging tracks were reconstructed at the time of each dive by modeling the filtered location data using a continuous-time correlated random walk model (Johnson et al., 2008). Time of day was a categorical variable (day or night) calculated using the start time of each dive with night being classified as a sun elevation < 0 (R package “maptools”).

We were also interested in how prey size category related to the mixed-layer depth (MLD) as it is likely driving prey capture relationships for both depth and temperature. Data from the annual Alaska Fisheries Science Center’s eastern Bering Sea bottom-trawl survey (available at <https://www.fisheries.noaa.gov/alaska/commercial-fishing/alaska-groundfish-bottom-trawl-survey-data>, Acuna and Lauth, 2008; Lauth and Acuna, 2009; Lauth, 2010) were used to estimate MLD, defined in this study as the depth at which temperature deviated by 0.2°C from a near surface (5.5 m) reference depth. MLD was estimated at each survey haul location and interpolated to dive locations using an inverse distance weighting method. MLD data from the annual surveys was used instead of temperature data from the tracking instruments because it has higher accuracy and it provided information throughout the fur seals’ habitat regardless of the depth of individual dives. For one fur seal (NFSF2018) that spent some time foraging off the Bering Sea shelf, the MLD was calculated using profile data from the closest Argo float (#4902930, June–August 2018, mldthermocline function in R by K. Evans, Roemmich et al., 2009). The average MLD over seven profiles was $27.5 \pm 1.5 \text{ m}$ (range: 22 to 32 m), which is similar to historical values reported in July and August for the Bering Sea basin (Roden, 1995; Johnson and Stabeno, 2017). The PCA depth in relation to the MLD was a categorical variable (above MLD, at MLD, below MLD). Above MLD included depths from the surface to 5 m above the MLD, at MLD included depths within $\pm 5 \text{ m}$ of the MLD, and below MLD included depths $> 5 \text{ m}$ below the MLD to the seafloor. Two-minute gridded elevation data for the North Pacific derived from ETOPO 2 were used to estimate the seafloor depth at each dive position to calculate the relative depth of prey captures (capture depth/bottom depth).

Statistical analysis

We used generalized linear mixed-effects models (R package “lme4”, R 3.6.0) (R Core Team, 2019) to examine prey size category (large and small) in relation to capture depth, time of day, and water temperature. MLD was not included in the models because of its collinearity with both depth and temperature. Models were also run with PCAs of unknown prey size excluded from the small size category for comparison. Temperature residuals were used to account for the negative relationship between depth and water temperature. “Animal Id”

was included as a random factor in all models and year was included as a fixed factor. We examined relationships between study year and fur seal mass, study year and daily mass change over the tracking period (mass change), mass change and the proportion of recorded dives with prey capture, and mass change and average prey captured per recorded dive using a linear regression after validating normality and homogeneity of variances. Summary statistics, including those presented in Tables 1 and 2, were calculated for each individual to account for large differences in the number of PCAs and presented as mean \pm se. Factors were considered significant at $P < 0.05$.

Results

Fur seal behavior

At instrumentation, fur seals ranged in mass from 30.0 to 44.8 kg (average: $37.9 \pm 1.2 \text{ kg}$, $n=12$) with no differences in mass among years ($F_{2,9} = 0.47$, $p = 0.64$, Table 1). Tracking durations ranged from 7.0 to 35.0 d ($15.4 \pm 3.0 \text{ d}$) covering 1 to 3 foraging trips that lasted $8.3 \pm 0.5 \text{ d}$ (range: 5.9 to 12.4 d, Table 1, Figure 1). In 2017, one fur seal was not recaptured after her satellite locations stopped while at-sea and her VHF tag was not heard again on the rookery. Mass change over the tracking period was $1.8 \pm 0.8 \text{ kg}$ (range: -1.6 to 6.4 kg, $n=11$, Table 1). The rate of mass change per day of tracking was $0.2 \pm 0.08 \text{ kg d}^{-1}$ and there were no differences among years ($F_{2,8} = 1.72$, $p = 0.24$, Table 1).

In 2017, software errors prevented three of the CATS cams from turning on and the two remaining CATS cams stopped after 255 videos were recorded. In 2018, one CATS cam didn’t function as programmed (NFSF0118) and the video recovered displayed intermittent color distortion which impacted our ability to analyze prey capture attempts. We ranked the video quality from 1 (no distortion) to 5 (can’t visualize any behavior) and removed videos classified as quality 4 (mostly distorted but can visualize some behavior) and 5. Because of the video quality, it is highly likely that some small prey captures were missed since small prey are harder to see. The inability to see small prey captures could impact some of the summary metrics calculated (e.g., PCA per hour or per dive) but would not impact the relationships between prey size and environmental covariates (e.g., depth and temperature). As a result, NFSF0118 was excluded from some summary metrics related to video data and prey capture where noted. Finally, in 2018, we were unable to download videos from one CATS cam.

Videos were recorded over $3.4 \pm 0.5 \text{ d}$ of each foraging trip (Table 1, Figure 1), with 60.3 total hours of video (hours per animal: $7.6 \pm 1.0 \text{ h}$, Table 1). Videos were recorded for $51.2 \pm 0.1\%$ of the dives during the recording period (range: 19.7 to 89.7%, Table 2, NFSF0118 excluded). Out of 3002 recorded prey

TABLE 1 Summary of tracking information and mass characteristics for 13 northern fur seals equipped with video cameras in 2017, 2018, and 2019.

Animal Id	Camera attached	Tracking duration (d)	Mass at capture (kg)	Mass change (kg)/Rate of change (kg day ⁻¹)	Trip duration ± SE	Trips	Video start	Video duration (d)	Total video (hh:mm)
NFSF0117 [#]	2017-09-06 11:06	23.4	37.2	-1.6/-0.07	8.55 ± 1.0	2	NA	NA	NA
NFSF0517	2017-08-31 10:36	7.1	NA	NA	5.91	1	2017-09-02 01:46	2.5	08:21
NFSF0617 [#]	2017-09-03 13:32	18.9	44.8	2.0/0.11	12.45	1	NA	NA	NA
NFSF0717	2017-09-02 16:08	12.9	38.8	-0.8/-0.06	8.75	1	2017-09-07 06:32	1.9	06:37
NFSF0817 [*]	2017-09-04 12:48	NA	39.8	NA	NA	NA	NA	NA	NA
NFSF1117 [#]	2017-09-04 14:51	8.8	31.8	2.8/0.32	8.11	1	NA	NA	NA
NFSF0118 [§]	2018-08-16 18:58	8.7	37.8	0	7.89	1	2018-08-17 23:46	5.4	04:00
NFSF0218	2018-08-17 10:15	7.0	36.6	2.4/0.34	6.20	1	2018-08-18 07:41	5.1	07:20
NFSF0318	2018-08-17 11:13	35.0	30.0	0.2/0.01	7.58 ± 0.2	3	2018-08-19 07:48	3.1	03:12
NFSF0418 [^]	2018-08-17 11:32	34.9	40.4	2.6/0.07	9.14 ± 0.2	3	NA	NA	NA
NFSF0219	2019-08-12 15:34	10.9	41.0	6.4/0.58	9.50	1	2019-08-13 23:08	4.4	13:09
NFSF0319	2019-08-13 11:58	9.1	35.4	5.8/0.64	8.15	1	2019-08-13 23:06	3.6	07:38
NFSF0419	2019-08-13 13:40	8.1	40.8	-0.4/-0.05	7.02	1	2019-08-15 01:48	2.4	10:16

*Animal not recaptured, [#]camera did not record, [^]videos could not be downloaded, [§]distortion on some videos. Video duration is the time between the first and last recorded videos. NA is not available.

capture attempts, 2224 were successful (Table 2). Capture success varied among individuals (Table 2) and was not different between prey size classes ($p=0.87$, Figure 3). Successful PCAs were recorded on 976 dives, which meant prey capture occurred on $41.2 \pm 5.1\%$ of the recorded dives (range: 29.3 – 68.4%, NFSF0118 excluded). The average number

of PCAs per recorded dive ranged from 0.4 to 2.2 (average: 0.87 ± 0.2 , NFSF0118 excluded). If only recorded dives with prey capture are considered, fur seals captured 1.9 ± 0.04 prey per feeding dive (range: 1.2 to 3.4). There were no relationships between mass change over the tracking period and the proportion of recorded dives with prey capture ($F_{1,5} = 0.11$,

TABLE 2 Dive and prey capture attempt (PCA) metrics during the video recording period for eight northern fur seals tracked in 2017, 2018, and 2019.

Animal Id	Dives with video	Total dives during recording period	Successful PCAs	Total PCAs	Size of prey			PCA depth (m) mean ± SE	PCA temperature (°C) mean ± SE	Proportion of PCA at night
					Large	Small	Unknown			
NFSF0517	259	355	109	177	103	4	2	38.9 ± 1.6	4.3 ± 0.3	0.83
NFSF0717	264	677	172	266	17	149	6	22.6 ± 1.0	5.1 ± 0.2	0.85
NFSF0118	128	869	23	34	19	4	0	57.5 ± 7.7	6.8 ± 0.6	0.78
NFSF0218	422	2030	970	1144	4	937	29	13.2 ± 0.2	8.6 ± 0.1	1.00
NFSF0318	133	676	61	93	16	43	2	33.8 ± 2.7	6.9 ± 0.2	0.80
NFSF0219	406	1025	307	453	27	212	68	23.8 ± 0.8	8.8 ± 0.2	0.99
NFSF0319	323	420	254	340	29	182	43	25.4 ± 0.6	7.9 ± 0.2	0.96
NFSF0419	356	397	328	495	8	290	30	27.1 ± 0.6	6.4 ± 0.2	0.96

Dives with video include any dive with some portion recorded. See methods for descriptions of relative prey size (large, small, or unknown).

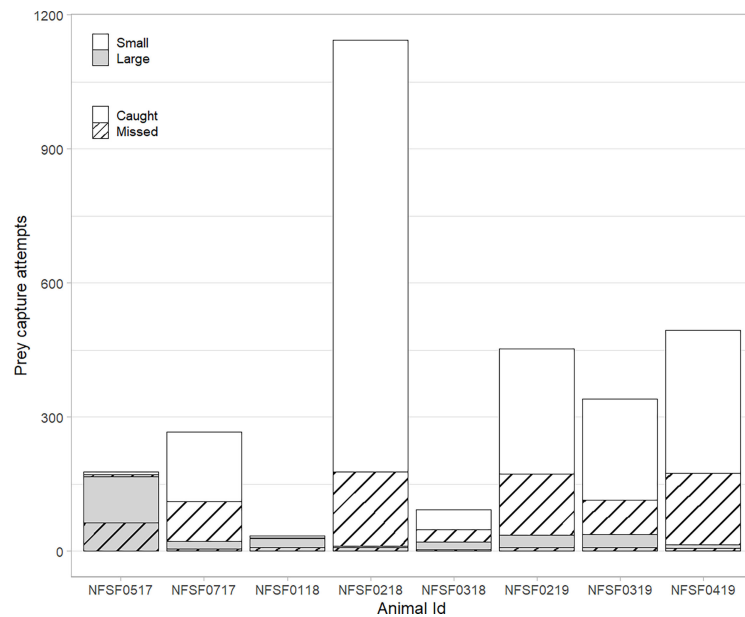


FIGURE 3

Prey capture success (caught= solid, missed= hatched) for eight northern fur seals by relative prey size (white= small, grey= large). Differences in total prey capture are primarily related to the duration of video recording (Table 1).

$p = 0.75$) or the average number of prey captures per recorded dive ($F_{1,5} < 0.001$, $p = 0.99$).

Small prey accounted for $70.5 \pm 13.2\%$ of all prey captures, but the percent of small prey captured varied between 5.5 and 99.6% per individual (Table 2). Successful PCAs occurred at depths ranging from the surface to 136.5 m (average: 30.3 ± 1.9 m, Table 2, Figures 4A, B) and temperatures ranging from 1.5 to 13.0 °C (average: 6.8 ± 0.2 °C, Table 2, Figure 4C). The average depth for video recorded dives was significantly deeper than average depth for all dives during the recording period ($F_{1,14} = 8.15$, $p=0.01$) due to the depth trigger of the CATS cam being set at 10 m (Figure 5). On numerous occasions, the videos continued to record during the ascent until the fur seals reached the surface which allowed us to observe prey captures between 0 and 10 m (Figure 4). In addition, due to the CATS cams having a minimum recording time, some dives less than 10 m were also recorded if they followed a short dive (i.e., less than 1 minute). There was a significant negative relationship between depth and water temperature for PCAs ($R^2 = 0.35$, $F_{1,2222} = 1214$, $p < 0.001$). Most PCAs occurred at night ($89.7 \pm 3.1\%$), which was relatively consistent among fur seals (Table 2). All fur seals but one had successful PCAs in each of the MLD categories (above, at, and below, Table 2, Figure 6) and the majority of individuals had the largest proportion of their PCAs occur below the MLD (Figure 6).

Relationship between prey size and depth, water temperature, and time of day

Large prey was captured in deeper water and more often during the day than small prey ($p < 0.001$ for depth and time of day). There was no relationship between prey size and the temperature residuals and no differences among years. These relationships were similar when the unknown prey size class was excluded from the small prey group and when NFSF0218 was excluded due to some foraging occurring in the Bering Sea basin (depth: $p < 0.001$, time of day: $p < 0.001$). On average, large prey were captured at nearly twice the depth of small prey (42.9 ± 3.7 m and 23.1 ± 1.8 m, respectively, Figure 4A) and at temperatures over 1.5 °C colder (6.0 ± 0.6 °C and 7.7 ± 0.5 °C, respectively, Figure 4C). The proportion of large fish caught during the day was 3 times higher than at night (0.77 ± 0.1 vs. 0.25 ± 0.1). For all fur seals combined, the highest proportion of PCAs occurred below the MLD regardless of size (large: 0.77 ± 0.9 , small: 0.62 ± 0.1 , Figure 6), but the proportion of PCAs for small prey above the MLD was double that of large prey (small: 0.25 ± 0.1 , large: 0.12 ± 0.1 , Figure 6). Only one fur seal, NFSF0218, had a higher proportion of PCAs above the MLD, which was consistent between prey sizes.

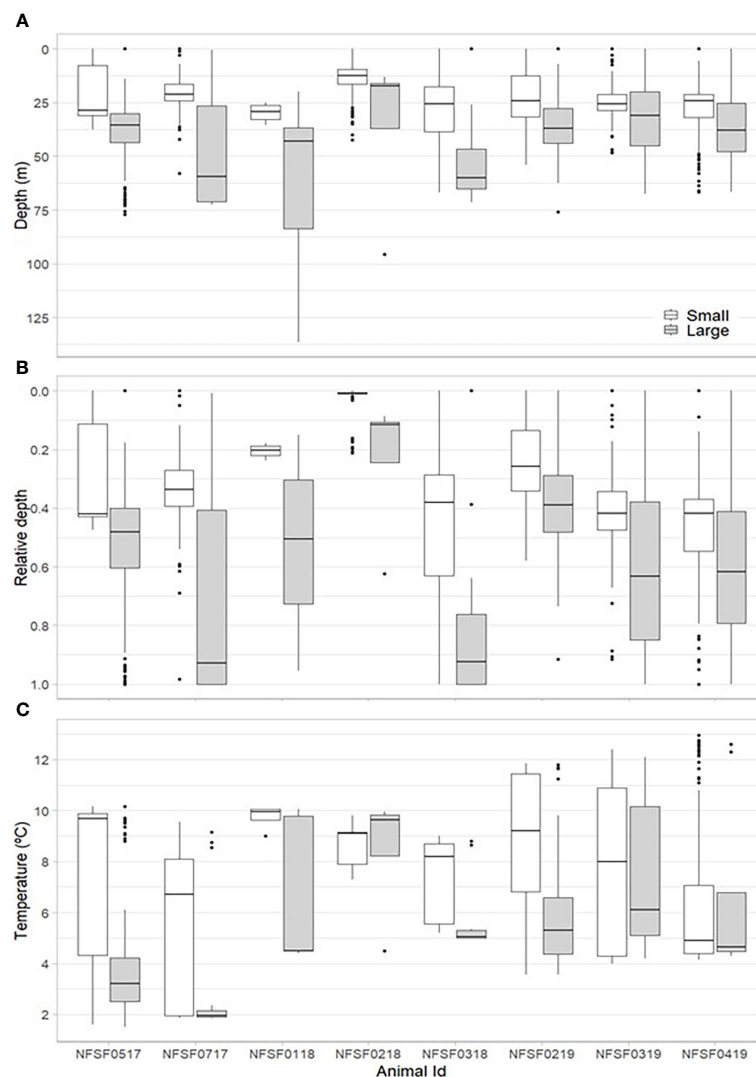


FIGURE 4

Boxplots depicting the depth (m, A), relative depth (depth/seafloor depth, B), and temperature (°C, C) where successful prey captures occurred for each fur seal by prey size (white= small, grey= large). Lines denote the median values, boxes encompass the first and third quartiles, points are outliers ($> 1.5 \times$ the inter-quartile range), and whiskers display the smallest or largest values beyond the inter-quartile range, excluding outliers.

Prey identification

Over 40,000 images that contained visible prey during a successful capture event were examined to identify the prey being consumed (Figure 2). Prey were identified to class for 841 successful PCAs (41% of successful captures) using at least one identifiable feature or movement patterns (fish: $n = 836$, cephalopod: $n = 5$) (Supplemental Material, Table S1). For the fish identified, 129 could be narrowed down to family (Supplemental Material, Table S1), with 93.8% being identified as Gadidae. All of the Gadidae were categorized as large fish. Five Salmonidae and three Clupeidae (likely Pacific herring, *Clupea pallasii*) were also identified. An additional three fish had

identifiable characteristics not consistent with family Gadidae, such as a highly forked tail (Supplemental Material Table S1). All Cephalopoda ($n=5$) were characterized as likely squid which could include several species from the family Gonatidae based on northern fur seal diet studies (Zeppelin and Ream, 2006).

Discussion

An understanding of fine-scale predator-prey relationships can provide insight into factors that influence an individual's foraging decisions and success. By combining animal-borne video cameras with tracking instruments that record diving patterns and

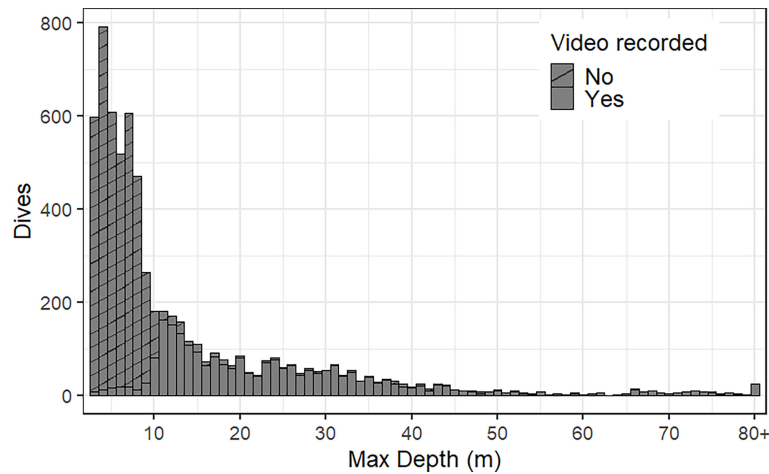


FIGURE 5
 Distribution of northern fur seal maximum dive depths during the video recording period. Most dives under 10 m did not have video recordings (stripe filled) due to the preset depth trigger. However, as a result of the CATS cam minimum recording duration (1 min), some shallower dives (< 10 m) were recorded if they immediately followed a recorded dive (solid filled) with a short duration. Dives from NFSF0118 were excluded because of issues with the CATS cam and recorded videos (see Results for details).

environmental characteristics, we were able to investigate the influence of prey size on northern fur seal foraging behavior. The incorporation of animal-borne video into marine predator tracking studies has exploded in recent years with videos helping to quantify prey encounter rates (e.g., [Watanabe and Takahashi, 2013](#); [Thiebot et al., 2016](#); [Oliver et al., 2022](#)), prey avoidance behavior ([Handley et al., 2018](#); [Mattern et al., 2018](#)), location and timing of foraging (e.g., [Yoshino et al., 2020](#); [Sutton et al., 2021](#)), and impacts of multi-species foraging groups ([Sutton et al., 2020](#); [Michel et al., 2022](#)). Studies examining the foraging success of individuals are critical for

understanding how changes to habitat and prey resources could impact overall population dynamics (e.g., [Lewis et al., 2001](#); [Petturelli et al., 2001](#)).

Although great strides have been made to increase capabilities while simultaneously reducing the size of animal-borne video cameras ([Moll et al., 2007](#); [Holton et al., 2021](#)), most studies still require cameras to go through cycles of on/off periods to extend recording duration (e.g., [Kernaléguen et al., 2016](#); [Volpov et al., 2016](#)). This can leave data gaps and result in missing rare behaviors ([Sutton et al., 2020](#); [Hinke et al., 2021](#)) or rare prey captures

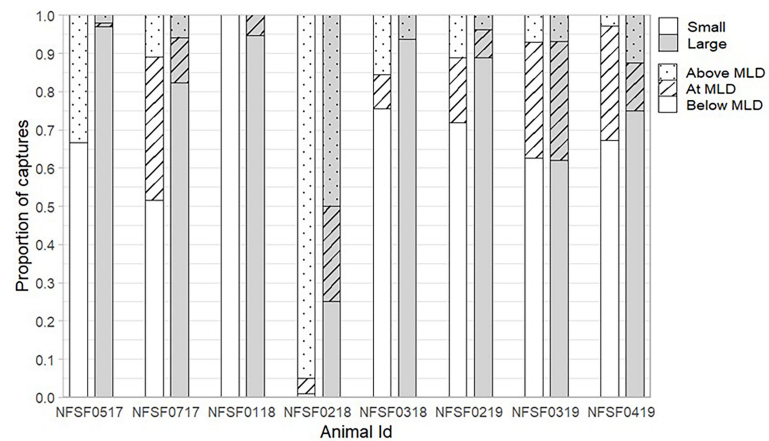


FIGURE 6
 Proportion of prey captures in relation to the mixed-layer depth (MLD) for each fur seal by prey size (white= small, grey= large). Total captures for each female by prey size are found in [Table 2](#). A description of each MLD category can be found in the methods.

(Pistorius et al., 2020; Hinke et al., 2021). Further, the additional animal handling requirements for video studies, which predominantly require that the animal is recaptured for instrument recovery, along with the increased financial cost of video cameras means that study sample sizes are generally small. These issues were factors in our study where only a small number of individuals could be tracked each year and video recordings did not cover the entire fur seal foraging trip (Table 1). In addition, other camera issues including failure to turn on, distorted video recordings, and shorter than expected recording durations further limited our sample size (Table 1). These challenges with small sample size also likely limited our ability to find relationships between foraging success and mass change over the tracking period. Regardless, our study provides greater insight into northern fur seal prey size selection, prey encounter rates, and foraging success, data which are not available for many large marine predators.

All fur seals foraged on a mix of small and large prey, although relative proportions varied among individuals. Past diet studies, which primarily sampled scat, have highlighted the importance of small pollock in the northern fur seal diet (Zeppelin and Ream, 2006; Sinclair et al., 2008; Call and Ream, 2012), but fewer studies have been able to assess the prominence of larger, adult pollock because enumerable hard parts (bones and otoliths) from larger fish rarely pass through the digestive system to be recovered in scat (Sinclair et al., 1996; Gudmundson et al., 2006; McHuron et al., 2020). Interestingly, we found nearly equal capture success for both small and large prey. Based on the schooling behavior of juvenile pollock, which can act as a mechanism to reduce predation risk (Landeau and Terbough, 1986; Magurran, 1990), we expected capture success to be lower for small prey. This was the case for Australian fur seals (*Arctocephalus pusillus doriferus*), where the highest success rates (up to 100%) occurred when fur seals targeted large, solitary prey in comparison to smaller, schooling baitfish (Meyers et al., 2021). In contrast, Sutton et al. (2021) found that all capture attempts by Macaroni penguins feeding on patches of krill were successful. Given that the majority of the fur seals' foraging occurred at night, we may be underestimating unsuccessful prey capture attempts due to the inability to visualize prey at a distance. This would be more pronounced for capture attempts on smaller prey. In addition, various head movements, including rapid head strikes that could have been prey capture attempts, were noted throughout the videos, but these could also be associated with other non-feeding behaviors. As a result, our estimates of the differences in capture success by size should be interpreted cautiously.

Foraging occurred predominantly at night for all individuals with little variation (Table 2). Juvenile and adult pollock (to a lesser extent) perform a diel vertical migration, (Smith, 1979; Adams et al., 2009), which could lead to a higher nighttime foraging efficiency as fur seals reduce underwater commuting time (Croxall et al., 1985; Trillmich, 1990; Kooyman et al., 1992). The complete lack of daytime diving by one fur seal (NFSF0218) was likely related to her spending some time foraging off the Bering Sea shelf (Figure 1).

Fur seals that feed in the Bering Sea basin are known to have a higher proportion of other prey species in their diet, with squid reaching up to 36% FO (Zeppelin and Ream, 2006). Squid, and other off-shelf prey species including myctophids and smoothtongue, migrate into deeper water during the day which means that fur seals are only able to reach these species at night (Roper and Young, 1975; Zeppelin and Ream, 2006; Sterling et al., 2014). For all fur seals, when foraging did occur during the day, there was a higher proportion of large prey being consumed. We also observed fur seals targeting both large and small fish aggregated among jellyfish found in shallow water (Supplemental Material, Figure S1). A similar foraging tactic was described for thick-billed murres (*Uria lomvia*) and researchers found the probability of foraging was positively related to fish densities around the jellyfish (Sato et al., 2015). This behavior could also be occurring at night as we observed fur seals move through jellyfish tentacles during capture events, but it was harder to document due to the limited sighting distance.

Prey were captured over a large range of depths and the clear relationship between depth and prey size reflects the age-depth stratification of the fur seal's primary prey (Traynor, 1986; Bailey, 1989). As adults, pollock are strongly associated with the seafloor, whereas juveniles can be found throughout the water column with higher densities above the thermocline (Smith, 1979; Swartzman et al., 1994; Olla et al., 1996). This pattern is also present in the prey captures as large prey were captured closer to the seafloor than small prey (Figure 4B). This size-based segregation has been suggested as a mechanism for age-0 pollock to reduce cannibalism by adults (Francis and Bailey, 1983). When diving deeper, such as during the day (Kooyman and Goebel, 1986; Goebel et al., 1991; Kuhn, 2011), fur seals may balance the trade-off of increased effort by selectively targeting larger fish (Costa, 1991; Blakeway et al., 2021). Costa, 1991 suggested this shift to consuming larger prey is similar to the central place foraging theory where the surface is the place of return and the increased travel to reach deeper depths favors selection of larger prey items. Gentoo penguins (*Pygoscelis papua*) showed a similar pattern, switching from foraging on krill in shallow waters to targeting fish during deeper dives (Croxall et al., 1988). One notable exception to our pattern of larger fish being caught at deeper depths could be when fur seals target salmon which spend a significant proportion of their time in shallow water (< 40 m, Supplemental Material, Video S1, Ogura and Ishida, 1995; Walker et al., 2007). Both our video results and diet studies, however, show salmon appear to be rare in the northern fur seal diet (3-15% FO) with prevalence varying annually and among breeding sites (Sinclair et al., 2008).

Larger prey were captured at lower temperatures than small prey but this was expected due to the relationship between depth and temperature in the Bering Sea. In the summer months, a stable thermocline can be found over much of the Bering Sea shelf (Stabeno et al., 2001; Stabeno et al., 2007). In addition, a subsurface "cold pool", which is defined as an isolated water mass less than 2.0° C, can form in the middle region of the shelf (50 –

100 m) due to the presence of winter sea ice (Stabeno et al., 2001; Stabeno et al., 2007; Grüss et al., 2021). These subsurface oceanographic features can play a role in the depth and geographic distribution of pollock (Wyllie-Echeverria and Wooster, 1998; Stabeno et al., 2001). During years with an extensive cold pool, the distribution of adult pollock is compressed and pushed to the outer shelf region as adult pollock tend to avoid the colder waters (Wyllie-Echeverria and Wooster, 1998; Eisner et al., 2020). If fur seals were targeting these larger fish away from the cold pool, then we would expect to see a relationship between prey size and temperature residuals (i.e., larger fish would be found in warmer than expected temperatures based on depth alone). This was not the case, but it's important to note that both 2018 and 2019 were considered warm years and the cold pool was not found within most of the fur seals foraging range (Janelli et al., 2019; Eisner et al., 2020). Only in 2017 were prey captured at or near 2°C (Figure 4C) and this was the case for both large and small prey.

The stable thermocline, which sets up in May and begins to break down in fall (Sept-Nov), can also act as a barrier to separate small and larger pollock within the water column (Traynor, 1986; Stabeno et al., 2001; Ladd and Stabeno, 2012). Juvenile pollock, which can be found in a range of temperatures and depths, primarily congregate in the mixed-layer above the thermocline, but become more demersal as they age (Bailey, 1989; Swartzman et al., 1994; Olla et al., 1996). Although we did find that large prey were captured almost exclusively below the mixed-layer depth, we were surprised that smaller prey were also often captured within or below the mixed-layer depth. The lack of small prey captures above the mixed-layer depth may be related to the programming of our cameras, as there was limited video recording from the surface to 10 m. This could, however, also be a result of a predator response behavior by the fish or a specific hunting tactic used by the fur seals. For example, the pollock could be responding to the presence of a predator by moving to deeper depths, below the mixed-layer (Sogard and Olla, 1993; Olla et al., 1996). During laboratory experiments, when an adult pollock was introduced, juvenile pollock responded by diving to the bottom even when a thermocline was present (Sogard and Olla, 1993). A similar response in the natural environment could explain the high proportion of small fish captured at or below the mixed-layer depth. Juvenile pollock have also been shown to form schools that can span over 10 m in depth (Stienessen et al., 2019). As a visual predator, fur seals could be using the backlight from the surface to target fish near the bottom of a school, at its deepest depth, which would result in the capture of juvenile prey deeper in the water column than expected based on average school depths. Capture attempts from below are well documented in other species including penguins, whales, and sharks (Klimley et al., 1992; Watanabe et al., 2004; Sutton et al., 2021). During the daytime when the surface could be identified we regularly observed fur seals targeting prey from below (Supplemental Material, Figure S1, Video S2).

Although most of the fur seals tracked in this study foraged on the Bering Sea shelf, a significant proportion of the population also feeds over deep water in the Bering Sea basin (Kooyman and Goebel, 1986; Goebel et al., 1991). The use of these different habitats has been shown to influence both diet and dive behavior (Zeppelin and Ream, 2006; Kuhn et al., 2014; Jeanniard-du-Dot et al., 2017) and we predict that this would influence prey encounter rates and foraging success as well. The single fur seal in this study that foraged in the Bering Sea basin did have a markedly higher number of prey captures per recorded dive than all of the others (2.2 vs. < 1 successful captures/recorded dive, Table 2). Future northern fur seal foraging studies using video cameras should aim to track more individuals that forage over the basin to investigate these differences. In addition, until further developments lead to more reliable animal-borne video cameras that are able to record for longer durations, future studies could also use the video data as a tool to validate other methods for identifying foraging behavior or prey capture attempts (e.g., Volpov et al., 2016; McGovern et al., 2019; Sutton et al., 2020).

Identifying foraging behavior using data from dive recorders is not new, but studies have found varying success and the metrics used to identify foraging are not consistent. For example, using just depth data, foraging dives by Australian fur seals were identified with 77% accuracy based on descent rate alone (Volpov et al., 2016). By incorporating accelerometers and magnetometers, McGovern et al. (2019) were able to not only identify foraging dives, but also individual prey encounters based on 3D dive patterns with 95% accuracy. The ability to transition away from video recorders, would result in both a reduction in the size and cost of instruments, and potentially make it possible to use instruments that do not need to be recovered (Cox et al., 2017; Heerah et al., 2019; Robinson et al., 2021). This could result in larger sample sizes and the tracking of sex or age-classes that do not predictably return to the rookery. However, this would also result in the loss of the other beneficial data collected from animal-borne videos (e.g., visualizing prey species and determining capture success).

Conclusions

The enhanced understanding of predator-prey relationships provided by animal-borne video cameras will be invaluable to better interpret years of historical northern fur seal biologging data and to provide baseline data for modeling future impacts of variations in prey resources. Previous northern fur seal studies have suggested that more frequent deep or daytime dives was related to increased consumption of adult pollock, but direct evidence wasn't available (Sinclair and Loughlin, 1994; Sterling, 2009). Sterling (2009) found that variations in fur seal dive depths correlated with changes in pollock age-class recruitment, as fur seals shifted from shallow diving in 1992 to deeper diving in 1995, possibly following the dominant 1992 pollock cohort. McHuron et al. (2020) showed that during years of low pollock

recruitment, the increased consumption of larger pollock may be necessary for fur seals to meet their energetic demands. The reduced abundance of age-0 and age-1 pollock in the fur seals foraging area in 2017 (Ianelli et al., 2019; Eisner et al., 2020) could have been a factor driving NFSF0517 to primarily target adult pollock during her foraging trip. Our results provide a direct link between dive behavior and prey consumption and demonstrate that changes in dive depth and the timing of dives can be used as an indicator of shifts in diet between small and large prey for northern fur seals.

As marine environments continue to change, either from climate-related or anthropogenic threats, it becomes crucial to understand relationships between marine predators and their prey. Walleye pollock distribution and recruitment are fundamentally linked to temperature variability in the Bering Sea (Kotwicki et al., 2005; Mueter et al., 2011; Eisner et al., 2020). With climate models predicting future warming in the Bering Sea, the predicted shift in pollock distribution and declines in abundance may have adverse impacts on not only northern fur seal populations, but other marine mammals and seabirds that rely on this prey resource (Springer et al., 1986; Mueter et al., 2011; Spencer et al., 2016; Ianelli et al., 2019; Eisner et al., 2020). Using a range of IPCC climate projections, Mueter et al. (2011) predicted pollock recruitment could decline by 32–58% in the Bering Sea by 2040–2050. Having the ability to collect data to quantify foraging behavior, visualize the prey being consumed, and identify factors affecting foraging success, will help inform models to predict the future impacts of climate-related changes to the northern fur seals' habitat and prey resources.

Data availability statement

The raw data supporting the conclusions of this article and associated R code used for analysis will be made available on request to the corresponding author, without undue reservation.

Ethics statement

Research was conducted under Marine Mammal Protection Act permit #14327 and approved by the National Marine Fisheries Service IACUC A/NW 2013-3/2016-2.

Author contributions

CK, JS, and CM study conception. CK and CM funding. CK and JS conducted data collection. CK, JS, MM, BB, AS, and AF analyzed data. CK wrote with input from JS, MM, BB, AS, AF, and CM. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.1015594/full#supplementary-material>

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