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# Linking northern fur seal behavior with prey distributions: the impact of temporal mismatch between predator studies and prey surveys

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## Abstract

**Background:** An essential part of foraging ecology research is identifying how the distribution and abundance of prey influence predator behavior. However, in marine systems, temporal or spatial mismatches often exist between prey surveys and predator tracking periods, especially for species with large foraging ranges. Using northern fur seals (*Callorhinus ursinus*) as a model, we investigated how conclusions about predator–prey relationships change with increasing temporal disparity between predator tracking periods and prey surveys. To measure foraging behavior, northern fur seals (*n* = 20) from St. Paul Island (Alaska, USA) were equipped with satellite tracking transmitters and time-depth recorders from July to October 2006. Fur seal dive and movement metrics were examined in relation to the relative abundance of the fur seals' primary prey, walleye pollock (*Gadus chalcogrammus*), reported from the annual eastern Bering Sea groundfish survey. Relationships between foraging behavior metrics and prey abundance were examined within the Bering shelf survey grid cells at three timescales: within 2 weeks of the prey survey, within 1 month, and over the northern fur seal reproductive season (>4 months).

**Results:** We found significant relationships between northern fur seal behavior and prey abundance, even with the limited sample size at the shortest temporal resolution (2 weeks). Changes in dive behavior that were associated with areas of abundant pollock (for example, increased vertical distance traveled and longer periods of diving) were consistent with previously reported metrics of pinniped foraging success. When behavioral metrics, such as vertical distance traveled and time spent diving, remained significantly related to prey abundance at multiple temporal scales, the relationship strength was reduced as temporal mismatch increased.

**Conclusion:** Our results suggest that relationships between behavioral metrics and prey abundance vary as temporal mismatch increases between prey surveys and predator tracking periods. For northern fur seals, pollock surveys conducted early in the reproductive season may still provide information useful to examine predator–prey relationships as the reproductive season progresses, albeit with diminished predictive power. Understanding predator–prey relationships, including the impact of varying temporal scales, is particularly valuable for guiding research and conservation strategies for northern fur seals as the population continues to decline.

**Keywords:** Bering Sea, *Callorhinus ursinus*, Dive behavior, Satellite telemetry, Walleye pollock

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## Background

A key aspect of foraging ecology research is understanding how predator behavior is influenced by the abundance and distribution of prey resources. In the marine environment, predator–prey relationships are challenging to discern given the vast three-dimensional scale and inability to make direct observations in most systems. In addition, measuring prey landscapes for wide-ranging marine predators is a massive undertaking, which can be costly in terms of both resources and time. As a result, few studies have been able to simultaneously measure prey availability and predator behavior over a predator's entire temporal and spatial foraging range (for example, [1, 2]). Incomplete overlap between predator and prey surveys can lead to spatial or temporal mismatches between datasets and potentially inaccurate conclusions about predator–prey relationships.

On a small scale, predator–prey interactions can be identified through transect surveys (for example, [3, 4]) or focal follow studies [1, 5]. These studies may benefit from direct observations of feeding while simultaneously measuring predator densities and prey patch characteristics, making it possible to address questions of fine-scale behavior [6–8]. However, these studies have limited spatial coverage and often examine only a small portion of the predators' full foraging range. This can result in spatial mismatches and may limit inferences about predator–prey relationships on a larger scale. For example, Vlietstra [9] showed that fluctuations in regional prey abundance can shape predator–prey density relationships at small spatial scales. For three marine bird species, predator densities were only correlated with local prey biomass when regional prey abundance was low [9]. Therefore, understanding larger prey landscapes may be critical for accurately interpreting predator–prey relationships.

Researchers can also examine predator–prey relationships by correlating predator behavior measured remotely, via bio-logging devices, with surveys of prey landscapes throughout the foraging range [10–12]. Bio-logging devices include instruments that provide at-sea locations (satellite or GPS) or measure underwater behavior, such as time-depth recorders and accelerometry tags [13, 14]. Bio-logging applications can provide highly detailed measures of behavior over long timescales (months to years); however, the expanded timescales may lead to temporal mismatch between measures of predator behavior and prey surveys [15–17]. For example, Garthe et al. [16] tracked northern gannets (*Sula bassana*) from late July to August 2003 to examine foraging behavior in relation to prey densities (capelin, *Mallotus villosus*) that were measured in mid-July. Although a relationship was found for capelin density and gannet foraging sites, the authors noted that it was surprising that the relationship was not stronger and suggested that movements of the spawning capelin, after the prey survey, could be responsible [16]. Without knowing the impact of temporal or spatial discrepancies, our understanding of predator–prey relationships may be inaccurate or incomplete.
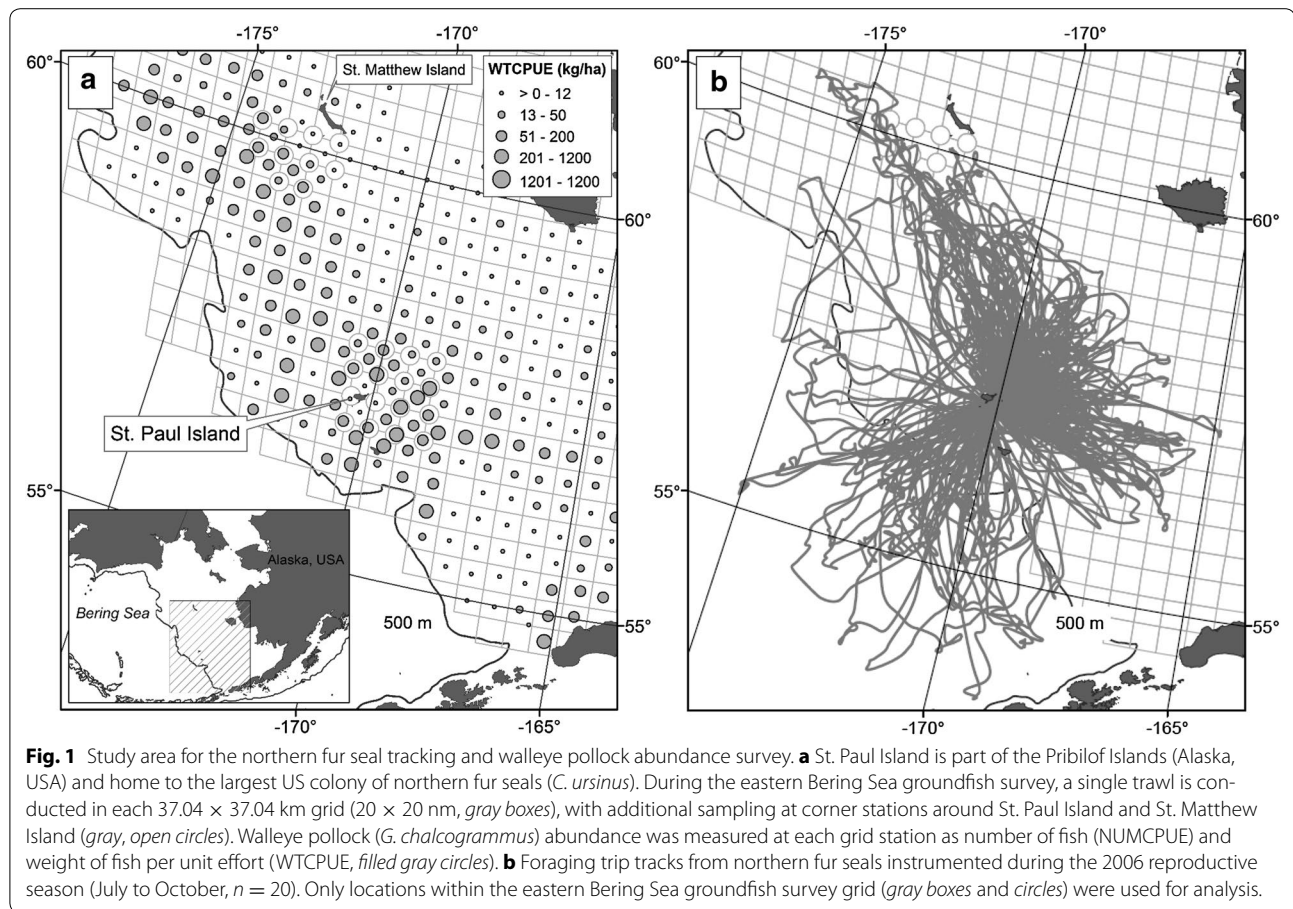
For northern fur seals (*Callorhinus ursinus*), understanding the influences of prey availability on foraging behavior is critical as the population in US waters has experienced unexplained decline since the mid-1970s [18]. The specific causes for the decline are unknown but could include disease or parasites, predation, entanglement in marine debris, incidental catch, environmental contaminants, or reduced prey availability (for example, from climate-related redistribution or commercial fisheries removal) [19]. In the United States, the largest colony of northern fur seals breeds on the Pribilof Islands (St. Paul and St. George islands, Alaska, Fig. 1a). During the reproductive season, between June and November, female fur seals are central place foragers because they balance short foraging trips to sea (approximately 4–10 days) with time on land nursing a single pup [20–23]. Being constrained to short foraging trips makes fur seals dependent on local prey resources around the breeding colonies to successfully rear their offspring [24–26].

As is the case with many marine predator–prey studies [15–17], temporal mismatches exist between prey surveys and predator tracking periods in this system. Diet studies based on scat indicate that northern fur seals foraging on the Bering Sea shelf predominantly consume walleye pollock (*Gadus chalcogrammus*), with frequency of occurrence ranging from 62 to 89% [22, 27, 28]. In addition, stable isotopes in northern fur seal tissue suggest that this diet is consistent throughout most of the reproductive season [27]. An annual groundfish survey that measures walleye pollock abundance is conducted on the Bering Sea shelf in early summer (late May to July) [29]. This survey covers the entire Bering shelf foraging habitat used by northern fur seals; however, fur seals rely on this prey resource from June to November [23]. To determine if this survey can provide valuable information about the influence of prey availability on northern fur seal behavior, it is necessary to know the potential impact of this temporal mismatch. Therefore, we investigated how relationships between northern fur seal behavior and prey abundance change with increasing temporal disparity between predator tracking periods and prey surveys.

## Results

### Fur sea behavior

Fur seals ($n = 20$) ranged in mass from 30.4 to 54.0 kg (average $39.9 \pm 1.3$ kg), and mass change was

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**Fig. 1** Study area for the northern fur seal tracking and walleye pollock abundance survey. **a** St. Paul Island is part of the Pribilof Islands (Alaska, USA) and home to the largest US colony of northern fur seals (*C. ursinus*). During the eastern Bering Sea groundfish survey, a single trawl is conducted in each 37.04 × 37.04 km grid (20 × 20 nm, *gray boxes*), with additional sampling at corner stations around St. Paul Island and St. Matthew Island (*gray, open circles*). Walleye pollock (*G. chalcogrammus*) abundance was measured at each grid station as number of fish (NUMCPUE) and weight of fish per unit effort (WTCPUE, *filled gray circles*). **b** Foraging trip tracks from northern fur seals instrumented during the 2006 reproductive season (July to October, *n* = 20). Only locations within the eastern Bering Sea groundfish survey grid (*gray boxes* and *circles*) were used for analysis.

$-2.9 \pm 0.9$ kg over the tracking period (range $-9.2$ to 4.8 kg, $n = 17$). Average tracking duration was $76.7 \pm 4.8$ days, with a range of 13–93 days. Two fur seals were not equipped with a time-depth recorder, three fur seals were not recaptured, and one time-depth recorder failed, which resulted in dive data from 14 fur seals. Location data were acquired from all fur seals ($n = 20$); however, for four fur seals, the platform terminal transmitters (PTTs) did not transmit through the duration of the study period. This was because one fur seal lost her PTT during the study, and the PTTs for the three fur seals that were not recaptured stopped transmitting before the end of the reproductive season. As a result, these four fur seals had abbreviated location records (13, 26, 58, and 59 days).

During the full reproductive season, fur seals spent 20,635 h ($n = 20$ location records) in 180 unique survey grids where 106,123 dives occurred ($n = 14$ depth records, Fig. 1b). Mean values for all behavior metrics during each temporal scale are presented in Table 1. At the 1 mo temporal scale, fur seals spent 4,087 h ($n = 20$ location records) in 88 unique grid cells where 10,837 dives occurred ($n = 14$ dive records). At the shortest

temporal scale (2 weeks), the fewest grid cells were used ($n = 23$ grids) and the total hours of use (363 h, $n = 13$ location records) and number of dives (1,221 dives, $n = 7$ dive records) were reduced.

### Pollock distribution and abundance

During the annual groundfish assessment survey, walleye pollock were captured at 96% of the survey stations with WTCPUE ranging from 0.002 to 1,031.7 kg/ha and NUMCPUE ranging from 0.17 to 1,617.6 fish/ha [29]. The highest densities were found northwest of St. Paul Island on the outer shelf region and just south of St. Paul Island (Fig. 1a, Figure ten in [29]). Within the grid cells that fur seals used, WTCPUE averaged $126.6 \pm 6.3$ kg/ha (0.01–1,016.1 kg/ha) and NUMCPUE averaged $171.8 \pm 8.7$ fish/ha (0.60–1,396.6 fish/ha).

### Relationships between fur seal behavior and prey

Fur seal behavior was related to walleye pollock abundance at all temporal scales examined, and in all but eight cases, the responses for WTCPUE and NUMCPUE were similar (Table 2). At the shortest temporal scale (2 weeks), multiple dive metrics were significant but time

**Table 1 Summary of behavior metrics by grid for each temporal scale**

|  | 2 weeks | 1 month | Full |
|---|---|---|---|
| Hours in grid/area (h/km$^2$) | 0.01 ± 0.002 (0.0007–0.04) | 0.02 ± 0.001 (0.0007–0.19) | 0.03 ± 0.001 (0.0007–0.37) |
| Transit rate (km/h) | 3.0 ± 0.33 (0.5–7.2) | 4.2 ± 0.11 (0.5–10.4) | 4.2 ± 0.09 (0.5–12.8) |
| Dives/grid hour (count/h) | 5.4 ± 0.84 (0.22–18.8) | 4.0 ± 0.21 (0.06–21.1) | 6.4 ± 0.21 (0.06–71.8) |
| Dives/grid area (count/km$^2$) | 0.06 ± 0.009 (0.0007–0.18) | 0.07 ± 0.004 (0.0008–0.50) | 0.19 ± 0.01 (0.0007–3.12) |
| Vertical distance/grid hour (m/h) | 433.3 ± 57.8 (3.6–1,383.8) | 285.4 ± 13.3 (1.4–1,509.7) | 386.6 ± 10.4 (1.4–2,436.0) |
| Vertical distance/grid area (m/km$^2$) | 5.8 ± 1.06 (0.02–25.1) | 5.2 ± 0.41 (0.01–57.8) | 11.3 ± 0.62 (0.01–185.9) |
| Bottom time/grid hour (min/h) | 2.8 ± 0.34 (0.02–6.6) | 2.4 ± 0.13 (0–19.6) | 3.9 ± 0.12 (0–28.7) |
| Bottom time/grid area (min/km$^2$) | 0.04 ± 0.006 (0.0001–0.12) | 0.04 ± 0.003 (0–0.43) | 0.12 ± 0.006 (0–1.51) |
| Percent bottom time | 26.6 ± 1.0 (16.4–36.0) | 29.9 ± 0.51 (0–50.9) | 33.1 ± 0.36 (0–62.5) |
| Dive time/grid hour (min/h) | 9.7 ± 1.3 (0.11–30.7) | 6.9 ± 0.32 (0.04–40.7) | 10.1 ± 0.26 (0.02–49.8) |
| Dive time/grid area (min/km$^2$) | 0.12 ± 0.02 (0.0007–0.39) | 0.12 ± 0.009 (0.0003–1.3) | 0.30 ± 0.02 (0.001–3.8) |
| Descent rate (m/s) | 1.0 ± 0.05 (0.54–1.6) | 1.04 ± 0.02 (0.26–1.8) | 1.02 ± 0.01 (0.19–2.7) |
| Ascent rate (m/s) | 0.93 ± 0.05 (0.49–1.4) | 0.91 ± 0.02 (0.34–1.7) | 0.90 ± 0.01 (0.25–1.7) |
| Wiggles/dive | 0.63 ± 0.05 (0–1.1) | 0.50 ± 0.02 (0–2.1) | 0.67 ± 0.01 (0–3.0) |
| Wiggles/grid hour (count/h) | 3.1 ± 0.48 (0–11.4) | 2.2 ± 0.19 (0–32.1) | 4.5 ± 0.17 (0–31.0) |
| Wiggles/grid area (count/km$^2$) | 0.04 ± 0.007 (0–0.2) | 0.04 ± 0.003 (0–0.5) | 0.12 ± 0.007 (0–1.8) |

Values are presented as mean ± SE and ranges are provided in parentheses.

**Table 2 Results of models used to examine relationships between walleye pollock abundance and northern fur seal behavior**

|  | Pollock catch per effort (WTCPUE/NUMCUPE) | | |
|---|---|---|---|
|  | 2 weeks | 1 month | Full |
| Hours in grid/area (h/km$^2$) | NS | NS | NS/$P = 0.02$ |
| Transit rate (km/h) | NS | NS | NS |
| Dives/grid hour (count/h) | $P = 0.04$/$P = 0.04$ | NS | NS |
| Dives/grid area (count/km$^2$) | $P = 0.03$/$P = 0.02$ | NS | NS |
| Vertical distance/grid hour (m/h) | $P = 0.01$/$P = 0.01$ | $P < 0.001$/$P < 0.001$ | $P = 0.03$/$P = 0.005$ |
| Vertical distance/grid area (m/km$^2$) | $P = 0.04$/$P = 0.04$ | $P = 0.003$/$P = 0.003$ | $P = 0.03$/NS |
| Bottom time/grid hour (min/h) | NS | NS | NS |
| Bottom time/grid area (min/km$^2$) | NS | NS | $P = 0.04$/NS |
| Percent bottom time | NS | NS | NS |
| Dive time/grid hour (min/h) | $P = 0.02$/$P = 0.03$ | $P = 0.03$/$P = 0.03$ | NS/$P = 0.02$ |
| Dive time/grid area (min/km$^2$) | NS/$P = 0.04$ | $P = 0.03$/$P = 0.04$ | NS |
| Descent rate (m/s) | NS | $P = 0.001$/$P = 0.001$ | $P = 0.03$/$P = 0.009$ |
| Ascent rate (m/s) | NS | $P < 0.001$/$P < 0.001$ | $P = 0.002$/$P < 0.001$ |
| Wiggles/dive | NS | $P = 0.002$/$P = 0.002$ | $P = 0.04$/$P = 0.02$ |
| Wiggles/grid hour (count/h) | NS | $P = 0.01$/NS | NS |
| Wiggles/grid area (count/km$^2$) | NS | $P = 0.003$/NS | $P = 0.04$/NS |

Behavior metrics were investigated at three temporal scales: within 2 weeks of the prey survey (2 weeks), within 1 month, and over the fur seal reproductive period (full, approximately 4 months). Pollock abundance was measured as catch per unit effort calculated as kilogram per hectare (WTCPUE) and number per hectare (NUMPUE). All behavior metrics that were significant were positively correlated with prey abundance, except hours per grid area. Behavioral variables that were not significant are denoted by NS.

spent in grid and transit rate were not. The significant dive metrics included measures of dive frequency, vertical distance traveled during a dive, and time spent diving (Table 2). Dives per hour in grid and by area increased significantly with WTCPUE ($t = 2.22$, $r^2 = 0.22$, $P = 0.04$ and $t = 2.34$, $r^2 = 0.22$, $P = 0.03$, respectively) and NUMCPUE ($t = 2.19$, $r^2 = 0.22$, $P = 0.04$ and $t = 2.45$, $r^2 = 0.23$, $P = 0.02$, respectively, Table 2). A similar positive relationship was found for the vertical distance traveled during a dive by hour in grid (WTCPUE: $t = 2.86$,

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$r^2 = 0.32$, $P = 0.01$; NUMCPUE: $t = 2.77$, $r^2 = 0.31$, $P = 0.01$) and by area (WTCPUE: $t = 2.16$, $r^2 = 0.21$, $P = 0.04$; NUMCPUE: $t = 2.26$, $r^2 = 0.22$, $P = 0.04$, Table 2). For total dive time per grid hour, both WTCPUE and NUMCPUE were significant ($t = 2.49$, $r^2 = 0.27$, $P = 0.02$ and $t = 2.40$, $r^2 = 0.25$, $P = 0.03$, respectively), but only NUMCPUE was significant for dive time by area ($t = 2.21$, $r^2 = 0.21$, $P = 0.04$, Table 2).

At the intermediate timescale (1 month), a similar pattern was found with multiple dive metrics related to walleye pollock abundance (Table 2). Vertical distance traveled per grid hour (WTCPUE: $t = 3.62$, $r^2 = 0.07$, $P < 0.001$, and NUMCPUE: $t = 3.68$, $r^2 = 0.07$, $P < 0.001$), vertical distance by area (WTCPUE: $t = 3.04$, $r^2 = 0.05$, $P = 0.003$, and NUMCPUE: $t = 2.98$, $r^2 = 0.04$, $P = 0.003$), dive time per grid hour (WTCPUE: $t = 2.14$, $r^2 = 0.02$, $P = 0.03$, and NUMCPUE: $t = 2.17$, $r^2 = 0.02$, $P = 0.03$), and dive time per area (WTCPUE: $t = 2.13$, $r^2 = 0.02$, $P = 0.03$, and NUMCPUE: $t = 2.06$, $r^2 = 0.02$, $P = 0.04$) were all positively related to prey abundance (Table 2), but with notably lower $r^2$ values. At the intermediate temporal scale, there was a positive relationship between descent rate and ascent rate for both WTCPUE ($t = 3.25$, $r^2 = 0.05$, $P = 0.001$, and $t = 4.30$, $r^2 = 0.09$, $P < 0.001$, respectively) and NUMCPUE ($t = 3.27$, $r^2 = 0.05$, $P = 0.001$, and $t = 4.32$, $r^2 = 0.09$, $P < 0.001$, respectively). Measures of wiggle behavior were also significant at the intermediate scale, but these metrics varied between WTCPUE and NUMCPUE (Table 2). The average number of wiggles per dive increased with WTCPUE ($t = 3.12$, $r^2 = 0.05$, $P = 0.002$) and NUM-CPUE ($t = 3.12$, $r^2 = 0.05$, $P = 0.002$); however, both the number of wiggles per grid hour and per grid area were only significantly related to WTCPUE ($t = 2.56$, $r^2 = 0.03$, $P = 0.01$, and $t = 3.05$, $r^2 = 0.05$, $P = 0.003$, respectively). As temporal scale increased, measures of dive frequency (by hour or area) which were significant at the 2-week scale were no longer significant (Table 2).

At the scale of the full northern fur seal reproductive season, some dive metrics remained significant, and for the first time, grid residence time was significantly related to prey abundance (Table 2). Similar to the intermediate timescale, descent rate and ascent rate increased with WTCPUE ($t = 2.12$, $r^2 = 0.01$, $P = 0.03$, and $t = 3.09$, $r^2 = 0.01$, $P = 0.002$, respectively) and NUMCPUE ($t = 2.60$, $r^2 = 0.01$, $P = 0.009$, and $t = 3.63$, $r^2 = 0.02$, $P < 0.001$, respectively). In addition, some measures of wiggle behavior remained significantly related to WTCPUE, such as average wiggles per dive ($t = 2.22$, $r^2 = 0.01$, $P = 0.04$) and wiggles per area ($t = 2.22$, $r^2 = 0.01$, $P = 0.04$); however, only wiggles per dive was related to NUMCPUE ($t = 2.56$, $r^2 = 0.01$, $P = 0.02$, Table 2). As with the other two temporal scales, vertical
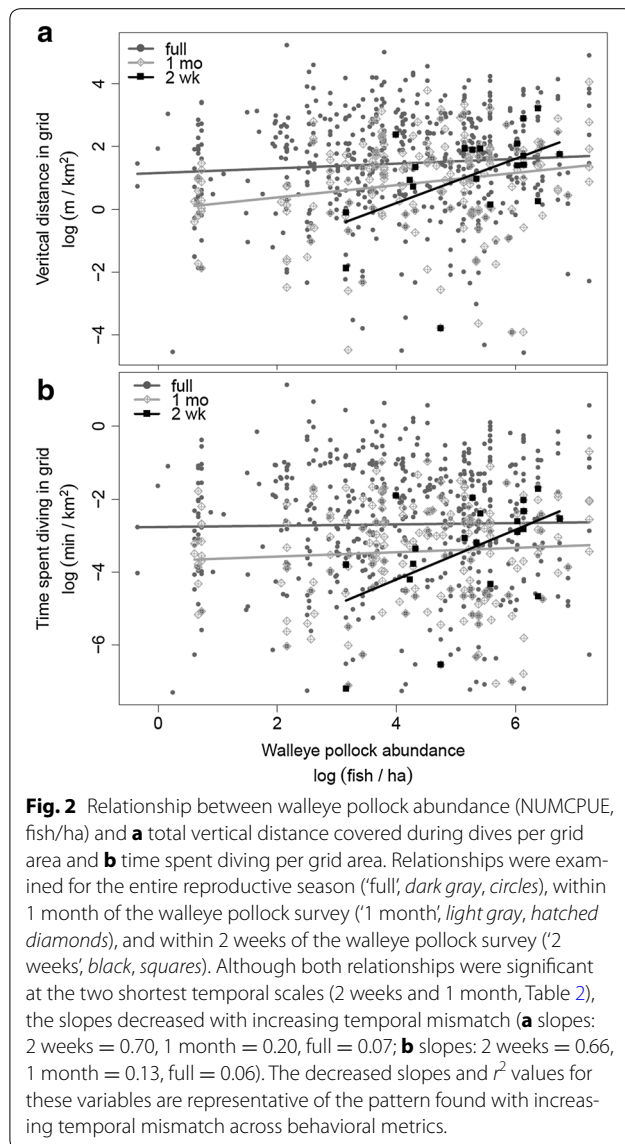
distance traveled during a dive and dive time in a survey grid increased with prey abundance. For vertical distance per hour in a grid, both WTCPUE ($t = 2.13$, $r^2 = 0.01$, $P = 0.03$) and NUMCPUE ($t = 2.77$, $r^2 = 0.01$, $P = 0.005$) were significant, but vertical distance by area was only related to WTCPUE ($t = 2.22$, $r^2 = 0.01$, $P = 0.03$). Dive time per grid hour was only correlated with NUMCPUE ($t = 2.4$, $r^2 = 0.01$, $P = 0.02$), whereas bottom time per grid area was only correlated with WTCPUE ($t = 2.0$, $r^2 = 0.01$, $P = 0.04$). Hours spent in grid was only related to NUMCPUE, but this was a negative relationship ($t = -2.25$, $r^2 = 0.01$, $P = 0.02$, Table 2).

Finally, when fur seal behavior metrics were significant at more than one scale, relationships changed with increasing temporal disparity. For example, vertical distance by area and time spent diving by area were significantly related to NUMCPUE at the shorter temporal scales (2 weeks and 1 month, Table 2). However, the $r^2$ values and slopes of these relationships declined as temporal disparity increased (Fig. 2a, b). This pattern of reduced slope and $r^2$ values with increased temporal disparity was found for all relationships that were significant at more than one temporal scale.

## Discussion
### Fur seal behavior and prey density
By spatially and temporally linking northern fur seal behavior with prey abundance, we were able to examine how relationships change in response to varying temporal disparity. The metrics of northern fur seal behavior that were significantly related to prey abundance at the shortest temporal scale are consistent with indices of foraging behavior identified in other marine predators, including northern fur seals in Russia (for example, [30–32]). Dive rate or dive frequency has been shown to increase when animals are successfully catching prey or when animals are on their main foraging grounds [30, 33, 34]. For example, when feeding occurred, gray seal (*Halichoerus grypus*) dive bouts had a greater number of dives than when prey were not captured [30]. Subantarctic fur seals (*Arctocephalus tropicalis*) significantly increased dive rate (dives/h) during the feeding phase of their foraging trips in areas where their main prey were abundant [33]. During this feeding phase, subantarctic fur seals also increased the vertical distance per hour during dives to over seven times greater than what was measured during the earlier transit phase [33]. An increase in vertical distance during diving was also found to be positively related to mass gain for northern fur seals breeding at Lovushki Island, Russia [32]. Although the mass gain was determined for an entire foraging trip, this suggests that successful foraging is related to diving effort for northern fur seals [32]. Associated with the increased diving

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**Fig. 2** Relationship between walleye pollock abundance (NUMCPUE, fish/ha) and **a** total vertical distance covered during dives per grid area and **b** time spent diving per grid area. Relationships were examined for the entire reproductive season ('full', *dark gray*, *circles*), within 1 month of the walleye pollock survey ('1 month', *light gray*, *hatched diamonds*), and within 2 weeks of the walleye pollock survey ('2 weeks', *black*, *squares*). Although both relationships were significant at the two shortest temporal scales (2 weeks and 1 month, Table 2), the slopes decreased with increasing temporal mismatch (**a** slopes: 2 weeks = 0.70, 1 month = 0.20, full = 0.07; **b** slopes: 2 weeks = 0.66, 1 month = 0.13, full = 0.06). The decreased slopes and $r^2$ values for these variables are representative of the pattern found with increasing temporal mismatch across behavioral metrics.

activity (frequency and distance covered), increased time spent diving has also been related to marine predator feeding behavior [35, 36]. In a captive setting, gray seals were found to significantly increase dive duration with increasing prey encounter rate [36]. For European shags (*Phalacrocorax aristotelis*), the amount of prey ingested was positively related to both the duration of a single dive and the duration of an entire dive bout [35].

Other metrics that have been associated with increased prey encounter rate for marine predators were not found to be significant for northern fur seals at the shortest temporal scale. For example, undulations (wiggles) during the bottom phase of a dive have been linked to prey capture attempts for species such as penguins and seals [31, 37, 38]. For northern fur seals in Russia, Skinner

et al. [32] did not find a relationship between wiggles and mass gain over a foraging trip and suggested this behavior may not reflect actual prey capture attempts in this species. For gray seals, accumulated bottom time was 3.5 times greater for feeding versus non-feeding bouts [30], but a similar relationship was not found for northern fur seals. However, many studies have shown that dive indices related to prey capture can vary significantly among species and may be shaped by the specific prey being targeted [39–41]. For example, when using the 'sit and wait' foraging strategy, harbor seal (*Phoca vitulina*) dives were found to have longer bottom times and lower bottom swim speeds than when employing an active foraging strategy [40]. As a result, future studies examining how predator–prey relationships change over time should validate these dive metrics to confirm they are indicative of foraging success or prey encounter for northern fur seals.

The one behavioral metric that appears to be consistently related to foraging behavior for marine predators, and that we found to be insignificant, is residence time in an area (for example, [42, 43]). Marine predators feeding on patchily distributed prey can increase foraging success by employing area-restricted search patterns in response to prey encounter [44–46]. This area-restricted search behavior should increase retention within a grid cell if animals are successfully foraging. For example, the swimming paths of basking sharks (*Cetorhinus maximus*) became more convoluted as prey density increased, resulting in sharks spending the greatest amount of time in the highest density prey patches [1]. Bailey and Thompson [44] showed that bottlenose dolphins (*Tursiops truncatus*) concentrated search effort in areas where feeding occurred compared to their movements throughout the rest of the study region. For northern fur seals, grid residence time was only significantly related to prey abundance at the longest temporal scale, which was a weak negative relationship. It has been previously suggested that northern fur seals forage while transiting, which may limit the number or intensity of area-restricted search periods during foraging trips, reducing residency times [47, 48]. In addition, other fur seal behaviors not related to feeding, such as resting and grooming, may impact time in a grid cell regardless of prey abundance. Finally, it is important to consider the constraints faced by female northern fur seals during the reproductive season, which may shape how fur seals allocate their time at sea. Trip durations are limited by the fasting duration of the dependent pup waiting onshore [23, 24, 49]. Therefore, if grids with higher densities of prey are distributed away from the rookery, females must spend a larger proportion of their time traveling, which may reduce the amount of time available to forage before needing to return to the rookery. To examine the impacts

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of this constraint, distance from the rookery could be included as a factor in further models examining the relationship between prey abundance and residence time [22, 50].

## Impacts of temporal disparity

As the temporal disparity increased, relationships between prey abundance and northern fur seal behavior changed. Metrics of dive rate lost significance with increased temporal disparity, but other dive variables, such as vertical distance traveled during a dive and total dive time, remained significant. Nevertheless, the strength of these relationships decreased as temporal mismatch between northern fur seal data and the prey survey increased, and at the scale of the full reproductive season, $r^2$ values for all relationships were nearly zero. Because many significant relationships persisted at the intermediate scale, this suggests that using fur seal behavioral data within 1 month of prey surveys may still provide valuable information to examine predator–prey relationships, albeit with diminished predictive power. This consistency at the intermediate temporal scale could be related to the behavior of the fur seals' prey, the stability of the environment, or the strong foraging site fidelity previously described for northern fur seals [51–54].

After spawning in the spring [55], walleye pollock migrate to the Bering shelf region to forage [53, 54]. For the purpose of stock assessment, it is assumed that walleye pollock do not change distribution during the 3-month survey period [56]. However, based on interannual variability in walleye pollock distribution in relation to water temperature, Kotwicki et al. [53] proposed that during the summer some walleye pollock may move to the north and northeast as water temperature increases and suitable habitat becomes more available. These movements appear to be based on fish size, with immature fish migrating a shorter distance and most of the larger fish not moving at all [53]. Therefore, if a survey grid is primarily composed of these relatively stationary size classes, measurements of abundance reported in June/July may accurately reflect localized abundance later in the summer.

Additionally, the early season surveys may be identifying hotspots for walleye pollock that are enhanced by physical or oceanographic features, resulting in high fish retention after the survey has occurred [52, 57–59]. The middle shelf region of the Bering Sea, which is defined by depths of 50–100 m, is characterized by a strong, persistent thermocline [60–64]. Thermoclines can act to aggregate prey, increasing encounter rate and foraging success for marine predators [54, 65–67]. In addition, at the inner front, which separates the middle and inner shelf regions, nutrient-rich bottom waters from the middle shelf can

be mixed with the surface layer, leading to prolonged primary production [57, 68]. The regional stability and localized enrichment could make this a profitable foraging area for fish and other marine predators, acting as a hotspot over the summer months.

A final factor that may be influencing the consistency in pollock–fur seal relationships at the intermediate temporal scale is foraging site fidelity by northern fur seals [51, 69]. When prey resources are predictable, predators can increase foraging success by returning to areas of previous success [70, 71]. Call et al. [51] found that most northern fur seals returned to foraging locations on subsequent trips over a $48 \pm 1.9$-day period (two to eight trips per individual). Therefore, even if changes in prey distribution occur at the intermediate temporal scale, fur seals could still be visiting grids that had previously been associated with high walleye pollock abundance before moving on to new foraging areas.

For northern fur seals, autumnal storms have been linked to disruptions in foraging behavior that result in changes to the foraging site fidelity that has been previously described and, in some cases, leads to increased foraging effort [22]. In 2006, in particular, Sterling [22] showed that, after a storm in early September, northern fur seals spent more time foraging than prior to the storm. These late season storms can impact lower trophic levels by dispersing nutrients and causing shifts in circulation patterns [57, 60], which may in turn lead to shifts in prey distribution or the disruption of features that lead to persistent hotspots (for example, [72]). As a result, these late season environmental changes may reduce the predictability of prey encounters and could be linked to the reduced strength of predator–prey relationships at the longest temporal scale, the entire reproductive season.

## Study limitations and future directions

For this study, as temporal mismatch between datasets was reduced, we were also faced with a reduction in the amount of data available to examine fur seal behavior. As a result of the small sample size at the 2-week scale, we limited model complexity to single-metric analyses. Complex models that include interactions between behavioral metrics (for example, [32]), including distance from the rookery, may be more suitable for examining predator–prey relationships for northern fur seals, but these types of models would require testing with a larger dataset. In addition, the limited power with the smaller sample size may have reduced our ability to find significance for some behavior metrics at the shortest temporal scale, such as ascent rate and wiggles, which were significant at other scales. Nevertheless, we believe this study provides a starting point for further analyses by identifying the impacts of temporal mismatch and emphasizing

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the need to take it into consideration for future research examining predator–prey relationships.

Although walleye pollock are the dominate prey of northern fur seals at the Pribilof Islands, diet can vary among breeding locations and years [27, 28, 73]. For this study, we assumed fur seals were foraging on walleye pollock and that other secondary prey species did not influence the behavioral metrics examined. This assumption is supported by diet data acquired from scat analyses for fur seals at the study locations in 2006 [22, 27]. At the Reef and Vostochni rookeries, walleye pollock frequency of occurrence in scat was 68.9 and 89.3%, respectively [22, 27]. An additional 25% frequency of occurrence of unidentified gadids were found in the scats from the Reef rookery, which likely included walleye pollock and would have resulted in an even higher frequency of occurrence at that location [22, 27].

An additional consideration is the coarse resolution of the prey survey data (20 × 20 nm grids). Predators can respond to their environment, including prey availability, at multiple spatial scales (for example, [74, 75]). Northern fur seals have been shown to respond to environmental factors from the scale of meters up to the entire foraging range [50, 76]. Here, we found that, even at this coarse spatial scale, significant relationships exist between fur seal behavior and prey abundance. The benefit of using this prey survey dataset is that it is collected annually and it covers the entire Bering shelf summer foraging range of northern fur seals. Recently, additional surveys of walleye pollock have occurred during the summer season, including biennial acoustic surveys of the mid-water column and late season mid-water trawl surveys [77–79]. Together, these surveys provide a comprehensive dataset for walleye pollock distribution in the Bering Sea, although the eastern Bearing Sea bottom trawl survey is still the most consistent and covers the largest range [29, 77–79]. Integrating these data on walleye pollock with continued studies of northern fur seal at-sea behavior, and having an understanding of the impacts of temporal mismatch, will allow for future research to examine fur seal behavior in relation to prey and to track how these relationships change over time.

### Conservation implications

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 is the most abundant forage fish in the Bering Sea [80] and many species of fish, seabirds, and marine mammals depend on this population as a prey resource [81, 82]. In addition, walleye pollock distribution and recruitment are fundamentally linked to temperature variability in the Bering Sea [53,

83, 84]. As climate models predict future warming in the Bering Sea, changes to walleye pollock distribution and abundance may have adverse impacts on northern fur seal populations [85, 86]. By identifying northern fur seal behaviors associated with prey encounter and potential foraging success, it may be possible to predict or model the impacts of climate-related changes to the northern fur seals' habitat and prey resources. This is particularly valuable for developing effective management and conservation strategies as the northern fur seal population continues to decline.

## Conclusion

By spatially and temporally linking predator tracking data with prey surveys, we were able to examine the impact of temporal disparity on our understanding of predator–prey relationships. Although relationships between northern fur seal behavior and walleye pollock abundance existed at all temporal scales, the correlation strength was noticeably diminished as temporal mismatch increased. For northern fur seals, it appears that prey surveys collected within 1 month of predator-tracking studies may still provide valuable information about the influence of prey abundance on predator behavior.

## Methods

### Fur seal dive and location analysis

Research was conducted on St. Paul Island, Alaska (USA, Fig. 1a) from 7 July to 18 October 2006. Adult female northern fur seals were instrumented at two rookeries, Reef ($n = 10$, 57.1°N, 170.3°W) and Vostochni ($n = 10$, 57.3°N, 170.1°W). Females with new-born pups were removed from a harem and weighed using a digital scale ($\pm 0.2$ kg). Bio-logging instruments were attached to the dorsal pelage using quick-set epoxy while the individuals were physically restrained. After multiple foraging trips, the fur seals were recaptured to recover instruments and reweighed prior to release.

Eighteen fur seals were equipped with an Mk9 time-depth recorder (TDR; Wildlife Computers, Redmond, USA) and a KiwiSat 101 (Sirtrack, Havelock North, New Zealand) PTT that provided at-sea locations. An additional two fur seals were equipped with only a PTT. For animals equipped with a TDR, dive depth and ambient water temperature were sampled at 5-s intervals (resolution and accuracy: 0.05 m $\pm$ 1% of depth reading and 0.05°C $\pm$ 0.01°C). To maximize transmission duration, PTTs were duty-cycled for 4 h on and 4 h off starting at 03:00 GMT. PTTs shut off after a 4-h dry period and restarted when submerged. To facilitate instrument recovery, each female was also equipped with a VHF tag (Advanced Telemetry Systems, Isanti, MN, USA).

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Dive data were processed using Instrument Helper (Wildlife Computers), with a dive defined by a minimum depth of 5 m and duration of 10 s. Dive depth (m), dive duration (s), number of wiggles (vertical excursions >1 m during bottom time), wiggle distance (total vertical distance covered by all wiggles, m), descent rate (m/s), and ascent rate (m/s) were calculated for each dive. Bottom time (s) was calculated as the time between the first and last inflection points at greater than 90% of the maximum dive depth, and percent bottom time was calculated as bottom time divided by dive duration. Vertical distance was the distance covered during descent and ascent plus the sum of wiggle distances in the bottom phase of the dive [32].

To remove erroneous locations, PTT locations were filtered based on a maximum transit rate of 3 m/s (R package 'argosfilter') [22, 69, 87, 88]. Foraging tracks were reconstructed by modeling the filtered PTT data using a continuous-time correlated random walk model [89]. Locations were modeled hourly to determine residence time (hours spent in each grid) and transit rate (km/h) and modeled for each dive for all other behavioral metrics.

### Prey survey

Walleye pollock distribution and abundance were measured during the NOAA Fisheries annual groundfish assessment survey from May to July 2006 [29], and data were downloaded from the Groundfish Assessment Program of the Alaska Fisheries Science Center (NOAA, http://www.afsc.noaa.gov/RACE/groundfish/survey_data/). Details of the survey study design can be found in Lauth and Acuna [29]. Bottom trawls were conducted in the center of 37.04 × 37.04 km (20 × 20 nm) grids on the Bering Sea shelf, with higher density surveying occurring around the Pribilof Islands at the corners of some grids (Fig. 1a). Trawls were conducted for 30 min at a transit speed of 1.54 m/s [29]. Walleye pollock weight [weight catch per unit effort (WTCPUE, kg/ha)] and density [fish per unit effort (NUMCPUE, fish/ha)] were calculated for each trawl. WTCPUE and NUMCPUE values were used as an index of relative abundance for comparison among grid cells (from hereon called 'abundance'). For walleye pollock stock assessment analyses, it is assumed that distributions remained stationary during the duration of the groundfish survey (30 May through 28 July) [56].

Although the groundfish survey focuses on walleye pollock distributed near the sea floor, primarily targeting fish that are generally 4 years and older [29, 90], we believe these data can be used as an index of the juvenile and adult walleye pollock available to fur seals. Walleye pollock are cannibalistic, and it is estimated that approximately 40% of the juvenile mortality results from consumption by older fish [90, 91]. This high level of

mortality occurs when there is spatial overlap between age classes [91, 92]. Bolt et al. [92] showed that over a 20-year period (1985–2006), between 55 and 85% of the bottom trawl survey stations had co-occurrence of young and adult walleye pollock. In 2006, a mid-water survey of walleye pollock, which included age 1 and older fish, also found little spatial segregation between the distributions of young and older walleye pollock (see Figures 1.10 and 1.20 in [90]). Therefore, we believe the bottom trawl survey data can be an indication of the walleye pollock available for northern fur seals on the Bering Sea shelf.

### Relationships between fur seal behavior and prey abundance

Using dive and movement variables previously suggested as metrics for increased prey encounter rate or foraging success in marine predators (for example, [30, 32, 93, 94]), we examined relationships between fur seal behavior and prey abundance in each survey grid utilized by fur seals. Because survey stations were not all the same size (due to the higher density sampling around the Pribilof Islands, Fig. 1a), behavior metrics that were based on counts within a grid cell were adjusted for grid area. For each fur seal, we calculated hours per grid area, average transit rate, dives per hour in grid, dives per grid area, vertical distance per hour in grid, vertical distance per grid area, bottom time per hour in grid, bottom time per grid area, average percent of bottom time during dives, average wiggles per dive, wiggles per hour in grid, wiggles per grid area, total dive time per hour in grid, total dive time per grid area, average descent rate, and average ascent rate (Table 2). Each dive and movement metric was determined at three temporal intervals: over the full reproductive season (July to October, 'full'), within 1 month of the prey survey ('1 month'), and within 2 weeks of the survey ('2 weeks'). Behavior metrics in a grid were assessed for each temporal scale by identifying the actual prey survey date and including only measurements that occurred within the specified time window. This spatial and temporal linking ensured that we were only measuring behavioral metrics that occurred within 2 weeks or 1 month of the prey survey.

We assumed that behavior metrics at the shortest timescale accurately reflected fur seals' response to prey abundance. If significant relationships were maintained as the temporal scales increased, this would suggest that walleye pollock distributions do not change significantly between July (during the survey period) and October. This temporal consistency in prey distributions would be only slightly longer than what is assumed for the stock assessment analyses (May to July) [56]. However, if the relationships break down with increasing temporal disparity, then significant shifts in the pollock distribution

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or fur seal diet may have occurred over the fur seal reproductive season.

We used linear mixed effect models (R package 'lme4') [88] to compare behavior metrics with walleye pollock catch weight (WTCPUE) and abundance (NUMCPUE). To account for variation in behavior among fur seals, animal ID was included as a random factor in all models. All relationships were considered significant at $P < 0.05$ and means are reported ±SE.

## Ethics statement

All northern fur seal research was conducted in accordance with and under the authority of the United States Marine Mammal Protection Act (National Marine Fisheries Service, NMFS Permit 782-1708). At the time of the study, there were no additional requirements by NMFS for institutional review of these procedures. Recently, an NMFS Institutional Animal Care and Use Committee was established for the Alaska Fisheries Science Center and the capture and handling protocols described here were approved by this committee.

## References
1. Sims DW, Quayle VA (1998) Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. Nature 393:460–464
2. Sveegaard S, Nabe-Nielsen J, Staehr K-J, Jensen TF, Mouritsen KN, Teilmann J (2012) Spatial interactions between marine predators and their prey: herring abundance as a driver for the distributions of mackerel and harbor porpoise. Mar Ecol Prog Ser 468:245–253
3. Benoit-Bird KJ, Kuletz K, Heppell S, Jones N, Hoover B (2011) Active acoustic examination of the diving behavior of murres foraging on patchy prey. Mar Ecol Prog Ser 443:217–235
4. Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R et al (2005) From wind to whales: trophic links in a coastal upwelling system. Mar Ecol Prog Ser 289:117–130
5. Hazen EL, Friedlaender AS, Thompson MA, Ware CR, Weinrich MT, Halpin PN et al (2009) Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. Mar Ecol Prog Ser 395:75–89
6. Benoit-Bird KJ, Au WWL (2009) Cooperative prey herding by the pelagic dolphin, *Stenella longirostris*. J Acoust Soc Am 125:125–137
7. Similä T (1997) Sonar observations of killer whales (*Orcinus orca*) feeding on herring schools. Aquat Mamm 23:119–126
8. Nowacek DP, Friedlaender AS, Halpin PN, Hazen EL, Johnston DW, Read AJ et al (2011) Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. PLoS One 6:e19173
9. Vlietstra LS (2005) Spatial associations between seabirds and prey: effects of large-scale prey abundance on small-scale seabird distributions. Mar Ecol Prog Ser 291:275–287
10. Ichii T, Bengston JL, Boveng PL, Takao Y, Jansen JK, Hiruki-Raring LM et al (2007) Provisioning strategies of Antarctic fur seals and chinstrap penguins produce different responses to distribution of common prey and habitat. Mar Ecol Prog Ser 344:277–297
11. Sims DW, Witt MJ, Richardson AJ, Southall EJ, Metcalfe JD (2006) Encounter success of free-ranging marine predator movements across a dynamic prey landscape. Proc R Soc Biol Sci Ser B 273:1195–1201
12. Womble JN, Blundell GM, Gende SM, Horning M, Sigler MF, Csepp DJ (2014) Linking marine predator diving behavior to local prey fields in contrasting habitats in a subarctic glacial fjord. Mar Biol 161:1361–1374
13. Kooyman GL (2004) Genesis and evolution of bio-logging devices: 1963–2002. Mem Natl Inst Polar Res 58:15–22
14. Rutz C, Hays GC (2009) New frontiers in biologging science. Biol Lett 5:289–292
15. Croxall J, Everson G, Kooyman GL, Ricketts C, Davis RW (1985) Fur seal diving behaviour in relation to vertical distribution of krill. J Anim Ecol 54:1–8
16. Garthe S, Montevecchi WA, Davoren GK (2007) Flight destinations and foraging behaviour of northern gannets (*Sula bassana*) preying on small forage fish in a low-Arctic ecosystem. Deep Sea Res II 54:311–320
17. Kai ET, Benhamou S, van der Lingen CD, Coetzee JC, Pichegru L, Ryan PG et al (2013) Are Cape gannets dependent upon fishery waste? A multi-scale analysis using seabird GPS-tracking, hydro-acoustic surveys of pelagic fish and vessel monitoring systems. J Appl Ecol 50:659–670
18. Towell RG, Ream RR, Sterling JT, Williams M, Bengtson JL (2013) Population assessment of northern fur seals on the Pribilof Islands, Alaska, 2012. In: Testa JW (ed) Fur seal investigations 2010–2011. U.S. Dep. Commer., NOAA Tech. Memo, Seattle. NMFS-AFSC-257, p 8–22
19. NMFS (2007) Conservation plan for the Eastern Pacific stock of northern fur seal (*Callorhinus ursinus*). National Marine Fisheries Service, Juneau
20. Gentry R, Holt JR (1986) Attendance behavior of northern fur seals. In: Gentry R, Kooyman GL (eds) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, pp 41–60
21. Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) An analysis of ecological systems. Ohio State University Press, Ohio, pp 154–177
22. Sterling JT (2009) Northern fur seal foraging behaviors, food webs, and interactions with oceanographic features in the eastern Bering Sea. Ph.D. thesis, University of Washington
23. Gentry RL (1998) Behavior and ecology of the northern fur seal. Princeton University Press, Princeton
24. Costa DP (1991) Reproductive and foraging energetics of high-latitude penguins, albatrosses and pinnipeds: implications for life-history patterns. Am Zool 31:111–130
25. Goebel ME, Bengtson JL, DeLong RL, Gentry RL, Loughlin TR (1991) Diving patterns and foraging locations of female northern fur seals. Fish Bull 89:171–179
26. Costa DP, Gentry R (1986) Free-ranging energetics of northern fur seals. In: Gentry R, Kooyman GL (eds) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, pp 79–101
27. Zeppelin TK, Orr AJ (2010) Stable isotope and scat analyses indicate diet and habitat partitioning in northern fur seals *Callorhinus ursinus* across the eastern Pacific. Mar Ecol Prog Ser 409:241–253
28. Zeppelin TK, Ream RR (2006) Foraging habitats based on the diet of female northern fur seals (*Callorhinus ursinus*) on the Pribilof Islands. Alask J Zool (Lond) 270:565–576

Kuhn *et al. Anim Biotelemetry  (2015) 3:26*

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29. Lauth RR, Acuna E (2007) Results of the 2006 Eastern Bering Sea continental shelf bottom trawl survey of groundfish and invertebrate resources. U.S. Dep. Commer., NOAA Tech. Memo NFMS-AFSC-176, Seattle

30. Austin D, Bowen WD, McMillan JI, Iverson SJ (2006) Linking movement, diving, and habitat to foraging success in a large marine predator. Ecology 87:3095–3108

31. Hanuise N, Bost C-A, Huin W, Auber A, Halsey LG, Handrich Y (2010) Measuring foraging activity in a deep-diving bird: comparing wiggles, oesophageal temperatures and beak-opening angles as proxies of feeding. J Exp Biol 213:3874–3880

32. Skinner JP, Mitani Y, Burkanov VN, Andrews RD (2014) Proxies of food intake and energy expenditure for estimating the time-energy budgets of lactating northern fur seals *Callorhinus ursinus*. J Exp Mar Biol Ecol 461:107–115

33. Georges JY, Bonadonna F, Guinet C (2000) Foraging habitat and diving activity of lactating subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. Mar Ecol Prog Ser 196:291–304

34. Hamer KC, Humphreys EM, Magalhães MC, Garthe S, Hennicke J, Peters G et al (2009) Fine-scale foraging behaviour of a medium-ranging marine predator. J Anim Ecol 78:880–889

35. Sato K, Daunt F, Watanuki Y, Takahashi A, Wanless S (2008) A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. J Exp Biol 211:58–65

36. Sparling CE, Georges JY, Gallon SL, Fedak M, Thompson D (2007) How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: a test of a simple model. Anim Behav 74:207–218

37. Bost CA, Handrich Y, Butler PJ, Fahlman A, Halsey LG, Woakes AJ et al (2007) Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. Deep Sea Res II 54:248–255

38. Iwata T, Sakamoto KQ, Takahashi A, Edwards EW, Staniland IJ, Trathan PN et al (2011) Using a mandible accelerometer to study fine-scale foraging behavior of free-ranging Antarctic fur seals. Mar Mamm Sci 28:345–357

39. Fuiman LA, Madden KM, Williams TM, Davis RW (2007) Structure of foraging dives by Weddell seals at an offshore isolated hole in the Antarctic fast-ice environment. Deep Sea Res II 54:270–289

40. Lesage V, Hammill MO, Kovacs KM (1999) Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. Can J Zool 77:74–87

41. Viviant M, Monestiez P, Guinet C (2014) Can we predict foraging success in a marine predator from dive patterns only? Validation with prey capture attempt data. PLoS One 9:e88503

42. Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. Ecology 84:282–288

43. Kareiva P, Odell G (1987) Swarms of predators exhibit "preytaxis" if individual predators use area-restricted search. Am Nat 130:233–270

44. Bailey H, Thompson P (2006) Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. J Anim Ecol 75:456–465

45. Bailleul F, Pinaud D, Hindell M, Charrassin JB, Guinet C (2008) Assessment of scale-dependent foraging behaviour in southern elephant seals incorporating the vertical dimension: a development of the first passage time method. J Anim Ecol 77:948–957

46. Trathan PN, Bishop C, Maclean G, Brown P, Fleming A, Collins MA (2008) Linear tracks and restricted temperature ranges characterise penguin foraging pathways. Mar Ecol Prog Ser 370:285–294

47. Kuhn CE, Tremblay Y, Ream RR, Gelatt TS (2010) Coupling GPS tracking with dive behavior to examine the relationship between foraging strategy and fine-scale movements in northern fur seals (*Callorhinus ursinus*). Endanger Species Res 12:125–139

48. Nordstrom CA, Battaile BC, Cotté C, Trites AW (2012) Foraging habitats of lactating northern fur seals are structured by thermocline depths and submesoscale fronts in the eastern Bering Sea. Deep Sea Res II. doi:10.1016/j.dsr2.2012.07.010

49. Boyd I (1999) Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. Behav Ecol 10:198–208

50. Johnson DJ, Hooten MB, Kuhn CE (2013) Estimating animal resource selection from telemetry data using point process models. J Anim Ecol 82:1155–1164

51. Call KA, Ream RR, Johnson D, Sterling JT, Towell RG (2008) Foraging route tactics and site fidelity of adult female northern fur seal (*Callorhinus ursinus*) around the Pribilof Islands. Deep Sea Res II 55:1883–1896

52. Hollowed AB, Barbeaux SJ, Cokelet ED, Farley E, Kotwicki S, Ressler PH et al (2012) Effects of climate variation on pelagic ocean habitats and their role in structuring forage fish distributions in the Bering Sea. Deep Sea Res II 65:230–250

53. Kotwicki S, Buckley TW, Honkalehto T, Walters G (2005) Variation in the distribution of walleye pollock (*Theragra chalcogramma*) with temperature and implications for seasonal migration. Fish Bull 103:574–587

54. Swartzman G, Stuetzle W, Kulman K, Powojowski M (1994) Relating the distribution of pollock schools in the Bering Sea to environmental factors. ICES J Mar Sci 51:481–492

55. Bacheler NM, Ciannelli L, Bailey KM, Duffy-Anderson JT (2010) Spatial and temporal patterns of walleye pollock (*Theragra chalcogramma*) spawning in the eastern Bering Sea inferred from egg and larval distributions. Fish Oceanogr 19:107–120

56. Smith GB, Bakkala RG (1982) Demersal fish resources of the eastern Bering Sea: Spring 1976. NOAA Technical Report NMFS SSRF-754, Seattle

57. Kachel NB, Hunt GL Jr, Salo SA, Schumacher JD, Stabeno PJ, Whitledge TE (2002) Characteristics and variability of the inner front of the southeastern Bering Sea. Deep Sea Res II 49:5889–5909

58. Swartzman G, Silverman E, Williamson N (1995) Relating trends in walleye pollock (*Theragra chalcogramma*) abundance in the Bering Sea to environmental factors. Can J Fish Aquat Sci 52:369–381

59. Stabeno PJ, Kachel N, Mordy C, Righi D, Salo S (2008) An examination of the physical variability around the Pribilof Islands in 2004. Deep Sea Res II 55:1701–1716

60. Stabeno PJ, Bond NA, Kachel NB, Salo SA, Schumacher JD (2001) On the temporal variability of the physical environment over the south-eastern Bering Sea. Fish Oceanogr 10:81–98

61. Stabeno PJ, Bond NA, Salo SA (2007) On the recent warming of the southeastern Bering Sea shelf. Deep Sea Res II 54:2599–2618

62. Wyllie-Echeverria T, Wooster WS (1998) Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fish Oceanogr 72:159–170

63. Bakkala RG, Wespestad VG, Low L-L (1987) Historical trends in abundance and current condition of walleye pollock in the eastern Bering Sea. Fish Res 5:199–215

64. Coachman LK (1986) Circulation, water masses, and fluxes on the southeastern Bering Sea Shelf. Cont Shelf Res 5:23–108

65. Kuhn CE (2011) The influence of subsurface thermal structure on the diving behavior of northern fur seals (*Callorhinus ursinus*) during the breeding season. Mar Biol 158:649–663

66. Ropert-Coudert Y, Kato A, Chiaradia A (2009) Impact of small-scale environmental perturbations on local marine food resources: a case study of a predator, the little penguin. Proc R Soc Biol Sci Ser B 276:4105–4109

67. Takahashi A, Matsumoto K, Hunt GL Jr, Shultz MT, Kitaysky AS, Sato K et al (2008) Thick-billed murres use different diving behaviors in mixed and stratified waters. Deep Sea Res II 55:1837–1845

68. Stabeno PJ, Hunt GL Jr (2002) Overview of the inner front and southeast Bering Sea carrying capacity programs. Deep Sea Res II 49:6157–6168

69. Robson BW, Goebel ME, Baker JD, Ream RR, Loughlin TR, Francis RC et al (2004) Separation of foraging habitat among breeding sites of a colonial marine predator, the northern fur seal (*Callorhinus ursinus*). Can J Zool 82:20–29

70. Bonadonna F, Lea MA, Dehorter O, Guinet C (2001) Foraging ground fidelity and route-choice tactics of a marine predator: the Antarctic fur seal *Arctocephalus gazella*. Mar Ecol Prog Ser 223:287–297

71. Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep Sea Res II 54:211–223

72. Warren JD, Santora JA, Demer DA (2009) Submesoscale distribution of Antarctic krill and its avian and pinniped predators before and after a gale. Mar Biol 156:479–491

73. Sinclair E, Loughlin T (1994) Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. Fish Bull 92:144–156

74. Fauchald P, Erikstad KE, Ksarsfjord H (2000) Scale-dependent predator–prey interactions: the hierarchical spatial distribution of seabirds and prey. Ecology 81:773–783

Kuhn *et al. Anim Biotelemetry* (2015) 3:26

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75. Fritz H, Said S, Weimerskirch H (2003) Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. Proc R Soc Biol Sci Ser B 270:1143–1148

76. Benoit-Bird KJ, Battaile BC, Nordstrom CA, Trites AW (2013) Foraging behavior of northern fur seals closely matches the hierarchical patch scales of prey. Mar Ecol Prog Ser 479:283–302

77. Helle J, Farley E, Murphy J, Feldmann A, Cieciel K, Moss J et al (2015) The Bering-Aleutian Salmon International Survey, (BASIS). Alaska Fish Sci Cent Q Rep, Seattle, pp 1–5. http://www.afsc.noaa.gov/Quarterly/jfm2007/jfm07feat.pdf. Accessed 9 Apr 2015

78. Honkalehto T, Ressler PH, Towler RH, Wilson CD (2011) Using acoustic data from fishing vessels to estimate walleye pollock (*Theragra chalcogramma*) abundance in the eastern Bering Sea. Can J Fish Aquat Sci 68:1231–1242

79. Parker-Stetter SL, Horne JK, Farley EV, Barbee DH, Andrews AG III, Eisner LB et al (2013) Summer distributions of forage fish in the eastern Bering Sea. Deep Sea Res II 94:211–230

80. Wespestad VG, Fritz LW, Ingraham WJ, Megrey BA (2000) On relationships between cannibalism, climate variability, physical transport, and recruitment success of Bering Sea walleye pollock (*Theragra chalcogramma*). ICES J Mar Sci 57:272–278

81. Livingston PA (1993) Importance of predation by groundfish, marine mammals and birds on walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasi* in the eastern Bearing Sea. Mar Ecol Prog Ser 102:205–215

82. Sinclair EH, Vlietstra LS, Johnson DS, Zeppelin TK, Byrd GV, Springer AM et al (2008) Patterns in prey use among fur seals and seabirds in the Pribilof Islands. Deep Sea Res II 55:1897–1918

83. Coyle KO, Eisner LB, Mueter FJ, Pinchuk AI, Janout MA, Cieciel KD et al (2011) Climate change in the southeastern Bering Sea: impacts on pollock stocks and implications for the oscillating control hypothesis. Fish Oceanogr 20:139–156

84. Stabeno PJ, Kachel NB, Moore SE, Napp JM, Sigler M, Yamaguchi A et al (2012) Comparison of warm and cold years on the southeastern Bering Sea shelf and some implications for the ecosystem. Deep Sea Res II 65:31–45

85. Lee HC, Delworth TL, Rosati A, Zhang R, Anderson WG, Zeng F et al (2013) Impact of climate warming on upper layer of the Bering Sea. Clim Dyn 40:327–340

86. Wang M, Overland JE, Stabeno P (2012) Future climate of the Bering and Chukchi Seas projected by global climate models. Deep Sea Res II 65:46–57

87. Freitas C, Lydersen C, Fedak MA, Kovacs KM (2008) A simple new algorithm to filter marine mammal Argos locations. Mar Mamm Sci 24:315–325

88. R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

89. Johnson DS, London JM, Lea MA, Durban JW (2008) Continuous-time correlated random walk model for animal telemetry data. Ecology 89:1208–1215

90. Ianelli JN, Barbeaux S, Honkalehto T, Kotwicki S, Aydin K, Williamson N (2006) Assessment of Alaska pollock stock in the Eastern Bearing Sea. In: Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea and Aleutian Islands region. North Pacific Fishery Management Council, Anchorage, pp 35–138

91. Mueter FJ, Ladd C, Palmer MC, Norcross BL (2006) Bottom-up and top-down controls of walleye pollock (*Theragra chalcogramma*) on the Eastern Bering Sea shelf. Prog Oceanogr 68:152–183

92. Boldt JL, Buckley TW, Rooper CN, Aydin K (2012) Factors influencing cannibalism and abundance of walleye pollock (*Theragra chalcogramma*) on the eastern Bering Sea shelf, 1982–2006. Fish Bull 110:293–306

93. Miller PJO, Johnson MP, Tyack PL (2004) Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. Proc R Soc Biol Sci Ser B 271:2239–2247

94. Simeone A, Wilson RP (2003) In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? Mar Biol 143:825–831