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ORIGINAL PAPER

Linking marine predator diving behavior to local prey fields in contrasting habitats in a subarctic glacial fjord

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Abstract Foraging theory predicts that animals will adjust their foraging behavior in order to maximize net energy intake and that trade-offs may exist that can influence their behavior. Although substantial advances have been made with respect to the foraging ecology of large marine predators, there is still a limited understanding of how predators respond to temporal and spatial variability in prey resources, primarily due to a lack of empirical studies that quantify foraging and diving behavior concurrently with characteristics of prey fields. Such information is important because changes in prey availability can influence the foraging success and ultimately fitness of marine predators. We assessed the diving behavior of juvenile female harbor seals (*Phoca vitulina richardii*) and prey fields near glacial ice and terrestrial haulout sites in Glacier Bay (58°40′N, −136°05′W), Alaska. Harbor seals captured at glacial ice sites dived deeper, had longer dive durations, lower percent bottom time, and generally traveled further to forage. The increased diving effort for seals from the glacial ice site corresponded to lower prey densities and prey at deeper depths at the glacial ice site. In contrast, seals captured at terrestrial sites dived shallower, had shorter dive durations, higher percent bottom time, and traveled shorter distances to access foraging areas with much higher prey densities at shallower depths. The increased diving effort for seals from glacial ice sites suggests that the lower relative availability of prey may be offset by other factors, such as the stability of the glacial ice as a resting platform and as a refuge from predation. We provide evidence of differences in prey accessibility for seals associated with glacial ice and terrestrial habitats and suggest that seals may balance trade-offs between the costs and benefits of using these habitats.

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Introduction

Foraging theory predicts that animals will adjust their foraging behavior in order to maximize net energy intake and that trade-offs may exist that can influence their behavior (Stephens and Krebs 1986). For large marine predators, such as cetaceans and pinnipeds, it is extremely difficult to directly observe their foraging behavior which takes place beneath the surface of the oceans, often at great depths, and in remote areas (Hooker et al. 2007; Hindell 2008; Gallon et al. 2013). Although quantifying the foraging behavior of marine predators may be challenging, an understanding of how marine predators adjust their behavior in relation to changes in prey availability is important as such changes may influence energetic intake which has implications for foraging success and ultimately fitness.

To date, only few studies have directly monitored the foraging behavior of pinnipeds and their prey fields in the wild (Davis et al. 1999; Bowen et al. 2002; Hooker et al. 2002; Ichii et al. 2007; Parrish et al. 2005; Naito et al. 2013), primarily due to the challenges associated with simultaneously quantifying marine predator behavior and prey availability over large spatial scales. However, evidence suggests that changes in the depth of prey may result in behavioral changes for pinnipeds that include diving deeper, increased dive durations, or increased time spent diving (Härkönen 1987; Feldkamp et al. 1989; Boyd et al. 1994; Tollit et al. 1998; Lea et al. 2006). Diving deeper may reflect increased search effort for deeper prey, with more time spent in transit and less time spent along the bottom portion of the dive, which is where foraging often takes place (Lesage et al. 1999; Austin et al. 2006). Reduced prey accessibility may also result in traveling greater distances to forage (Croxall et al. 1985; Boyd et al. 1991; Boyd 1999; Horning and Trillmich 1997), which may result in increased energetic costs that could have fitness-level consequences (Bowen et al. 2002; Costa 2008).

Precipitous declines in several pinniped populations in the North Pacific Ocean (Pitcher 1990; Merrick et al. 1987; Towell et al. 2006; Small et al. 2008) have highlighted the need for a better understanding of the functional relationships between pinnipeds and their prey, particularly the behavioral and demographic responses of pinnipeds to changes in prey availability. However, only a few studies have directly investigated linkages between prey fields and the foraging and diving behavior of individual pinnipeds in Alaska (e.g., Sigler et al. 2009; Benoit-Bird et al. 2013).

Harbor seals (*Phoca vitulina*) are the most widely distributed pinniped in the northern hemisphere and occupy a diverse array of haulout habitats along the North Pacific Rim, including small islands, beaches, and glacial ice emanating from tidewater glaciers. Hypothesized reasons for the use of different haulout habitats by harbor seals include proximity to prey resources, reduced risk of predation, local bathymetry, and reduced wave exposure (Brown and Mate 1983; Härkönen 1987; Thompson et al. 1989; Nordstrom 2002; Montgomery et al. 2007; Grigg et al. 2009, 2012; Sharples et al. 2012). While some of the largest aggregations of harbor seals in Alaska are found seasonally using glacial ice as a resting substrate in tidewater glacial fjords (Calambokidis et al. 1987; Mathews and Pendleton 2006; Womble et al. 2010; Hoover-Miller et al. 2011), previous studies of harbor seal diving and foraging behavior in Alaska have focused only on seals that use terrestrial haulout sites (Frost et al. 2001; Lowry et al. 2001; Small et al. 2005; Hastings et al. 2004). Thus, our understanding of how harbor seals may adjust their foraging and diving behavior in different habitats is extremely limited.

Here, we consider the implications of the use of glacial ice and terrestrial habitats on the diving and foraging behavior of juvenile female harbor seals in Glacier Bay, a subarctic glacial fjord in Alaska. Glacier Bay provides a unique opportunity for a comparative approach because harbor seals utilize two distinct habitats, glacial ice and terrestrial sites, as resting platforms within the same marine ecosystem. While these habitats are in relatively close proximity to one another, the marine waters in and adjacent to these habitats contrast sharply in their physical and biological characteristics which likely plays a role in structuring prey communities and prey accessibility for harbor seals. At the glacial ice site in Johns Hopkins Inlet, seafloor depths range up to 370 m with water masses characterized by large quantities of freshwater runoff, colder water temperatures, a high degree of stratification, and lower productivity. In contrast, the marine waters adjacent to the primary terrestrial sites in the Beardslee Islands are characterized by shallower sea floor depths up to 140 m, warmer water temperatures, and strong mixing (Etherington et al. 2007).

Given the distinct physical and biological characteristics associated with the marine waters in and adjacent to glacial ice and terrestrial habitats in Glacier Bay, our primary working hypothesis was that prey availability, including depth and density of prey, would differ in these contrasting habitats and would influence the diving and foraging behavior of harbor seals. Harbor seals are suitable models for assessing their diving behavior relative to indices of prey availability in glacial ice and terrestrial habitats in Glacier Bay because during the breeding season, harbor seals display a high degree of fidelity to glacial ice and terrestrial habitats (Blundell et al. 2011) and exhibit relatively restricted movements (Womble and Gende 2013). Our specific objectives were to assess (1) the diving behavior of juvenile female harbor seals and (2) indices of local prey accessibility (density and depth) near harbor seal haulout sites in contrasting glacial ice and terrestrial habitats in Glacier Bay, Alaska. Our primary question was to determine whether prey availability differed in glacial ice and terrestrial habitats and how differences in prey availability in contrasting habitats influenced harbor seal diving and foraging behavior.

Materials and methods

Study area

Glacier Bay (58°40′N, −136°05′W) is a subarctic glacial fjord in southeastern Alaska that constitutes a part of Glacier Bay National Park (Fig. 1). Distinct oceanographic and circulation patterns (Etherington et al. 2007; Hill et al. 2009), as a result of rapid and repeated advances and retreats of tidewater glaciers over the past 225 years (Field
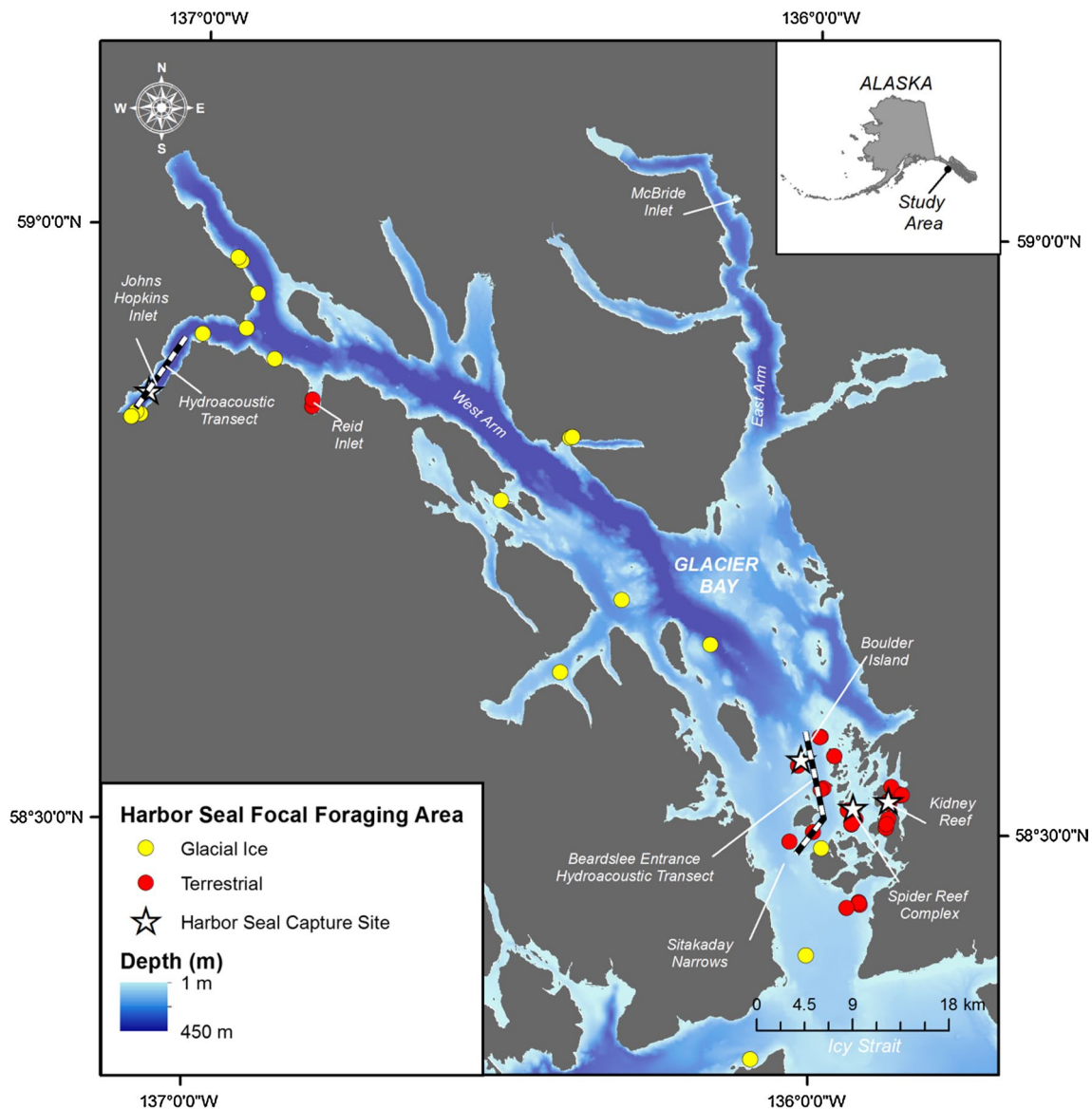
Fig. 1 Study area in Glacier Bay, Alaska, with juvenile female harbor seal capture locations (*white stars*). Focal foraging areas (FFA) of harbor seals captured at glacial ice are indicated by *yellow circles*, and FFAs for harbor seals captured at terrestrial sites are indicated by *red circles*. Hydroacoustic surveys in the Beardslee Entrance and Johns Hopkins Inlet are indicated by *black* and *white lines*

1947; Hall et al. 1995), have resulted in high levels of primary productivity (Etherington et al. 2007) and large concentrations of zooplankton and forage fish (Robards et al. 2003; Arimitsu et al. 2008).

During the harbor seal breeding (May–June) and molting (August) periods, ~66 % of seals in Glacier Bay inhabit the primary glacial ice site in Johns Hopkins Inlet and ~22 % of seals are found in and adjacent to the Beardslee Island archipelago (Fig. 1). Harbor seals are also found at smaller terrestrial sites that are scattered throughout Glacier Bay and at 2 small glacial ice sites in McBride Inlet (East Arm) and Tarr Inlet (West Arm) (Mathews and Pendleton 2006; Womble et al. 2010) (Fig. 1).

Harbor seal captures and instrument deployment

Juvenile female harbor seals ($N = 12$ seals) were captured between mid-April and early May from 2004 to 2007 at both terrestrial ($N = 6$ seals) and glacial ice ($N = 6$ seals) sites (Table 1). Seals were captured at terrestrial sites in lower Glacier Bay (Fig. 1) using a multifilament seine net (e.g., Frost et al. 2001; Lowry et al. 2001). At the primary glacial ice site in Johns Hopkins Inlet (Fig. 1), seals were captured using monofilament gillnets deployed from inflatable skiffs (Blundell et al. 2011). Seals were placed in hoop nets and transferred to a larger vessel where they were weighed (to the nearest 0.1 kg) and measured (to the

Table 1 Juvenile female harbor seals instrumented with time-depth recorders and VHF tags in terrestrial ($n = 6$) and glacial ice habitats ($n = 6$) Glacier Bay, Alaska

Animal ID#	Mass (kg)	Capture date	Capture site	Capture habitat
PV04GB06	45.1	4/14/2004	Kidney Reef	Terrestrial
PV04GB11	33.2	4/16/2004	Boulder Island	Terrestrial
PV06GB25	32.8	5/1/2006	Kidney Reef	Terrestrial
PV07GB03	32.7	4/21/2007	Spider Reef Complex	Terrestrial
PV07GB04	31.4	4/21/2007	Spider Reef Complex	Terrestrial
PV07GB06	30.2	4/21/2007	Spider Reef Complex	Terrestrial
PV05GB24	41.0	4/27/2005	Johns Hopkins Inlet	Glacial Ice
PV05GB25	39.0	4/27/2005	Johns Hopkins Inlet	Glacial Ice
PV05GB29	35.0	4/27/2005	Johns Hopkins Inlet	Glacial Ice
PV06GB05	29.8	4/26/2006	Johns Hopkins Inlet	Glacial Ice
PV06GB11	34.9	4/27/2006	Johns Hopkins Inlet	Glacial Ice
PV06GB18	47.3	4/28/2006	Johns Hopkins Inlet	Glacial Ice

nearest cm). Seals were physically restrained and sedated with 0.25 mg/kg of diazepam administered intravenously prior to the application of telemetry devices. The age of seals was determined morphometrically; for this study seals >3 years old were classified as adults, while seals <3 years of age were classified as juveniles (Blundell and Pendleton 2008).

Diving data

The diving behavior of harbor seals was recorded using electronic MK-9 time-depth recorders (TDRs) (Wildlife Computers, Redmond, Washington, USA) which measure pressure to calculate depth to a resolution of 0.5 m (±1 %). TDRs were attached to the pelage on the dorsum of the seal, lateral to the lumbar vertebrae, using 5-min epoxy and were programmed to record depth every 2 s and temperature, light levels, and conductivity every 20 s. TDRs were embedded in syntactic foam to make the package buoyant after it detached from the seal during the annual molting period. An MM230B VHF transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA) was also included in the flotation package to allow for VHF-tracking and retrieval of the shed TDRs. Flotation packages (~480 g) had slight positive buoyancy and a sloped leading edge to reduce drag (Blundell et al. 2011). These relatively small (~1 % of body weight), slightly buoyant tags are not likely to negatively affect harbor seals as experimental manipulation of buoyancy simulating 12–26 % subcutaneous fat did not alter diving metabolism (Fahlman et al. 2008). Tags were also considerably less than the maximum 5 % of body weight recommended for telemetry studies (Cuthill 1991).

TDRs were shed during the annual molt and were retrieved using boats, fixed-winged aircraft (float-equipped Cessna 206), and kayaks. After instrument retrieval, TDR data were downloaded and processed using software supplied by the manufacturer (Wildlife Computers, Instrument Helper version 2.0). The data were zero-offset corrected to account for any drift in the zero reading of the depth sensor. The Dive Analysis Toolkit within Instrument Helper was used to identify and classify individual dives from the zero-offset corrected data. Only dives ≥4 m were analyzed to avoid including instrument noise in the data (e.g., Bowen et al. 1999; Lesage et al. 1999).

Focal foraging areas

Vessel-based behavioral observations were conducted to identify focal foraging areas for a subset of the instrumented seals and to provide an index of where instrumented harbor seals focused their foraging effort. Focal foraging areas were determined by conducting real-time vessel-based VHF-tracking (e.g., Lea and Wilson 2006) of individual seals from the R/V *Capelin* (8.5 m) and a Boston Whaler (6.7 m). Vessel surveys ($N = 87$ survey days) were conducted every other week for 4- to 5-day periods in May and June from 2004 to 2007. A survey day ranged from 6 to 12 h between 06:00 and 21:30 h ($N = 687$ total survey hours), primarily during daylight hours to facilitate safe navigation. During each vessel survey, VHF radio frequencies of tagged seals were scanned continuously while transiting within the detection range of all known haulout sites used by harbor seals in lower, middle, and upper Glacier Bay. After a VHF signal was detected, 2 observers visually located the seal on the surface of the water using hand-held binoculars (Swarovski 10 × 42 and Zeiss 20 × 60); radio tags were individually color coded to confirm a match between telemetry frequency and the seal being observed. Once the VHF-tagged seal was located and confirmed by both observers, surface positions (latitude, longitude) of seals were recorded using a global positioning system (Garmin GPS Map 76) on the vessel. An area was designated as a focal foraging area if a seal dove repeatedly in the same general area for >1 h. The distance between focal foraging areas and the site where harbor seals were captured was measured using ArcMap 9.3 (ESRI, Redlands, CA, USA).

Prey availability

Hydroacoustic surveys ($n = 13$) were conducted to provide an index of local prey availability near primary haulout sites in (1) the Beardslee Entrance, adjacent to terrestrial sites (Spider Reef, Boulder Island, Flapjack Island) used by seals in lower Glacier Bay and in (2) Johns Hopkins

Inlet, the primary glacial ice site used by seals (Fig. 1). Hydro acoustic surveys were conducted in conjunction with vessel-based tracking of tagged harbor seals and were conducted every other week from May to mid-July during daylight hours from 06:00 and 21:00 h. Transects in the Beardslee Entrance ($N = 7$ surveys) were conducted from the northwest side of Young Island to the northern end of Flapjack Island and covered an average of 30 km/survey. Transects in Johns Hopkins Inlet ($N = 6$ surveys) were conducted from Jaw Point to approximately 1 km from the terminus of Johns Hopkins glacier and covered an average of 25 km/survey. Hydroacoustic transects were oriented perpendicular to shore and were spaced 0.6–0.8 km apart.

During each hydroacoustic survey, acoustic backscatter data were collected using a portable 38-kHz split-beam Simrad EK60 echo-integration system with a 12° beam angle and stored on disk. The echo-sounder transducer was towed in a hydrodynamic fin alongside the R/V *Capelin* at 9 km/h^{-1}. Location data from a GPS were collected simultaneously. Hydroacoustic data were the sum of the returning echoes of fish below the boat. Hydroacoustic data were classified by 0.183-km length intervals and 10-m depth intervals and corrected for instrument calibration using the echo-integration software Sonar Data Echoview (Sigler et al. 2004).

Statistical analysis

Diving behavior

Non-metric multidimensional scaling (NMS), a multivariate ordination technique (Kruskal 1964; Mather 1976), was used to assess the predominant gradients in overall diving behavior (e.g., Lesage et al. 1999; Lea et al. 2002) of harbor seals captured in glacial and terrestrial sites. NMS was used to reduce the dimensions of the multivariate dive data and is well suited for data that are on multiple scales and are not normally distributed (McCune and Grace 2002). Six parameters were derived from the diving record of each seal including (1) average dive depth (m), (2) dive duration (s), (3) dive rate (h^{-1}), (4) percent time diving (%), (5) wiggle count (number of vertical movements within the bottom portion of the dive), (6) diving efficiency (bottom time/(dive duration + surface duration) (Ydenberg and Clark 1989). The primary data matrix (12 seals or sample units × 6 dive parameters) consisted of the grand mean of each of the six dive parameters for each seal. The secondary data matrix (12 × 2 variables) included categorical variables (capture year, capture habitat) associated with each seal. All dive parameters were transformed by normalizing each parameter by the maxima (McCune and Grace 2002).

Non-metric multidimensional scaling was conducted using Sørenson's distance (Bray and Curtis 1957), in slow

and thorough autopilot mode using random starting configurations in PC-ORD v. 6.0. To evaluate whether NMS extracted stronger axes than expected by chance, a Monte Carlo randomization test was performed which compared the final stress from the original data with final stress from multiple runs ($N = 250$) of randomized data (McCune and Mefford 2011). A random starting configuration was used for each run, and dimensionality was selected by comparing the final stress values among the best solutions and by visually inspecting a scree plot of real data in relation to randomized data (McCune and Grace 2002).

Differences in the overall diving behavior of seals captured at terrestrial and glacial ice sites were assessed using multiresponse permutation procedures (MRPP) (Mielke and Berry 2001) based on a rank-transformed Sørenson distance matrix (McCune and Mefford 2011). MRPP provided a chance-corrected within-group agreement (A) that described within-group homogeneity, compared to the random expectation. All multivariate statistical analyses were conducted using PC-ORD v. 6.0 (McCune and Mefford 2011).

We used Mann–Whitney U tests (Hollander and Wolfe 1973) to evaluate differences in individual diving parameters of harbor seals from glacial ice and terrestrial sites. Mann–Whitney U tests were implemented in R using the {coin} package (Hothorn et al. 2008). Results were considered significant at $P < 0.05$.

Trip durations

Trip durations of harbor seals were estimated by dividing the observed time into 'dry' and 'wet' intervals, based on data from the wet-dry sensor on the TDR. A time interval was defined as 'dry' if the wet-dry sensor measurement of conductivity was continuously ≥248 and 'wet' if conductivity was <248. This value was determined by examining graphs of TDR conductivity and depth measurements (corrected for surface error) to judge at what level seals appeared to be truly hauled out. For analysis of 'trips,' we used all wet intervals >30 min duration (Blundell et al. 2011).

Prey availability

Hydroacoustic backscatter data were expressed as the nautical area scattering coefficient (NASC; m^2/nmi), a relative measure of prey density. The NASC values were integrated over 0.183-km length intervals and 10-m depth bins. An average prey index was calculated for each hydroacoustic survey (Fig. 1) which accounted for both the density and the depth of the prey as both attributes are important to consider in the context of harbor seal diving behavior. The average prey index was calculated as:

$$\text{Average Prey Index} = \frac{1}{n} \sum_{i=1}^{n} \sum_{j=1}^{m_i} \left(\frac{\text{NASC}}{d} \right)$$

where n is the number of 0.183-km long samples in the survey and m_i is the number of 10-m depth bins in the ith sample (which varies with water depth). Each NASC value is divided by the lower bound of the depth bin (d). The average prey index accounts for the density and depth of prey and implies that accessing deeper prey has a higher cost (e.g., Härkönen 1987).

Results

Diving behavior

The average deployment period of TDRs on juvenile female harbor seals was 60.5 ± 9.9 days for a total of 726 seals days from May through June 2004–2007. The mass of juvenile harbor seals captured at the glacial ice site ($X \pm SD = 37.8 \pm 6.0$ kg, $n = 6$) was not significantly different than the mass of harbor seals captured at the terrestrial sites ($X \pm SD = 34.2 \pm 5.4$ kg, $n = 6$) (Mann–Whitney U test, $U = 10$, $N_1 = 6$, $N_2 = 6$, $P = 0.24$). Curvilinear length did not differ between seals captured at glacial ice ($X \pm SD = 118.1 \pm 8.4$ cm, $n = 6$) and terrestrial sites ($X \pm SD = 119.0 \pm 8.4$ cm, $n = 6$) (Mann–Whitney U test, $U = 17$, $N_1 = 6$, $N_2 = 6$, $P = 0.94$).

Distinct separation in the diving behavior of seals from glacial ice and terrestrial habitats was reflected in the NMS ordination plot (Fig. 2). The stable, three-dimensional solution (NMS, final stress = 2.4, final instability <0.00001, iterations = 61) explained 96.9 % of the variation with three major gradients capturing most of the variance in diving behavior. Dominant gradients along Axis 1 were strongly correlated with dive depth and dive duration. Axis 2 was correlated with percent time diving, and Axis 3 was correlated with dive efficiency. Multiresponse permutation procedures (MRPP) confirmed differences in diving behavior between glacial ice and terrestrial habitats (MRPP, $A = 0.15$, $P = 0.009$) but not years (MRPP, $A = 0.11$, $P = 0.13$).

Several diving parameters differed for seals captured in glacial ice and terrestrial habitats. Average dive depths for seals captured at glacial ice ($X \pm SE = 38.0 \pm 5.5$ m, $n = 6$) were deeper than for seals captured at terrestrial sites ($X \pm SE = 26.0 \pm 2.0$ m, $n = 6$) (Mann–Whitney U test, $U = 31$, $N_1 = 6$, $N_2 = 6$, $P = 0.04$) (Table 2). Maximum dive depths were also substantially deeper for seals captured at glacial ice sites ($X \pm SE = 267.3 \pm 31.3$ m, $n = 6$) than for seals from terrestrial sites ($X \pm SE = 132.0 \pm 19.1$ m, $n = 6$) (Mann–Whitney U test, $U = 33$, $N_1 = 6$, $N_2 = 6$, $P = 0.02$) (Table 2). Six harbor seals (5 from glacial ice site and 1 from terrestrial site) dived to depths exceeding 200 m and 3 seals from the glacial ice site dived to depths exceeding 300 m. The maximum dive depth of any seal was 326 m (dive duration = 17.7 min) and was attained by a
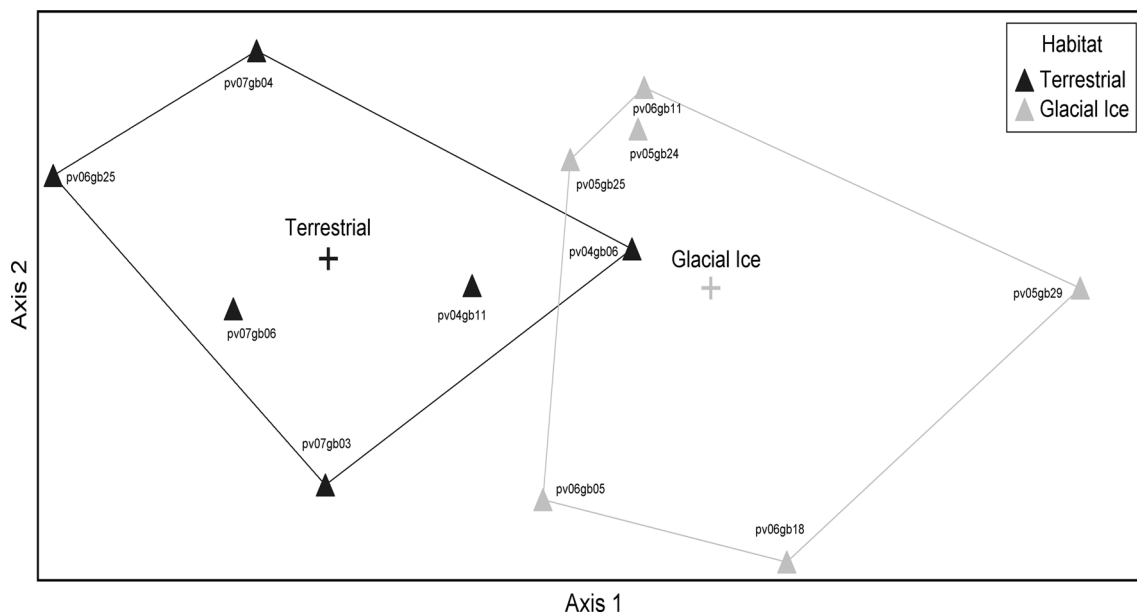
Fig. 2 Ordination of non-metric multidimensional scaling (NMS) of diving behavior of juvenile female harbor seals captured in terrestrial (*black triangles*) ($n = 6$) and glacial ice (*gray triangles*) ($n = 6$) habitats in Glacier Bay, Alaska. Dominant gradients along *Axis 1* were correlated with dive depth and dive duration. *Axis 2* was correlated with percent time diving. Group centroids for each habitat group are shown by *plus* (+) *symbols*

Table 2 Diving parameters and trip durations for juvenile female harbor seals from terrestrial ($n = 6$) and glacial ice ($n = 6$) habitats in Glacier Bay, Alaska

| Diving parameter	Terrestrial	Glacial ice	P value
Average dive depth (m)	26.0 (2.0)	38.0 (5.5)	0.04*
Maximum dive depth (m)	132.0 (19.1)	267.3 (31.3)	0.02*
Dives per hour (h^{-1})	10.7 (0.6)	9.4 (0.6)	0.24
Time spent diving (%)	0.4 (0.0)	0.5 (0.0)	0.008*
Dive intensity	0.2 (0.0)	0.2 (0.0)	0.04*
Dive duration (min)	2.4 (0.1)	2.9 (0.2)	0.04*
Surface time (min)	2.6 (0.2)	2.5 (0.3)	0.937
Bottom time (min)	1.4 (0.0)	1.5 (0.1)	0.70
Wiggles	2.1 (0.2)	2.7 (0.1)	0.064
Descent speed (m/s)	1.0 (0.0)	0.9 (0.0)	0.132
Ascent speed (m/s)	0.9 (0.0)	0.9 (0.0)	0.169
Diving efficiency	0.4 (0.01)	0.4 (0.0)	0.009*
Vertical distance traveled per day (km^{-1})	11.1 (0.5)	15.5 (1.6)	0.04*
Percent bottom time (%)	0.6 (0.01)	0.5 (0.0)	0.002*
Average trip duration (h)	10.9 (2.4)	14.0 (3.4)	0.26
Maximum trip duration (h)	94.6 (54.5)	192.0 (63.6)	0.05*

Values are mean and standard error (SE) of the mean

* Indicates significance at $P = 0.05$ based on Mann–Whitney U tests

juvenile female (seal# PV05GB29) captured at the glacial ice site.

Dive durations of seals captured at the glacial ice site (X ± SE = 2.9 ± 0.2 min, $n = 6$) were greater than for seals captured at terrestrial sites (X ± SE = 2.4 ± 0.1 min, $n = 6$) (Mann–Whitney U test, $U = 31$, $N_1 = 6$, $N_2 = 6$, $P = 0.04$). The percent of time spent along the bottom portion of the dive was less for seals captured at the glacial ice site than for seals captured at terrestrial sites (Mann–Whitney U test, $U = 36$, $N_1 = 6$, $N_2 = 6$, $P = 0.002$) (Table 2). Similarly, the diving efficiency of seals was also lower for seals captured in the glacial ice site than for seals captured at terrestrial sites (Mann–Whitney U test, $U = 2$, $N_1 = 6$, $N_2 = 6$, $P = 0.009$) (Table 2). The percent of time spent diving was greater for seals captured at the glacial ice site than at the terrestrial site (Mann–Whitney U test, $U = 34$, $N_1 = 6$, $N_2 = 6$, $P = 0.008$).

Overall, seals from terrestrial sites had a greater percentage of dives occurring in shallower waters than did seals from glacial ice sites. For seals captured at terrestrial sites, 92 % of dives occurred in the upper 50 m of the water column. In contrast, for seals captured at the glacial ice site, 71 % of dives occurred in the upper 50 m of the water column (Fig. 3a, b) (Table 3). The majority of dives for seals from both habitats (99.9 % for terrestrial and 94.1 % for glacial ice) occurred in the upper 100 m of the water
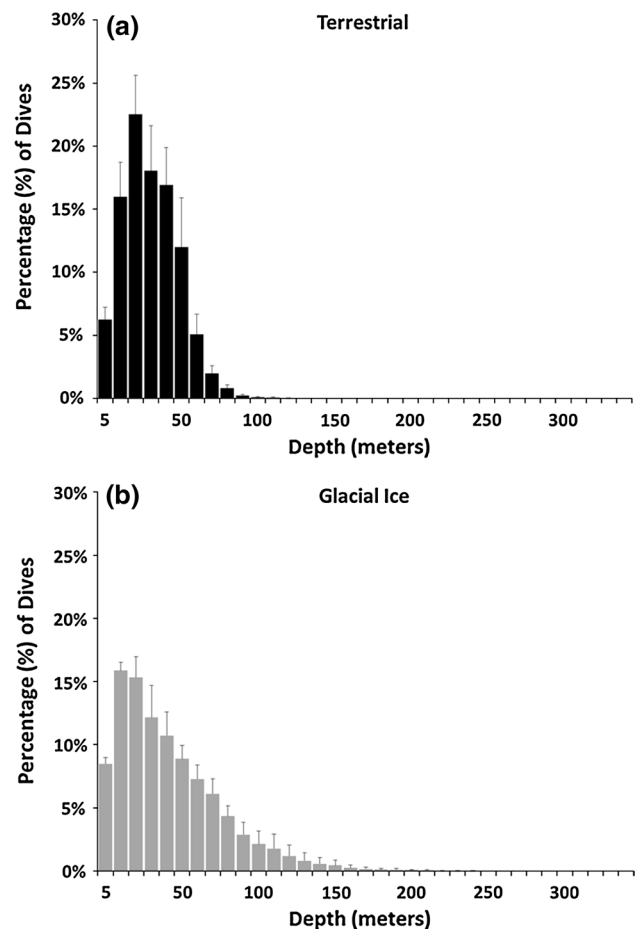
Fig. 3 Percentage of dives (± SE) by depth (m) for juvenile female harbor seals captured at **a** terrestrial ($n = 6$) and **b** glacial ice ($n = 6$) sites in Glacier Bay, Alaska

Table 3 Percentage of dives by juvenile female harbor seal with corresponding percentage of nautical area scattering coefficient (NASC) (m^2/nm^2) by depth for glacial ice and terrestrial habitats in Glacier Bay National Park

Depth bin (m)	Percentage (%) of dives		Percentage (%) of NASC	
	Terrestrial (%)	Glacial ice (%)	Terrestrial (%)	Glacial ice (%)
0–50	91.7	71.4	54.8	41.5
51–100	8.2	22.8	30.5	11.1
101–150	0.1	4.9	14.8	8.0
151–200	0.0	0.7	0.2	4.9
201–250	0.0	0.1	0.2	5.4
251–300	0.0	0.0	0.4	29.0

column (Table 3). A diurnal pattern of diving activity was apparent for seals from both habitats, with deeper dives typically occurring from 0500 to 2000 hours and shallower dives occurring during nighttime hours from 2100 to 0400 hours (Fig. 4).

Fig. 4 Dive depth (m) (± SE) of juvenile female harbor seals captured at terrestrial (n = 6) (*black bars*) and glacial ice (n = 6) (*gray bars*) habitats in Glacier Bay, Alaska, in relation to time of day (h)
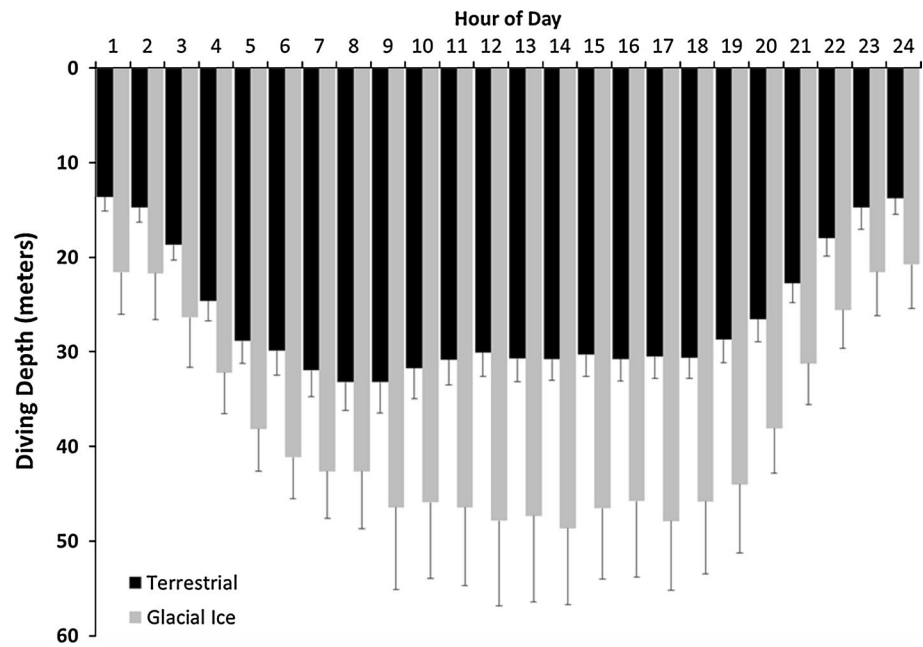
Trip durations

The maximum trip duration for seals (X ± SE = 192.0 ± 63.6 h) captured at the glacial ice site was substantially longer than for seals (X ± SD = 94.6 ± 54.5 h) (Mann–Whitney U test, $U = 1$, $N_1 = 6$, $N_2 = 6$, $P = 0.05$) captured at terrestrial sites. However, the average trip durations for seals (X ± SD = 14.0 ± 3.4 h) captured at the glacial ice site were not substantially different than for seals captured at terrestrial sites (X ± SD = 10.9 ± 2.4 h) (Mann–Whitney U test, $U = 4$, $N_1 = 6$, $N_2 = 6$, $P = 0.26$).

Focal foraging areas

Harbor seals captured at the glacial ice site generally traveled greater distances to FFA (median = 12.0 km, range 2.3–84.2 km; n = 24) than seals that were captured at terrestrial sites (median = 4.2 km, = 8.23 ± 15.5 km, range 0.1–63.3 km; n = 28); however, the median distances traveled to FFA were not significantly different (Mann–Whitney U test, $U = 4$, $N_1 = 6$, $N_2 = 4$, $P = 0.11$). Focal foraging areas of seals captured at terrestrial sites occurred in close proximity to the capture sites, predominantly in the lower-bay region in the vicinity of the Beardslee Island archipelago, Sitakaday Narrows, and Bartlett Cove in waters typically <100 m deep (Fig. 1). However, one juvenile female captured at the terrestrial site was documented on several occasions in Reid Inlet, a glacially influenced inlet, in the upper West Arm approximately 70 km from the Spider Reef capture site (Fig. 1). In contrast, FFAs of seals captured at the glacial ice site occurred primarily in the upper West Arm, most commonly outside of Johns Hopkins Inlet, and were much more dispersed than those for seals from terrestrial capture sites. In some cases, FFAs of seals from the glacial ice site extended to the mouth of Glacier Bay, approximately 100 km away (Fig. 1).

Prey availability

Prey availability, or the nautical area scattering coefficient (NASC), was consistently higher in Beardslee Entrance near the terrestrial sites (X ± SD = 55.2 ± 20.1 m^2nmi^2) than at the glacial ice site (X ± SD = 2.1 ± 1.1 m^2nmi^2) in Johns Hopkins Inlet (Mann–Whitney U test, $U = 20$, $N_1 = 7$, $N_2 = 6$, $P = 0.02$) (Fig. 5a). The average prey index, which accounted for both the density and depth of the prey, was also consistently higher near the terrestrial site (X ± SD = 1.8 ± 1.4) than at the glacial ice site (X ± SD = 0.1 ± 0.05) (Mann–Whitney U test, $U = 20$, $N_1 = 7$, $N_2 = 6$, $P = 0.02$) (Fig. 5b), demonstrating that prey were not only higher in density but also shallower in the water column and more accessible to harbor seals near the terrestrial site. Bottom depths in areas where hydro acoustic surveys were conducted near terrestrial sites in the Beardslee Entrance were much shallower (X ± SD = 65.1 ± 16.8 m; range = 12.9–141.7 m) than at the glacial ice site in Johns Hopkins Inlet (X ± SD = 284.3 ± 76.0 m; range = 32.2–356.4 m). At the terrestrial site, 85 % of NASC was found in the upper 100 m of the water column, whereas only 53 % of NASC was found in the upper 100 m of the water column at the glacial ice site (Table 3).
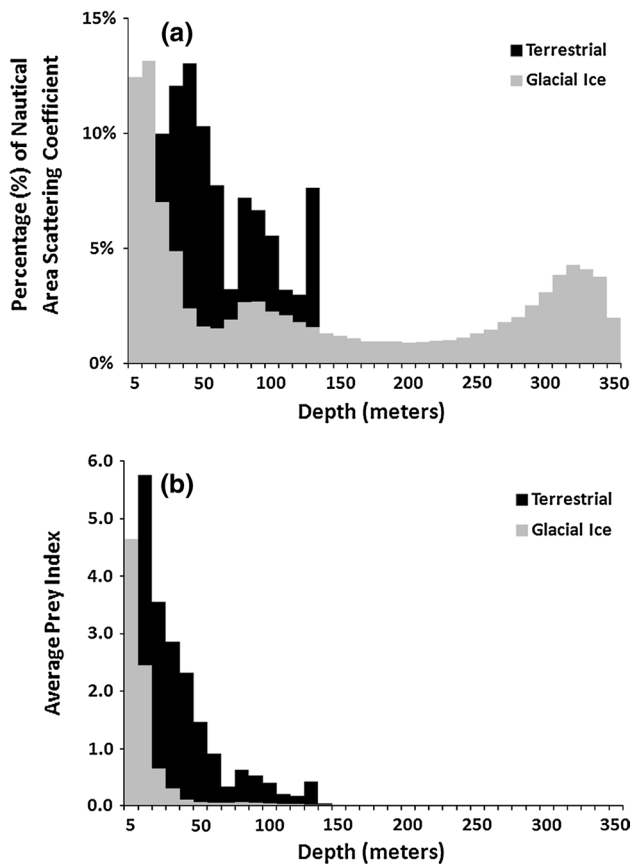
Fig. 5 Percentage of nautical area scattering coefficient ((NASC) m2/nmi2) (**a**) and average prey index (**b**) for hydroacoustic surveys at the terrestrial site in the Beardslee Entrance (*black bars*) and at the glacial ice site in Johns Hopkins Inlet (*gray bars*) in Glacier Bay, Alaska

Discussion

To our knowledge, this is the first study to concurrently assess harbor seal diving behavior and local prey fields near glacial ice and terrestrial haulout habitats and to consider the implications of using these contrasting habitats on harbor seal diving and foraging behavior. Numerous studies have suggested that prey distribution and depth were likely important factors influencing the diving behavior of harbor seals (Härkönen 1987; Tollit et al. 1998; Lesage et al. 1999; Lowry et al. 2001; Frost et al. 2001; Eguchi and Harvey 2005; Hastings et al. 2004; Grigg et al. 2009, 2012; Sharples et al. 2012). However, previous studies in Alaska have focused only on seals from terrestrial sites (Frost et al. 2001; Hastings et al. 2004) and have not directly measured prey fields of harbor seals. Our study allowed us to explore relationships between harbor seal diving behavior and prey distribution with empirical data.

Our study demonstrates that prey accessibility differed between glacial ice and terrestrial habitats and likely played

a role in influencing the diving and foraging behavior of harbor seals. Seals captured at the glacial ice site in Johns Hopkins Inlet generally dived deeper, had longer dive durations, lower percent bottom time, and traveled farther to foraging areas compared to seals captured at terrestrial sites. In contrast, seals captured at the terrestrial sites dived to shallower depths, had shorter dive durations, higher percent bottom time, and foraged in lower Glacier Bay near terrestrial capture sites.

Prey densities were higher and foraging conditions were likely better near the terrestrial sites and these conditions may confer less effort for seals during foraging. The lower reaches of Glacier Bay where terrestrial haul-out sites were located and where seals were regularly found diving are characterized by shallower seafloor depths, intense tidal currents, moderate stratification, and strong mixing which promote localized upwelling conditions and highly productive areas (Etherington et al. 2007; Renner et al. 2012). The majority (85 %) of prey density (NASC) occurred in the upper 100 m of the water column in the Beardslee Entrance adjacent to the terrestrial site. Aggregations of forage fish and other large marine predators, including Steller sea lions (*Eumetopias jubatus*) and humpback whales (*Megaptera novaeangliae*), were also consistently observed in the Beardslee Entrance near the terrestrial sites during hydroacoustic and opportunistic aerial surveys (J. N. Womble, *personal observation*). Previous studies of prey communities in the same region near the terrestrial sites in central and lower Glacier Bay commonly detected dense aggregations of walleye pollock (*Theragra chalcogramma*), Pacific sandlance (*Ammodytes hexapterus*), salmon (*Oncorhynchus* sp.), and capelin (*Mallotus villosus*) (Robards et al. 2003; Arimitsu et al. 2008).

In contrast, the physical environment of the glacial ice site in Johns Hopkins Inlet is characterized by a deep recently deglaciated fjord with seafloor depths ranging up to 370 m. Oceanographic surveys in the upper West Arm of Glacier Bay near Johns Hopkins Inlet have documented colder water temperatures, large amounts of freshwater runoff, higher levels of stratification, and lower levels of productivity (Etherington et al. 2007). Indices of prey density were consistently lower at the glacial ice site, and only 53 % of prey density (NASC) was found in the upper 100 m of the water column. The diversity of prey species was also lower in the upper West Arm region of Glacier Bay and included pollock, sandlance, capelin, sculpin, smelt, and myctophids (Abookire et al. 2002; Robards et al. 2003). In contrast to lower Glacier Bay, Steller sea lions and humpback whales were rarely observed in Johns Hopkins Inlet and upper West Arm of Glacier Bay (J. N. Womble, *personal observation*).

Foraging on a diverse array of prey types that differ in density, energy content, size, depth, and handling time can

influence foraging strategies, prey profitability, and ultimately foraging costs of harbor seals (Bowen et al. 2002). Harbor seals in Glacier Bay have a relatively diverse diet including pelagic and demersal species such as walleye pollock, Pacific salmon, capelin, sandlance, eulachon (*Thaleichthys pacificus*), sculpin, greenling (*Hexagrammos* sp.), Pacific cod (*Gadus macrocephalus*), herring (*Clupea pallasii*), Arrowtooth flounder (*Atheresthes stomias*), myctophids, and flatfish (Mathews 2002; Herreman et al. 2009). Pelagic fish species were more common in seal diet at the glacial ice site than at terrestrial sites (Blundell et al. 2011), and many of the pelagic species (e.g., myctophids, eulachon) are much higher in lipid content and energy density than other prey species (Van Pelt et al. 1997; Vollenweider et al. 2011). Myctophids, such as northern lampfish (*Stenobrachius leucopsarus*), are typically found in the deeper waters (200–1,000 m) (Frost and McCrone 1979); however, they have been documented at much shallower depths (10–100 m) in the Glacier Bay/Icy Strait region (Abookire et al. 2002; Renner et al. 2012). Northern lampfish were also commonly detected in mid-water trawls and in the diet of Steller sea lions nearby regions in Lynn Canal and Frederick Sound (Womble and Sigler 2006; Sigler et al. 2009; Csepp et al. 2011).

Capelin were more common in seal diet at the glacial ice site than at the terrestrial site (Herreman et al. 2009). Although capelin are not as high in lipid and energy content as eulachon or myctophids, they are higher in lipid content than many other prey species (Vollenweider et al. 2011). High catch-per-unit effort and abundance of capelin has been documented in colder waters near glacial areas, in the Beardslee Entrance area near terrestrial sites, and also in areas over shallow sills that were backed by deep basins (Arimitsu et al. 2008). The availability of dense aggregations of capelin in several regions of Glacier Bay at relatively shallow depths (<30 m) (Arimitsu et al. 2008) likely provides an important prey resource for harbor seals.

The differences in prey availability in the glacial ice and terrestrial habitats likely have behavioral consequences for diving and foraging effort of harbor seals and are consistent with the proximate behavioral responses of diving marine vertebrates to reduced prey accessibility or increases in the depth of prey (e.g., Feldkamp et al. 1989; Boyd et al. 1994; Boyd 1999; Staniland et al. 2010). For air-breathing diving marine vertebrates, diving deeper can result in more time spent in the transit, including the ascent, and descent phases of the dive, and less time spent searching for and acquiring prey, which may occur during the bottom phase of dives (Lesage et al. 1999; Costa 2008). As a result of lower percent bottom time, seals from the glacial ice site likely had less time available to search for and acquire prey. Conversely, seals using terrestrial haul-out sites likely encountered greater prey in nearby waters at shallower depths and in higher density which resulted in less foraging effort via shallower dives, less vertical distances traveled, and ultimately higher foraging efficiency.

Local bathymetry near haulout sites and foraging areas is also a factor that may influence the dive behavior of harbor seals (Härkönen 1987; Tollit et al. 1998; Hastings et al. 2004; Eguchi and Harvey 2005; Grigg et al. 2012). Bathymetric conditions contrast sharply in the glacial ice and terrestrial habitats: Johns Hopkins Inlet is a deep tidewater glacial fjord with seafloor depths extending up to 370 m, whereas the Beardslee Entrance is characterized by seafloor depths ranging up to 140 m and low to moderate substrate complexity. Although the bathymetric range was much greater at the glacial ice site, only 5 % of dives for seals from the glacial ice site occurred at depths >100 m. A few seals occasionally dived to depths exceeding 200–300 m; however, dives to these deeper depths did not occur regularly and likely represent rare performance events. Given that seals from the glacial ice site did not regularly exploit the large range of bathymetric conditions available to them at the glacial ice site suggests that other factors such as the vertical distribution of prey and/or their ability to maximize time at depth (Houston and Carbone 1992) may have influenced their diving behavior.

The foraging and diving behavior of pinnipeds can also be constrained by numerous intrinsic factors including body size, age, and physiology (Kooyman 1989). Diving abilities typically increase with increasing body size in pinnipeds (Schreer and Kovacs 1997), and younger harbor seals have more limited diving abilities than adult seals due to reduced oxygen stores and biochemically immature muscles (Burns et al. 2005; Prewitt et al. 2010). Younger or juvenile divers that are smaller in body size and have lower aerobic thresholds than adults could be more sensitive to reductions in prey availability than older more experienced divers (Burns 1999; Horning and Trillmich 1999). We focused on juvenile female harbor seals to minimize any confounding factors related to age, mass, body size, and sex (e.g., Thompson et al. 1998; Frost et al. 2001, 2006; Hastings et al. 2004; Eguchi and Harvey 2005). Reproductive status may also influence harbor seal diving behavior (Boness et al. 1994; Bowen et al. 1999) as adult females with dependent young are likely constrained by the need to return to shore to provision dependent young.

Even though seals utilizing glacial ice sites generally exerted increased diving and foraging effort compared to seals from terrestrial sites, the diving behavior of harbor seals in Glacier Bay was similar to that found for harbor seals in other regions of Alaska (Frost et al. 2001; Hastings et al. 2004) and elsewhere (Thompson et al. 1998; Tollit et al. 1998; Bowen et al. 1999; Lesage et al. 1999; Gjertz et al. 2001; Krafft et al. 2002; Eguchi and Harvey 2005; Sharples et al. 2012). The majority of dives by seals in

Glacier Bay occurred within the upper 100 m of the water column and were within the estimated aerobic dive limit of 8.9 min (Bowen et al. 1999; Thompson and Fedak 2001).

Higher prey densities and shallower prey depths for seals near terrestrial sites may confer the advantage of reduced foraging effort; however, the majority of seals (>66 %) in Glacier Bay are found at the glacial ice site in Johns Hopkins Inlet during the breeding period (Mathews and Pendleton 2006; Womble et al. 2010). Thus, suggesting that there may be additional benefits or trade-offs associated with using the glacial ice habitat that may not be related to prey availability. Companion studies in Glacier Bay have documented several lines of evidence consistent with this premise. First, the availability of floating ice as a haul-out platform provides a stable platform for resting and a refuge from predators. Seals using glacial ice spent a greater proportion of time dry (per hour) or hauled out (0.26) than seals from terrestrial sites (0.16), and tide height did not influence the proportion of time spent hauled out by seals at the glacial ice site (Blundell et al. 2011). In contrast to the stable ice platform, the primary terrestrial site at Spider Reef is often completely submerged twice daily during high tides thereby being less consistently available as a haulout platform for seals. Second, despite the lower prey availability noted in our study, seals captured at the glacial ice site had diets higher in pelagic fishes, including capelin and eulachon, compared to seals captured at terrestrial sites (Herreman et al. 2009; Blundell et al. 2011). Thus, the types and quality of fish available to seals in and near glacial ice may offset the added effort to acquire them. Third, observations suggest that both aquatic and terrestrial predators may be less common in and near the glacial ice habitat. Attempted and successful predation events by transient killer whales (*Orcinus orcas*) and Steller sea lions on harbor seals have been observed at terrestrial and glacial ice sites (Matkin et al. 2007; Womble et al. 2007; Mathews and Adkison 2010). However, anecdotal evidence suggests that the risk of predation may be lower at the glacial ice site (Womble and Conlon 2010). Finally, there may be a reduced likelihood of inter-specific aggression and/or competition (Mathews and Pendleton 2006; Herreman et al. 2009) in glacial ice habitat as Steller sea lions and humpback whales, both of which are increasing substantially in the Glacier Bay region (Mathews et al. 2011; Saracco et al. 2013) and forage on similar prey species as harbor seals, are not as common in the glacial ice habitat as they are near the terrestrial site.

We provide evidence of differences in prey accessibility for harbor seals in contrasting glacial ice and terrestrial habitats and suggest that harbor seals may balance trade-offs between the costs and benefits of using these habitats. It is currently unknown if there are fitness-level consequences for seals that use these contrasting habitats; however, determining whether or not there are fitness-level consequences will require quantifying survival and reproductive rates in each habitat and identifying sources of age-specific mortality (e.g., Horning and Mellish 2012).

Studies of this nature that concurrently measure marine predator diving behavior and prey fields are greatly needed as the distribution of prey is a primary factor influencing predator foraging behavior. We acknowledge that our study was based on relatively small samples sizes which may limit our scope of inference; however, small samples have provided tremendous insight into the foraging behavior of pinnipeds in relation to prey fields (e.g., Davis et al. 1999; Parrish et al. 2000; Hooker et al. 2002). Although monitoring marine predators' foraging behavior and their prey fields can be logistically challenging due to the spatial and temporal scales at which marine predators forage, such studies can provide much needed empirical data that can be used to provide a better understanding of the functional relationships between marine predators and their prey and to improve existing foraging models (Hindell 2008). Ultimately, understanding the diving and foraging strategies of individuals is essential, not only for understanding the behavior of individuals and their responses to changes in prey availability, but also for linking individual behavior to population level effects.

GLBA-2005-SCI-0003, GLBA-2006-SCI-0003, GLBA-2007-SCI-0003, and associated Glacier Bay National Park and Preserve Waivers to park regulations. Animal use protocols used in this research were reviewed and approved by the Institutional Animal Care and Use Committee at the State of Alaska Department of Fish and Game (protocol 07-16).

References

Abookire AA, Piatt JF, Speckman SG (2002) A nearsurface, daytime occurrence of two mesopelagic fish species (*Stenobrachius leucopsarus* and *Leuroglossus schmidti*) in a glacial fjord. Fish Bull 100:376–380

Arimitsu ML, Piatt JF, Litzow MA, Abookire AA, Romano MD, Robards MD (2008) Distribution and spawning dynamics of capelin (*Mallotus villosus*) in Glacier Bay, Alaska: a cold water refugium. Fish Oceanogr 17:137–146

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

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

Blundell GM, Pendleton GW (2008) Estimating age of harbor seals *Phoca vitulina* with incisor teeth and morphometrics. Mar Mamm Sci 24:577–590

Blundell GM, Womble JN, Pendleton GW, Karpovich SW, Gende SM, Herreman JK (2011) Use of glacial ice and terrestrial habitats by harbor seals in Glacier Bay, Alaska: costs and benefits. Mar Ecol Prog Ser 429:277–290

Boness DJ, Bowen WD, Oftedal OT (1994) Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seals. Behav Ecol Sociobiol 34:95–104

Bowen WD, Boness DJ, Iverson SJ (1999) Diving behaviour of lactating harbour seals and their pups during maternal foraging trips. Can J Zool 77:978–988

Bowen WD, Tulley D, Boness DJ, Bulheier BM, Marshall GJ (2002) Prey dependent foraging tactics and prey profitability in a marine mammal. Mar Ecol Prog Ser 244:235–245

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

Boyd IL, Lunn NJ, Barton T (1991) Time budgets and foraging characteristics of lactating Antarctic fur seals. J Anim Ecol 60:577–592

Boyd IL, Arnould JPY, Barton T, Croxall JP (1994) Foraging behavior of Antarctic fur sea lions during periods of contrasting prey abundance. J Anim Ecol 63:703–713

Bray JR, Curtis JT (1957) An ordination of the upland forest communities in southern Wisconsin. Ecol Monogr 27:325–349

Brown RF, Mate BR (1983) Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. Fish Bull 81:291–301

Burns JM (1999) The development of diving behavior in juvenile Weddell seals: pushing the physiological limits in order to survive. Can J Zool 77:737–747

Burns JM, Costa DP, Frost K, Harvey JT (2005) Development of body oxygen stores in harbor seals: effects of age, mass, and body composition. Physiol Biochem Zool 78:1057–1068

Calambokidis JB, Taylor BL, Carter SD, Steiger GH, Dawson PK, Antrim LD (1987) Distribution and haul-out behavior of harbor seals in Glacier Bay, Alaska. Can J Zool 65:1391–1396

Costa DP (2008) A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. Aquat Conserv 17:S44–S52

Croxall JP, Everson I, Kooyman GL, Ricketts C, Davis RW (1985) Fur seal diving behavior in relation to vertical distribution of krill. J Anim Ecol 54:1–8

Csepp DJ, Vollenweider JJ, Sigler MF (2011) Seasonal abundance and distribution of pelagic and demersal fishes in southeastern Alaska. Fisheries Res 108:307–320

Cuthill I (1991) Field experiments in animal behaviour: methods and ethics. Anim Behav 42:1007–1014

Davis RW, Fuiman LA, Williams RM, Collier SO, Hagey WP, Kanatous SB, Kohin S, Horning M (1999) Hunting behavior of a marine mammal beneath the Antarctic fast ice. Science 238:993–995

Eguchi T, Harvey JT (2005) Diving behavior of the Pacific harbor seal (*Phoca vitulina richardi*) in Monterey Bay, California. Mar Mamm Sci 21:283–295

Etherington LL, Hooge PN, Hooge ER, Hill DF (2007) Oceanography of Glacier Bay, Alaska: implications for biological patterns in a glacial fjord estuary. Estuaries Coasts 30:927–944

Fahlman A, Hastie GD, Rosen DAS, Naito Y, Trites AW (2008) Buoyancy does not affect diving metabolism during shallow dives in Steller sea lions *Eumatopias jubatus*. Aquat Biol 3:147–154

Feldkamp SD, DeLong RL, Antonelis GA (1989) Diving patterns of California sea lions, *Zalophus californianus*. Can J Zool 67:872–883

Field WO (1947) Glacier recession in Muir Inlet, Glacier Bay, Alaska. Geogr Rev 37:369–399

Frost BW, McCrone LE (1979) Vertical distribution, diet vertical migration, and abundance of some mesopelagic fishes in the eastern subarctic Pacific Ocean in summer. Fish Bull US 76:751–770

Frost KJ, Simpkins MA, Lowry LF (2001) Diving behavior of subadult and adult harbor seals in Prince William Sound, Alaska. Mar Mammal Sci 17:813–834

Frost KJ, Simpkins MA, Small RJ, Lowry LF (2006) Development of diving by harbor seal pups in two regions of Alaska: use of the water column. Mar Mamm Sci 22:617–643

Gallon SL, Bailleul F, Charassin J-B, Guinet C, Bost C-A, Handrich Y, Hindell M (2013) Identifying foraging events in deep-diving southern elephant seals, *Mirounga leonina*, using acceleration data loggers. Deep Sea Res II 88–89:14–22

Gjertz I, Lydersen C, Wiig Ø (2001) Distribution and diving of harbor seals (*Phoca vitulina*) in Svalbard. Polar Biol 24:209–214

Grigg EK, Klimley AP, Allen SG, Green DE, Elliot-Fisk DL, Markowitz H (2009) Spatial and seasonal relationships between Pacific harbor seals (*Phoca vitulina richardii*) and their prey, at multiple scales. Fish Bull 107:359–372

Grigg EK, Allen SG, Craven-Green DE, Klimley AP, Markowitz H, Elliot-Fisk DL (2012) Foraging distribution of Pacific harbor seals (*Phoca vitulina richardii*) in a highly impacted estuary. J Mamm 93:282–293

Hall DK, Benson CS, Field WO (1995) Changes of Glaciers in Glacier Bay, Alaska using ground and satellite measurements. Phys Geogr 16:27–41

Härkönen TJ (1987) Influence of feeding on haul-out patterns and sizes of sub-populations in harbour seals. Neth J Sea Res 21:331–339

Hastings KK, Frost KJ, Simpkins MA, Pendleton GW, Swain UG, Small RJ (2004) Regional differences in diving behavior of harbor seals in the Gulf of Alaska. Can J Zool 82:1755–1773

Herreman JK, Blundell GM, Ben-David M (2009) Evidence of bottom-up control of diet driven by top-down processes in a declining harbor seal *Phoca vitulina richardi* population. Mar Ecol Prog Ser 374:287–300

Hill DF, Ciavola S, Etherington L, Klaar M (2009) Estimation of freshwater runoff into Glacier Bay, Alaska and incorporation into a tidal circulation model. Estuar Coast Shelf Sci 82:95–107

Hindell M (2008) To breathe or not to breathe: optimal strategies for finding prey in the dark, three-dimensional environment. J Anim Ecol 77:847–849

Hollander M, Wolfe DA (1973) Nonparametric statistical methods. Wiley, New York

Hooker SK, Boyd IL, Jessop M, Cox O, Blackwell J, Boveng PL, Bengston JL (2002) Monitoring the prey-field of a marine predator: combining digital imaging with datalogging tags. Mar Mamm Sci 18:680–697

Hooker SK, Biuw M, McConnell BJ, Miller PJO, Sparling CE (2007) Bio-logging science: logging and relaying physical and biological data using animal-attached tags. Deep Sea Res II 54:177–182

Hoover-Miller A, Atkinson SA, Conlon S, Prewitt J, Armato P (2011) Persistent decline in the abundance of harbor seals, *Phoca vitulina richardsi*, over three decades in Aialik Bay, an Alaskan tidewater glacial fjord. Mar Ecol Prog Ser 424:259–271

Horning M, Mellish J-A (2012) Predation on an upper-trophic marine predator, the Steller sea lion, evaluating high juvenile mortality in a density-dependent conceptual framework. PLoS ONE 7(1):e30173. doi:10.1371/journal.pone.0030173

Horning M, Trillmich F (1997) Ontogeny of diving behaviour in the Galápagos fur seal. Behaviour 134:1211–1257

Horning M, Trillmich F (1999) Lunar cycles in diel prey migrations exert a stronger effect on the diving of juveniles than adult Galápagos fur seals. Proc R Soc Lond B Biol Sci 266:1127–1132

Hothorn T, Hornik K, van de Wiel MA, Zeileis A (2008) Implementing a class of permutation tests: the coin package. J Stat Softw 28(8):1–23

Houston AI, Carbone C (1992) The optimal allocation of time during the diving cycle. Behav Ecol 3:255–265

Ichii R, Bengtson JL, Boveng PL, Takao Y, Jansen JK, Hiruki-Raring LM, Cameron MF, Okamura H, Hayashi T, Naganobu M (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

Kooyman GL (1989) Diverse divers: physiology and behavior. In: Johansen K, Farner DS (eds) Zoophysiology series, vol 23. Springer, New York

Krafft BA, Lydersen C, Gjertz I, Kovacs KM (2002) Diving behavior of sub-adult harbor seals (*Phoca vitulina*) at Prins Karls Forland, Svalbard. Polar Biol 25:230–234

Kruskal JB (1964) Nonmetric multi-dimensional scaling: a numerical method. Psychometrica 29:1–27

Lea M-A, Wilson B (2006) Techniques for real-time, active tracking of sea lions. In: Trites AW, Atkinson SK, DeMaster DP, Fritz LW, Gelatt TS, Rea LD, Wynne KM (eds) Sea lions of the world. Alaska Sea Grant College Program. University of Alaska Fairbanks, Fairbanks, Alaska

Lea M-A, Hindell M, Guinet C (2002) Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Iles Kerguelen. Polar Biol 23:269–279

Lea M-A, Guinet C, Cherel Y, Duhamel G, Dubroca L, Pruvost P, Hindell M (2006) Impacts of climatic anomalies on provisioning strategies of a Southern Ocean predator. Mar Ecol Prog Ser 310:77–94

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

Lowry LF, Frost KJ, Ver Hoef JM, DeLong RA (2001) Movements of satellite-tagged subadult and adult harbor seals in Prince William Sound, Alaska. Mar Mamm Sci 17:835–861

Mather PM (1976) Computational methods of multivariate analysis in physical geography. Wiley, London

Mathews EA (2002) Diet of harbor seals at a glacial fjord and a terrestrial haulout in Glacier Bay, 1996–2001. Unpublished report to Glacier Bay National Park and Preserve, Resource Management Division, P.O. Box 140, Gustavus, AK 99801

Mathews EA, Adkison MD (2010) The role of predation by Steller sea lions in a large population decline of harbor seals. Mar Mamm Sci 26:803–836

Mathews EA, Pendleton GW (2006) Declines in harbor seal (*Phoca vitulina*) numbers in Glacier Bay National Park, Alaska, 1992–2002. Mar Mamm Sci 22:170–191

Mathews EA, Womble JN, Pendleton GW, Jemison LA, Maniscalco JM, Streveler G (2011) Population expansion and colonization of Steller sea lions in the Glacier Bay region of southeastern Alaska: 1970s to 2009. Mar Mamm Sci 27:852–880

Matkin DR, Straley JM, Gabriele CM (2007) Killer whale feeding ecology and non-predatory interactions with other marine mammals in the Glacier Bay region of Alaska. In: Piatt JF, Gende SM (eds) Proceedings of the Fourth Glacier Bay Science Symposium, October 26–28, 2004. US Geological Survey Scientific Investigations Report 2007–5047, pp 155–158

McCune B, Grace JB (2002) Analysis of ecological communities. MJM Software Design, Gleneden Beach

McCune B, Mefford MJ (2011) PC-ORD multivariate analysis of ecological data version 6.0. MjM software. Gleneden Beach, Oregon

Merrick RL, Loughlin TR, Calkins DG (1987) Decline in the abundance of the northern sea lions in Alaska, 1956–1986. Fish Bull 85:351–365

Mielke PW, Berry KJ (2001) Permutation methods: a distance function approach., Springer series in statisticsSpringer, New York

Montgomery RA, Hoef Ver, Boveng PL (2007) Spatial modeling of haul-out site use by harbor seals in Cook Inlet, Alaska. Mar Ecol Prog Ser 341:257–264

Naito Y, Costa DP, Adachi T, Robinson PW, Fowler M, Takahashi A (2013) Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. Funct Ecol. doi:10.1111/1365-2435.12083

Nordstrom CA (2002) Haul-out selection by Pacific harbor seals (*Phoca vitulina richardii*): isolation and perceived predation risk. Mar Mamm Sci 18:194–205

Parrish FA, Craig MP, Ragen TJ, Marshall GJ, Buhleier BM (2000) Identifying diurnal foraging habitat of endangered Hawaiian monk seals using a seal-mounted video camera. Mar Mamm Sci 16:392–412

Parrish FA, Marshall GJ, Littnan CL, Heithaus M, Canja S, Becker B, Braun B, Antonelis GA (2005) Foraging of juvenile monk seals at French Frigate Shoals, Hawaii. Mar Mamm Sci 21:93–107

Pitcher KW (1990) Major decline in the number of harbor seals on Tugidak Island, Gulf of Alaska. Mar Mamm Sci 6:121–134

Prewitt JS, Freistroffer DV, Scheer JF, Hammill MO, Burns JM (2010) Postnatal development of muscle biochemistry in nursing harbor seal (*Phoca vitulina*) pups: limitations to diving behavior? J Comp Physiol B 180:757–766

Renner M, Arimitsu ML, Piatt JF (2012) Structure of marine predator and prey communities along environmental gradients in a glaciated fjord. Can J Fish Aquat Sci 69:2029–2045

Robards MD, Drew GS, Piatt JF, Anson JM, Abookire AA, Bodkin J, Hooge P, Speckman S (2003) Ecology of selected marine communities in Glacier Bay: zooplankton, forage fish, seabirds and marine mammals. United States Geological Survey-Alaska Science Center, Department of the Interior. Anchorage, Alaska, 156 p

Saracco JF, Gabriele CM, Neilson JL (2013) Population dynamics and demography of humpback whales in Glacier Bay and Icy Strait, Alaska. Northwest Nat 94:187–197

Schreer JF, Kovacs KM (1997) Allometry of diving capacity in air-breathing vertebrates. Can J Zool 75:339–358

Sharples RJ, Moss SE, Patterson TA, Hammond PS (2012) Spatial variation in foraging behaviour of a marine top predator (*Phoca*

vitulina) determined by a large-scale satellite tagging program. PLoS ONE 7(5):e37216. doi:10.1371/journal.pone.0037216

Sigler MF, Womble JN, Vollenweider JJ (2004) Availability to Steller sea lions of an ephemeral prey resource, a pre-spawning aggregation of eulachon in southeastern Alaska. Can J Fish Aquat 61:1475–1484

Sigler MF, Tollit DJ, Vollenweider JJ, Thedinga JF, Csepp DJ, Womble JN, Wong MA, Rehberg MJ, Trites AW (2009) Foraging response of a marine predator, the Steller sea lion, to seasonal changes in prey availability. Mar Ecol Prog Ser 388:243–261

Small RJ, Lowry LF, Ver Hoef JM, Frost KJ, Delong RA, Rehberg MJ (2005) Differential movements by harbor seal pups in contrasting Alaska environments. Mar Mamm Sci 21:671–694

Small RJ, Boveng PL, Byrd GV, Withrow DW (2008) Harbor seal population decline in the Aleutian Archipelago. Mar Mamm Sci 24:845–863

Staniland IJ, Gales N, Warren NL, Robinson SL, Goldsworthy SD, Casper RM (2010) Geographic variation in the behaviour of a central place forager: Antarctic fur seals foraging in contrasting environments. Mar Biol 157:2383–2396

Stephens DW, Krebs JW (1986) Foraging theory. Princeton University Press, Princeton

Thompson D, Fedak MA (2001) How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. Anim Behav 61:287–296

Thompson PM, Fedak MA, McConnell BJ, Nicholas KS (1989) Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). J Appl Ecol 26:521–535

Thompson PM, Mackay A, Tollit DJ, Enderby S, Hammon PS (1998) The influence of body size and sex on characteristics of harbor seal foraging trips. Can J Zool 76:1044–1053

Tollit DJ, Black AD, Thompson PM, Mackay A, Corpe HM, Wilson B, VanParijs S, Grellier K, Parlane S (1998) Variation in harbour seal diet and dive depths in relation to foraging habitat. J Zool (London) 244:209–222

Towell RG, Ream RR, York AE (2006) Decline in northern fur seal (*Callorhinus ursinus*) pup production on the Pribilof Islands. Mar Mamm Sci 22:486–491

Van Pelt TI, Piatt JF, Lance BK, Roby DD (1997) Proximate composition and energy density of some North Pacific forage fishes. Comp Biochem Physiol A Physiol 118:1393–1398

Vollenweider JJ, Heintz RA, Schaufler L, Bradshaw R (2011) Seasonal cycles in whole-body proximate composition and energy content of forage fish vary with water depth. Mar Biol 158:413–427

Womble JN, Conlon S (2010) Observation of Steller sea lion (*Eumetopias jubatus*) predation on a harbor seal (*Phoca vitulina richardii*) in the Glacier Bay region of southeastern Alaska. Aquat Mamm 36:129–137

Womble JN, Gende SM (2013) Post-breeding migrations of a top predator, the harbor seal (*Phoca vitulina richardii*), from a marine protected area in Alaska. PLoS ONE 8(2):e55386. doi:10.1371/journal.pone.0055386

Womble JN, Sigler MF (2006) Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. Mar Ecol Prog Ser 325:281–293

Womble JN, Gende SM, Blundell GM (2007) Dive behavior of a harbor seal (*Phoca vitulina richardii*) in the presence of transient killer whales (*Orcinus orca*) in Glacier Bay National Park. Mar Mamm Sci 23:203–208

Womble JN, Pendleton GW, Mathews EA, Blundell GM, Bool NM, Gende SM (2010) Harbor seal (*Phoca vitulina richardii*) declines continues in the rapidly changing landscape of Glacier Bay National Park, Alaska, 1992–2008. Mar Mamm Sci 26:686–697

Ydenberg RC, Clark CW (1989) Aerobiosis and anaerobiosis during diving by western grebes: an optimal foraging approach. J Theor Biol 139:437–449