



Space use of a dominant Arctic vertebrate: Effects of prey, sea ice, and land on Pacific walrus resource selection



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ABSTRACT

Sea ice dominates marine ecosystems in the Arctic, and recent reductions in sea ice may alter food webs throughout the region. Sea ice loss may also stress Pacific walrus (*Odobenus rosmarus divergens*), which feed on benthic macroinvertebrates in the Bering and Chukchi seas. However, no studies have examined the effects of sea ice on foraging Pacific walrus space use patterns. We tested a series of hypotheses that examined walrus foraging resource selection as a function of proximity to resting substrates and prey biomass. We quantified walrus prey biomass with 17 benthic invertebrate families, which included bivalves, polychaetes, amphipods, tunicates, and sipunculids. We included covariates for distance to sea ice and distance to land, and systematically developed a series of candidate models to examine interactions among benthic prey biomass and resting substrates. We ranked candidate models with Bayesian Information Criterion and made inferences on walrus resource selection based on the top-ranked model. Based on the top model, biomass of the bivalve family Tellinidae, distance to ice, distance to land, and the interaction of distances to ice and land all positively influenced walrus foraging resource selection. Standardized model coefficients indicated that distance to ice explained the most variation in walrus foraging resource selection followed by Tellinidae biomass. Distance to land and the interaction of distances to ice and land accounted for similar levels of variation. Tellinidae biomass likely represented an index of overall bivalve biomass, indicating walrus focused foraging in areas with elevated levels of bivalve and tellinid biomass. Our results also emphasize the importance of sea ice to walrus. Projected sea ice loss will increase the duration of the open water season in the Chukchi Sea, altering the spatial distribution of resting sites relative to current foraging areas and possibly affecting the spatial structure of benthic communities.

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1. Introduction

Climate warming presents a significant threat to biodiversity in the 21st century, and species have responded with range shifts in response to changing biotic and abiotic environmental variables (Burrows et al., 2011; Sheffield Guy et al., 2016). Arctic ecosystems are particularly responsive to climate warming with temperatures increasing over 3 times the global rate due to a complex interaction of positive feedback loops (Comiso and Hall, 2014). In the Arctic, recent reductions in sea ice extent and thickness have the potential to significantly alter both terrestrial and marine ecosystems in the region (Post et al., 2013). Arctic sea ice extent during the September minimum declined 13% from 1979 to 2015 (National Snow and Ice Data Center Sea Ice Index, Accessed 9 March 2016) and recent model projections indicate that the Arctic

Ocean may have at least one ice free summer by 2040–2060 (Wang and Overland, 2012).

In the Pacific Arctic marine environment, sea ice loss has the potential to alter nutrient flow dynamics and generate cascading effects within food webs. Sea ice and light govern ecosystem processes that generate seasonal pulses of primary production and limit zooplankton populations, which increases organic carbon availability to benthic communities via pelagic-benthic coupling (Grebmeier et al., 1988, 1989, 2015). Reductions in sea ice coverage and increasing ocean temperatures, however, could increase zooplankton populations and associated grazing on organic carbon, decreasing pelagic-benthic coupling and the amount of carbon available to the benthos (Grebmeier et al., 2015). Thus, Arctic marine mammals will likely face numerous challenges associated with climate warming in the next 80 years, including changes in nutrient cycles, benthic production, and habitat (i.e. sea ice loss) (Kovacs et al., 2011; Laidre et al., 2008).

One such Arctic marine mammal facing these challenges within the next century is the Pacific walrus (*Odobenus rosmarus divergens*). Pacific

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walrus feed on benthic macroinvertebrates (e.g., bivalves, gastropods, polychaetes) in shallow waters (<200 m) on the continental shelf in the Bering and Chukchi seas, and haul-out to rest between foraging trips (Fay, 1985, 1982). Walrus typically rest on sea ice, but they also haul-out on land during ice-free periods (Fay, 1985; Jay et al., 2012). Sea ice is especially important for females with young because it provides a safe platform for calving, nursing, and resting. Pelagic-benthic coupling partially contributes to elevated benthic production in parts of the Chukchi Sea, providing ideal areas for walrus to forage (Grebmeier et al., 1989, 2006a, 2015). In addition, ocean acidification has the potential to impact bivalve development and alter benthic communities (Fabry et al., 2009; McClintock et al., 2009). Consequently, climate warming, ocean acidification, and sea ice loss have the potential to reduce walrus prey and habitat, which could affect movements, space use, energy budgets, and possibly population abundance (Jay et al., 2011, Taylor and Udevitz 2015, Wang and Overland 2015).

The Pacific walrus winters in the Bering Sea from Bristol Bay, Alaska to Kamchatka, Russia (Fay, 1982). As sea ice melts throughout the spring and summer, females and young migrate with the retreating ice through the Bering Strait and into the Chukchi Sea while most males remain in the Bering Sea (Fay, 1985, 1982). In the summer and early autumn, females, young, and some male walrus range from the East Siberian Sea to the western Beaufort Sea, but are primarily concentrated within the Chukchi Sea (Fay, 1985; Jay et al., 2012).

Reliably predicting and understanding the effects of climate warming and sea ice loss on Pacific walrus requires knowledge of contemporary resource selection patterns in the Chukchi Sea. However, information on Pacific walrus resource selection is limited to research conducted in the Bering Sea during late winter and spring (Jay et al., 2014). Thus, our overall goal was to obtain information on walrus resource selection in the Chukchi Sea to inform conservation and management efforts. Specifically, our objective was to examine resource selection of foraging female Pacific walrus as a function of potential benthic prey and proximity to haul-out substrates. To achieve our objective, we developed resource selection functions (RSFs) with a use-availability design and included covariates that accounted for potential prey and availability of sea ice and land.

2. Methods

2.1. Tag deployment and telemetry

We attached satellite tags (Telonics, Mesa, Arizona, USA) to 362 walrus in May–October from 2008 to 2012 throughout the Bering and Chukchi seas using crossbows or jab sticks (Jay et al., 2006, 2012). Tags used the Argos satellite system to estimate animal locations based on the Doppler Shift. Walrus were tagged when hauled-out on sea ice or land, and all tags had a barbed head that embedded into the walrus' blubber layer on impact. Although the duty cycle of tags varied throughout the study, all tags were programmed to transmit 6–16 h per day centered on local noon (Beatty et al., 2016). We identified the sex of most tagged walrus from sexually dimorphic features (Fay, 1985), dependent young attendance, or via genetic testing of remotely collected biopsies (Fischbach et al., 2008). The sex of a small number of animals was not identified and these individuals were classified as unknown sex ($n = 10$). We focused tag deployments on adult females ($n = 311$), although some tagged individuals were male ($n = 41$).

Satellite tags were equipped with sensors to monitor walrus behavior at 1-h intervals, and the processing of these sensor data is described elsewhere (Fischbach and Jay, 2016). Briefly, one of three distinct behaviors was assigned to each 1-h interval: 1) foraging, 2) in water not-foraging, and 3) hauled-out. Walrus tagging protocols were approved by the U.S. Geological Survey, Alaska Science Center Institutional Animal Care and Use Committee under a federal permit (U.S. Fish and Wildlife Service permits Nos. MA801652-4, MA801652-5, MA801652-6).

We filtered Argos locations with an algorithm based on spatial redundancy, movement rates, and turning angles (Douglas et al., 2012). We used this filter because it considers both primary and alternate Argos locations as well as class Z locations. We filtered locations with the distance, angle, and rate method with parameters identical to values in Udevitz et al. (2009). We then selected the location closest to local noon (Coordinated Universal Time – 11 h) for each day from each walrus to generate a dataset of daily locations. If two locations on a given day were temporally equidistant from local noon, we selected the location with the highest Argos location class. We removed all males and unknowns, walrus with <3 daily locations, and daily locations that occurred within 24 h of tagging. Thus, our final dataset of daily locations included female walrus with ≥ 2 daily locations.

We restricted our study area to areas of the Chukchi Sea with relatively high densities of benthic sampling to minimize error associated with geospatial modeling of potential prey taxa (Appendix A). To generate our study area polygon, we started on the area with the highest density of benthic sampling stations (i.e. the northeast Chukchi Sea) and systematically expanded the study area polygon to include sampling stations that were <125 km from the nearest sampling station. We then buffered this polygon with 10 km to generate our final study area polygon, which included an 187,504 km² area in the south-central and eastern Chukchi Sea (Fig. 1, Fig. A1).

2.2. Defining availability and resource covariates

We examined walrus resource selection based on a daily time step with discrete choice models. In discrete choice models, each used resource unit is paired with a set of available resource units. We defined used resource units as the daily walrus locations within the study area whereas available resource units were generated using a step selection function to account for animal movement (Fortin et al., 2005). For each focal used resource unit $s_i = (x_i, y_i)$, we identified the location from the previous day [~ 24 h apart; $s_{i-1} = (x_{i-1}, y_{i-1})$] and defined walrus behavior associated with the resource unit s_i with the mode of behavior over the ~ 24 h period from s_{i-1} to s_i . Our objective was to examine resource selection of foraging animals because space use patterns are linked to animal behavior (Wilson et al., 2012). Thus, we retained only daily walrus locations associated with foraging and discarded daily locations categorized as in-water not foraging or hauled-out. We drew 49 turning angle and step length values with replacement from the empirical distribution of daily time step movements of foraging walrus to project 49 available resource units from the previous location s_{i-1} . We chose 49 as the number of available locations because previous research has demonstrated that as few as 20 available locations in matched studies generate stable parameter estimates (Northrup et al., 2013).

We included a series of covariates in our discrete choice models to characterize resources associated with used and available resource units. We first included variables to characterize benthic macrofaunal biomass proximate to each resource unit to represent potential walrus prey (Blanchard et al., 2013; Dasher et al., 2015; Dunton et al., 2014). Although our benthic dataset included 192 families, our modeling approach required identification of a smaller number of benthic taxa. We used a hexagonal overlay procedure to select 17 benthic families to include in our analysis (Appendix A, Table 1). To obtain continuous surfaces of benthic biomass ($\log \text{gC m}^{-2}$), we used universal kriging to interpolate natural log family-level biomass onto a 500 m grid according to year to account for large-scale temporal differences in sampled benthic communities (Appendix A). In addition to specific benthic families, we also developed a continuous surface of total benthic biomass. We then calculated the mean log biomass value for our benthic variables within a 2 km radius around each used and available resource unit. We specifically used 2 km because this value corresponds to the median Argos observation error across all location classes for other pinnipeds (Costa et al., 2010).

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