Oceanographic characteristics associated with autumn movements of bowhead whales in the Chukchi Sea

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ABSTRACT

Each fall, bowhead whales in the Bering-Chukchi-Beaufort (BCB) population migrate westward from summering grounds in the Beaufort Sea through the Chukchi Sea to the northern coast of Chukotka, Russia. Routes whales use when crossing the Chukchi Sea vary by year; in some years, whales migrate directly to the northern coast of Chukotka while in other years, whales may pause migration and linger, presumably to feed, in the central Chukchi Sea. To investigate how whale movements may be related to oceanographic variables we examined bowhead whale habitat selection within the Chukchi Sea in autumn (September–November) at two spatial scales. First, at the landscape scale (i.e. the Chukchi Sea), we compare oceanographic variables (e.g. temperature, salinity, and current velocity) at locations within used and randomly available tracks (i.e. paths of travel) to determine how oceanographic features are associated with where whales cross the Chukchi Sea in autumn. Second, at a local scale, we examine how directed travel or lingering within a whale's track is associated with oceanographic variables (e.g. temperature, salinity, and current velocity). Whale location data for 24 bowhead whales were paired with oceanographic data from a pan-arctic coupled ice-ocean model for 2006–2009. At the landscape scale, we found that whales generally followed water of Pacific origin characterized by temperatures < 0 ºC and salinities between 31.5–34.25. Bowhead whales avoided Alaskan Coastal Water and Siberian Shelf Water, the latter of which defines the western limit of their range, likely due to lower intrinsic densities of zooplankton prey. At the local scale, within their tracks, whales were more likely to interrupt directed movements and linger in areas characterized by stronger gradients in bottom salinity.

Key words: Balaena mysticetus, Chukchi Sea, Alaskan Coastal Current, Bering Shelf Water, Anadyr Water, resource selection, correlated random walk, behavioral state-space model

1. Introduction

Bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort (BCB) population typically winter in the Bering Sea over the continental shelf, north of the southern boundary of sea ice (Moore and Reeves, 1993; Citta et al., 2012). In April, most bowhead whales migrate northward into the Chukchi Sea, follow the Alaskan coast past Point Barrow, and then proceed eastward to summering grounds in the Canadian Beaufort Sea (Moore and Reeves, 1993). Between August and October, whales in the Canadian Beaufort Sea begin to migrate westward, following the Alaskan coast back to Point Barrow. From Point Barrow, whales cross the Chukchi Sea to the Chukotka coast and slowly proceed southward as winter approaches (Fig. 1). In the Chukchi Sea, ice typically begins to form in November, and by the end of December most bowhead whales have returned to the Bering Sea (Quakenbush et al., 2010; Quakenbush et al., 2012; Citta et al., 2012). This is the migratory pattern followed by most BCB bowhead whales (~17,000; Givens et al., 2013); a small number of whales (~500; Melnikov and Zeh, 2007) are known to migrate from the Bering Sea to the Chukchi Sea in spring and then spend the entire summer in the Chukchi Sea (Melnikov and Zeh, 2007; Citta et al., 2012) before returning to the Bering Sea in winter.

Bowhead whales feed by filtering zooplankton through their baleen; the BCB population primarily consumes small crustaceans, especially calanoid copepods (mostly *Calanus hyperboreus* and *C. glacialis*), euphausiids (mostly *Thysanoessa raschii*), and, to a lesser extent, gammarid (order Gammaridea) and hyperid (order Hyperiidea) amphipods, and mysids (Lowry et al. 2004). Research has shown that bowhead whales target dense aggregations of zooplankton (Moore et al., 1995; Laidre et al., 2007) which energetic models suggest they need to meet their caloric requirements (see review in Lowry, 1993). As such, oceanographic features that may aggregate prey, such as fronts or stratified layers, are sometimes targeted by feeding whales (e.g., Moore et al., 1995; Ainley et al., 2007; Davies et al., 2014; Citta et al., 2015; see review in Bost et al., 2009).

Here, we focus on the movements of bowhead whales as they cross the Chukchi Sea in autumn (September−November). Within the Chukchi Sea, there are two areas where zooplankton aggregate, both of which are also bowhead whale aggregation areas. First, zooplankton concentrate along a salinity front (i.e. gradient) formed between the relatively fresh water in the Siberian Coastal Current (SCC) and saltier Bering Sea/Anadyr Water (BSAW; Fig. 1) along the northern coast of Chukotka, Russia. Moore et al. (1995) observed bowhead whales feeding on aggregations of *T. raschii* along this salinity front. Weingartner et al. (1999) showed that downwelling-favorable winds from the northwest promote the maintenance of this front. Second, at the boundary between the Chukchi and Beaufort seas, zooplankton are known concentrate at Point Barrow (Ashjian et al., 2010; Okkonen et al., 2011), where they are upwelled onto the shelf northeast of the point during east or southeast winds. When east winds weaken or when winds are from the south or southwest, a strong front forms between Barrow Canyon and the shelf, promoting the retention and aggregation of zooplankton on the shelf (Ashjian et al., 2010; Okkonen, 2011). Ashjian et al. (2010) found that bowhead whales were more likely to aggregate at Point Barrow and in larger groups, when zooplankton were aggregated there.

However, the movements and feeding behavior of bowhead whales between Point Barrow and the Russian coast (i.e. in the central and northern Chukchi Sea) are relatively unstudied. Satellite telemetry show great variation in the routes bowhead whales choose during the fall migration; some whales migrate directly across the northern Chukchi Sea, some linger in the central Chukchi Sea, and others migrate south along the Alaskan coast (Quakenbush et al., 2010, 2012; Fig. 2). Currents in the Chukchi Sea are complex (Fig. 1); zooplankton move northwards with BSAW (e.g. Berline et al., 2008; Eisner et al., 2013), flows encountering Herald and Hannah shoals (Fig. 1) may create local eddies or stratified layers that aggregate zooplankton, and copepods are known to be upwelled and advected onto the Chukchi Shelf from deeper waters in the Arctic Basin (Ashjian et al., 2002). As such, the central and northern Chukchi Sea may provide feeding opportunities for whales as they migrate from Point Barrow to the Chukotka coast.

In this manuscript we examine bowhead whale habitat selection within the Chukchi Sea in autumn (September–November) at two spatial scales. First, at what we call the landscape scale (i.e. within the Chukchi Sea), we compare oceanographic variables (e.g. temperature, salinity, and current velocity) at locations within travel paths used by bowhead whales with what is randomly available to whales within Chukchi Sea during the autumn migration. The goal of this analysis is to determine what, if any, oceanographic features are associated with where whales choose to cross the Chukchi Sea in autumn. Second, at what we call the local scale, we compare, within an individual whale track, oceanographic features where the whales travel with those where the whales linger. The goal of this second analysis is to determine what oceanographic features are associated with whales pausing migratory movements, presumably to feed. Because there are no oceanographic data directly coincident with the tagged bowhead whale locations, the oceanographic data for both analyses come from a pan-arctic coupled ice-ocean model (RASM; Maslowski et al., 2012).

The movements of bowhead whales in the Chukchi Sea are of particular interest in the autumn. This is when sea-ice extent is at a minimum and when most industrial activities, such as shipping and petroleum exploration and development, typically occur. Two arctic shipping routes pass through the Chukchi Sea: The Great Northern Route to Asia follows the Chukotka Coast, and the route through the Canadian Archipelago (i.e. the Northwest Passage) follows the Alaskan coast. Oil and gas lease areas exist in both the U.S. and Russian waters within the Chukchi Sea (Fig. 2), although there are currently no plans to proceed with drilling.

2. Methods

2.1. Tagging

Tagging methods are the same as used in Quakenbush et al. (2010, 2012) and Citta et al. (2012, 2015). Satellite-linked transmitters were attached to bowhead whales using the system developed by the Greenland Institute of Natural Resources (Heide-Jørgensen et al., 2001, 2003). Location data were collected via the Advanced Research and Global Observation Satellite (ARGOS) data collection and location system (Fancy et al. 1988, Rodgers 2001). We deployed SPOT, SPLASH, and Mk10 tags, manufactured by Wildlife Computers (Redmond, Washington) and a CTD (i.e. Conductivity-Temperature-Depth) tag, manufactured by the Sea Mammal Research Unit (St. Andrews, Scotland). Tags were attached to whales by subsistence whalers using a 2-m or 4-m long fiberglass or wooden pole as a jab-stick (Heide-Jørgensen et al., 2003). The pole system included a tip designed to collect a skin sample (biopsy) during tag deployment, which was later used to determine the sex of whales by amplification of either zinc finger (ZFX and ZFY) genes (Morin et al., 2005) or USP9X and USP9Y genes (Bickham et al., 2011), both of which are sex determining regions within bowhead whale DNA. Whale length was estimated visually by subsistence whalers at the time of tagging. Calves less than 1 year of age and cows with calves were avoided, as stipulated by research permits.

2.2 Bowhead whale location processing

We fit a two-state switching correlated random walk (CRW) model, as described in Jonsen et al. (2005) and Breed et al. (2009), to bowhead whale location data. Although the CRW model is complex, is the results are relatively easy to understand. We used the model to statistically estimate whale locations at 6-hr intervals based on locations obtained irregularly via the Argos satellite network. Unprocessed locations typically have an error ranging from a few hundred meters to many kilometers. The CRW model allows us to statistically estimate the location of a whale, providing a better estimate of the whale's true location, and will also classify each location as being associated with directed movement or lingering behaviors. Embedded within the model are two sets of movement parameters, one associated with directed movements and one associated with lingering behavior, and a parameter that allows us to classify the behavior associated with each estimated location. In practice, the model works well with track data for bowhead whales because they generally exhibit two distinct modes of travel, one in which whales move in a relatively direct fashion to a specific area and another in which they 'zig-zag' (i.e. linger) for multiple days or even months. Location estimates from the CRW model were used for all subsequent analyses.

The CRW model will predict the true location of an animal in intervals for which there are no satellite location data. Although these predictions are usually reasonable if the gap in data collection is not too long, we only used estimated locations and their behavioral state from intervals in which satellite data were collected. If no data were collected within a 6-hr interval, the estimated location and behavioral state were not used for analysis. Prior to fitting CRW models, we removed extreme outliers that were > 300 km from where whales could be located, as these lie outside the location error distributions that are typically used with state-space modeling. After fitting the CRW model, we removed estimated locations that fell on land. More details on how the model was parameterized and fit to the bowhead whale data are provided in the Supplementary Material.

2.3 Oceanographic model

We used the same oceanographic model as was used in Citta et al. (2015). However, instead of summarizing model output over seasonal periods in areas of concentrated whale use, we link daily model output with whale locations and movement behavior. The model is a subset of the Regional Arctic System Model (RASM; Maslowski et al., 2012), which in full configuration includes the Los Alamos Sea Ice Model (CICE) and Parallel Ocean Program (POP), Weather Research and Forecasting Model (WRF) and Variable Infiltration Capacity (VIC) land hydrology model coupled using the Community Earth System Model (CESM) flux coupler (CPL7). Here we replaced the atmospheric and land models with prescribed realistic atmospheric reanalyzed data from the Common Ocean Reference Experiment version 2 (CORE2) 1948–2009 reanalysis. The model is configured on a rotated spherical 1/12-degree and

45-level grid, with eight levels in the upper 50 m. The domain covers the entire Northern Hemisphere marine cryosphere and extends southward to ~30°N latitude in the North Pacific and ~40–45° N latitude in the North Atlantic. The high spatial resolution and the large domain allow simulation of most of the important processes in the Arctic Ocean, including those over the shelves and in the upper ocean of the deep basin, and allows for realistic exchanges between the Arctic and the lower latitude oceans. Model output was available for four years (2006–2009) of the seven-year study period (2006–2012).

2.4 Habitat variables

We chose seven oceanographic variables: (1) bottom salinity, (2) bottom temperature (°C), the gradients of (3) bottom salinity (psu/km), (4) temperature (°C/km), and (5) velocity (cm/s/km) within 20 km, and squared terms for (6) bottom salinity and (7) bottom temperature to allow for more flexible model fitting. We focused on bottom values because dive histograms indicated that bowhead whales generally dove to or near the seafloor in the Chukchi Sea and most dive profiles were “square shaped” indicating extended time near the bottom. In areas deeper than 200 m, we used oceanographic values at 200 m. To identify whale locations associated with frontal features, we calculated the gradients in salinity, temperature, and current velocity across three grid points in the x and y dimensions and used the maximum gradient within 20 km (~ 3 grid cells) of a whale location as the gradient associated with that location.

Both the Chukotka coast and Wrangel Island have prominent nearshore salinity gradients (fronts). We know little about the front surrounding Wrangel Island; however, Moore et al. (1995) observed whales feeding on aggregations of euphausiids in saline waters (~32 psu) on the seaward side of the front between the Siberian Coastal Current and BSAW near Vankarem on the Chukotka coast (Fig. 2). Given the observations of Moore et al. (1995) and that fresher water along the Russian coast originates from river systems, we do not expect zooplankton prey or whales to be preferentially found on the fresh side of this front. Because the ocean model grid spacing (~9.3 km) is of the same order as the internal Rossby radius of deformation in the Arctic (Nurser and Bacon, 2014), fronts and boundary currents, such as those in the Russian coastal areas, exhibit greater widths in the model domain than in actuality. A consequence of this is that modeled temperatures, salinities, and velocities occurring near coastal fronts will tend to differ from co-located measured values more so than at locations far from coastal areas. To account for these greater differences, we treated whale movements occurring within 75 km of the coasts of Chukotka and Wrangel Island separately from whale movements occurring in the central Chukchi. Within this 75-km-wide buffer, we examined whale movements only as functions of temperature, salinity, and velocity gradients and not as functions of temperature, salinity, or velocity directly. All variables were standardized prior to model fitting; to standardize, we subtracted the mean value of the covariate and then divided by the standard deviation.

2.5 Landscape scale habitat selection

To examine what oceanographic variables are associated with where bowhead whales choose to cross the Chukchi Sea, we compared locations along the actual whale track (i.e. used locations) with a set of locations taken from simulated tracks (i.e. available locations). Such “use vs. availability” designs are commonly used in biology to assess the relationship between animals and their environment; specifically, we want to compare what an animal used, in this case where a bowhead whale traveled, with what an animal could have used (e.g. Manley et al 2002; McDonald, 2013). Simulated tracks were constrained to occur within a bounding box defined by the September–November distribution of tagged bowhead whales. For each bowhead whale track, we simulated tracks that started at the same location as the real whale. To preserve a similar pattern of spatial autocorrelation, we kept the same step lengths between locations as the real whale, but allowed a random component to enter the turn angle. We examined a variety of methods for allowing randomness to affect turn angles. Most real whales started near Point Barrow, traveled to the Chukotka coast, and then headed southeast to the Bering Sea. This created a complex distribution of turn angles that was difficult to reproduce without having the simulated track look either too much or too little like the real track. We settled on scaling (multiplying) the real whale's turn angle by a random number drawn from a half normal distribution with mean equal to $1/\theta$ and variance $(\pi\text{-}2)/(2^*\theta^2)$. We truncated the distribution at zero and set θ equal to 2, which made drawing a scale parameter of 0 approximately 30% as likely as drawing a scale parameter of 1. In effect, this simulates a track that has the same step lengths as the real whale, but is randomly straightened to allow the simulated track to sample areas not sampled by the real whale. By using a half normal distribution, we ensured that most turn angles are similar to those used by the real whale. When a simulated track struck land, we included a random deflection parameter (random normal with μ=0 radians and SD=1) to allow a whale to randomly choose a direction that did not fall on land (Fig. 4).

Using simulated tracks to generate the set of available locations has three advantages. First, we correctly account for the relationship between distance and time in determining what locations are truly available to be selected. When whales start near Point Barrow, locations far away (e.g. Chukotka or Wrangel Island) are effectively not available to the whale for many days.

When quantifying selection, locations that are not available should not be included in the comparison. Simulated tracks started where the actual whale started and had identical step lengths, explicitly accounting for how availability differs as a function of time and the distance traveled. Second, we allow the available sample to be sufficiently different than the used sample. We want to compare oceanographic characteristics where whales are located with what is available at a large scale, including places that were not selected. Simulated tracks allow the sampling of resources at a sufficiently large scale. Third, oceanographic variables are correlated in space and, ideally, our available sample will exhibit similar patterns of autocorrelation. Because simulated tracks have the same step lengths as real tracks, patterns of spatial autocorrelation will be similar.

As noted above, whale locations and oceanographic characteristics are expected to be autocorrelated in space. Autocorrelation in the data does not bias the point estimates (i.e. the regression coefficients) but is expected to negatively bias the variances, which will lead to confidence limits and *p*-values that are too small. To account for autocorrelation in animal movements we used the tracks, rather than the locations themselves, as the sample units when estimating population-level means and variances. We simulated 25 random tracks for every real bowhead whale track. We then paired each track with a random track and used logistic regression to estimate 25 sets of regression coefficients for each whale. We then used the mean and standard deviation of the 25 independent fits of the logistic regression coefficients for our estimates and error terms. The 25 independent logistic regression coefficients were fit using a hierarchical model, with each whale treated as a random effect, so we could estimate the population level estimates and error terms. This is a “two-stage” approach (e.g. Fieberg et al., 2010) and assumes that the mean regression coefficients are normally distributed (an assumption we examined); regression models were fit using R version 3.1 (R Core Team 2014). Prior to model fitting, all variables were standardized by subtracting the mean from the value and then dividing by the standard deviation. This method for estimation is essentially a Monte Carlo approach, therefore we cannot use a likelihood-based method of statistical model selection, such as AIC. Instead, we used a backward stepwise procedure where we subtracted terms one at a time and only retained those that were significant at P=0.05. Because we are using output from an oceanographic model, we took a highly conservative approach to constructing our statistical models and only considered additive effects (i.e. no interactions). Because the scale of our intercept will be influenced by the size of our available dataset, we did not use the intercept when interpreting our coefficients (see Manley et al., 2002; McDonald, 2013) and scaled the resulting probabilities between 0 and 1; i.e. we examined relative rather than absolute selection. As noted above, within the Russian coastal areas, we examined whale activities only in relationship to gradients of oceanographic variables (i.e. salinity, temperature, and velocity) at whale locations and not in relationship to the variables themselves.

For statistically modelling whale movements in the central Chukchi Sea, our set of used and available locations was limited to the central Chukchi. For statistically modelling whale movements in the Russian coastal areas, we limited the used set to those located within the coastal buffer, but allowed paired available locations to be included if they were located outside the coastal buffer. Simulated paths (i.e. available locations) often veered outside of the coastal buffer when real whales (i.e. used locations) remained within the buffer.

2.6 Local scale habitat selection

To assess habitat selection at a local scale, we compared oceanographic conditions between locations associated with "directed travel" and "lingering" behaviors within the tracks of bowhead whales. In effect, we are asking what oceanographic features are associated with a whale stopping to feed along its path of travel. In this analysis, we are only comparing oceanographic variables along a whale's track and are not making any comparisons with randomly available locations. We used a generalized linear mixed model framework to determine the probability of switching from traveling to lingering as a function of our oceanographic variables. Locations associated with lingering were coded as '1' and locations associated with directed travel were coded as '0', allowing us to statistically model whale movements and oceanographic conditions using a logistic link and a binomial error distribution. To account for repeated observations, each observation was indexed by time of collection and then modeled with a spatial power covariance structure (Schabenberger and Pierce, 2001; Littell et al., 2006; Kaps and Lamberson, 2009). This covariance structure is a generalization of the more commonly used first-order auto-regressive (i.e. AR(1)) model. The AR(1) model assumes that all sampling intervals are equally spaced in time. The spatial power model accounts for the time elapsed between each pair of observations and therefore relaxes the requirement that data be sampled at equal time intervals. If all time intervals are equal in duration, this model reduces to the AR(1) model. To account for a limited number of whales, individual whales were specified as random intercepts. Models were fit using Proc GLIMMIX in SAS/STAT software version 9.3 (SAS Institute Inc., 2011).

We examined the same set of covariates when estimating the probability of lingering as for our resource selection analysis (see above). As with the prior analysis, we used backward stepwise selection and only retained variables that were significant at P=0.05. Again, within the

Russian coastal areas we only considered the gradients of salinity, temperature, and current velocity, not their point values.

3. Results

From 2006 to 2010 and in 2012, satellite tags provided enough location data to estimate locations and behaviors for 39 whales, 1 in 2006, 1 in 2007, 11 in 2008, 11 in 2009, 11 in 2010, and 4 in 2012 (Table 1). One transmitter, B08-07, provided locations in both 2008 and 2009. Of the 39 whales, 26 (67%) were tagged in Alaskan waters, mostly near Barrow, and 13 (33%) were tagged in Canadian waters, mostly near Tuktoyaktuk and Atkinson Point. Sex was determined for 23 whales; 9 (39%) were female and 14 (61%) were male. Twelve of the 39 whales (31%) were ≥13 m and considered mature. No females with dependent calves were tagged.

A total of 6,359 locations were estimated by the CRW model, of which 38% (2,461) were classified as lingering, 39% (2,477) as traveling, and 22% (1,421) as "unknown" (i.e., not classified as either lingering or traveling); most unknown locations occurred between bouts of traveling and lingering, and thus represent transitional behavior. Because lingering locations overlie each other in space, we plotted the kernel density of lingering locations by year (Duong and Hazelton 2005, Duong 2007). Kernel densities of lingering locations revealed two main patterns of movement across the Chukchi Sea. Specifically, bowhead whales spent relatively little time lingering within the central Chukchi Sea in 2008 and 2010 (Fig. 3a and 3c) compared to 2009 and 2012 (Fig. 3b and 3d). Neither the whale tagged in 2006 nor the one tagged in 2007 lingered in the central Chukchi, before reaching the Russian coast.

3.1 Landscape scale habitat selection

Data from 24 whales were used to examine resource selection during 2006–2009 in the central Chukchi Sea. An example temperature-salinity map with bowhead whale locations is presented for one two-week period (16–31 October 2009) in Fig. 5. Temperature-salinity maps with whale locations for 2008–2009 are presented in the Appendix (see Supplementary Material).

The data supported two different regression models. The first model included standardized bottom temperature (β_{logit}=-1.72; *SE*=0.66, *P*=0.02), standardized bottom temperature squared (β_{logit}=-1.11; *SE*=0.54, *P*=0.05), and the gradient of bottom velocity (β_{logit}=1.64; *SE*=0.43, *P*<0.01). The second model included standardized bottom salinity (β_{logit}=-0.34; *SE*=0.25, *P*=0.19), standardized bottom salinity squared (β_{logit}=-0.48; *SE*=0.22, *P*<0.04), and the gradient of bottom velocity (β_{logit}=1.30; *SE*=0.50, *P*=0.02). Neither salinity nor temperature were statistically significant when included in a model together, because these two variables were largely correlated and indicative of the same water masses (see Discussion). The intercepts are not presented because we cannot address the true probability of finding a whale within any habitat type (Manley et al. 1993, McDonald 2013). However, the selection coefficients indicate preference and can be interpreted on a relative scale. Tagged whales generally followed bottom water characterized by temperatures less than 0 ºC and salinities 31.5–34.25 psu, and were most likely to be found in water -1.2°C and +32.75 psu (Fig. 6). Although both models indicate that whales prefer to travel in the vicinity of high bottom velocity gradients, selection was for the highest velocity gradients observed (Fig. 7). The average velocity gradient at used locations was only 0.7 cm/s/km and only 5% of used locations occurred where the velocity gradient was > 2 cm/s/km. As such, the strong velocity gradients that whales selected were rarely available.

Data from 21 whales were used to examine resource selection during 2006–2009 in the Russian coastal areas (i.e. the Chukota coast and Wrangel Island). The final regression model only included the gradient of bottom salinity (β_{logit}=12.86; SE=1.33, $P<0.001$). However, the distribution of coefficients was not normally distributed and this coefficient is biased high. Recall that we paired each real whale track with 25 simulated tracks and then used logistic regression to estimate 25 sets of regression coefficients. We used the mean and standard deviation of the 25 independent fits of the logistic regression coefficients for our estimates and error terms. This approach assumes that the mean regression coefficients are normally distributed and this assumption was severely violated in the Russian coastal area. The distribution of coefficients for the salinity gradient had a mean of 84.5 and a median of only 5.0 (i.e., the distribution has a long positive tail). This can easily be observed in the distribution of salinity gradients in the set of used and available locations (Fig. 8). Hence, while the selection coefficient is biased high, whales are clearly selecting the strong salinity gradient along the Russian coast.

3.2 Local scale habitat selection

Data from 24 whales were used to model the probability whales lingered in the central Chukchi during 2006–2009. Of the 24 whales, 15 (63%) lingered in the central Chukchi for at least one 6-hr interval. The final regression model included an intercept (β_{logit}=-0.8583, SE=0.23, $P<0.001$), and the gradient of bottom salinity (β_{logit}=0.0917; SE=0.03, $P<0.01$).

Salinity gradients varied from approximately 0–0.4 psu/km (average=0.05, sd=0.04). The probability of lingering was near 0.3 for salinity gradients < 0.04 psu/km and approached 0.5 for gradients near 0.4 psu/km (Fig. 9). Within the Russian coastal areas, the probability of lingering was not related to any of the variables we modeled.

4. Discussion

We examined habitat selection of bowhead whales at two spatial scales. At the landscape scale, we found that bowhead whales generally followed water of Pacific origin characterized by temperatures <0 ºC and salinities between 31.5–34.25 psu. Bowhead whales avoided Alaskan Coastal Water and Siberian Shelf Water (the latter of which defines the western limit of their range) likely due to lower intrinsic densities of zooplankton prey. At the local scale, within the track of a whale, individuals were more likely to stop traveling and linger in areas characterized by stronger gradients in bottom salinity.

4.1 Habitat selection in the central Chukchi Sea

Bowhead whales migrating through the Chukchi Sea showed an affinity for relatively cold, salty water (Fig. 6). This finding is substantial, as the affinity for these oceanographic variables helps explain some aspects of fall migratory behavior across the central Chukchi Sea. This water is mostly of Bering Sea origin, including mainly Pacific Winter Water (PWW) and, to a lesser extent, Bering Shelf/Anadyr Water (BSAW), a composite water mass that, through winter cooling, transforms into PWW (Fig. 6). Euphausiids are not believed to reproduce in the Chukchi Sea (Neibauer and Schell, 1993; Siegel, 2000; Berline et al., 2008). Rather, the whales' association with these cold, saline waters is likely because euphausiids are advected northward from the Bering Sea by currents (Berline et al., 2008). Although some euphausiids may overwinter in PWW, most likely travel north with BSAW and then aggregate near the seafloor during their diurnal migration or when entering diapause in the late fall. To a much lesser extent, whales also used Atlantic Water (AW), which upwells along the Chukchi shelf break (Fig. 6). We suspect that whales may use AW because large copepod prey are known to be present north of the shelf break in AW (e.g. *C. glacialis* and *C. hyperboreus*; Ashjian et al., 2003) or because euphausiids advected north with PWW and BSAW may aggregate at the pycnocline between AW and PWW/BSAW.

Bowhead whales in the central Chukchi Sea also clearly avoided water that was either relatively fresh or relatively warm, including Alaskan Coastal Water (ACW) and Siberian Shelf Water (SSW) (Fig. 6). Much of the warm water reported in this study is characteristic of ACW carried northward by the Alaskan Coastal Current (ACC) and is freshened by discharges from the Yukon and Kuskokwim rivers. Temperature, salinity, and zooplankton sampling in the northern Bering and southern Chukchi seas in September of 2007 showed that BSAW has a higher abundance of large calanoid copepods and euphausiids than ACW, especially where BSAW occurs near the seafloor (Eisner et al., 2013). Although the mean flow of the ACC is northward through Bering Strait and through Barrow Canyon, this current is often disrupted by strong and/or prolonged winds from the north and northeast, displacing ACW from the Alaskan coast to intrude into the central Chukchi where these warm, fresh waters appear to be avoided by bowhead whales (e.g. Fig. 5). Of particular interest is how the affinity for cold water reasonably explains why some bowhead whales will migrate down the Alaskan coast instead of traversing the Chukchi Sea to Chukotka (see Supplemental Material). Bowhead whales migrating down the Alaskan coast only did so when the ACC was disrupted and colder, saltier water was present.

The other water mass avoided by tagged bowhead whales was SSW. Waters west of Wrangel Island are largely dominated by relatively fresh (<31.5 psu), cold SSW (<0.5 ºC) (e.g. Fig. 5; see also Supplemental Material) that originates as river discharge along the northern Russian coast and, therefore, is not expected to have high concentrations of zooplankton prey. Tagged whales rarely entered SSW, corroborating the likely absence of zooplankton prey and delineating the western boundary of the range of BCB bowhead whales.

Interestingly, there was little evidence that bowhead whales followed frontal features when choosing where to cross the Chukchi Sea. We detected some selection for large velocity gradients (Fig. 7), yet these velocity gradients were rare. The rarity of such gradients suggests that they do not determine the path whales choose to follow during migration. We suspect that bowhead whales know within what water masses they are likely to find zooplankton and they simply choose to remain within those water masses.

Whales were more likely to linger in areas characterized by higher salinity gradients, which are indicative of frontal features where zooplankton tend to aggregate. However, the probability that a whale lingers in the vicinity of a salinity front only increases from ~30% to ~50% (Fig. 9). Although the relatively weak response may be due to issues associated with ocean model resolution, we suggest that the weak response is more likely a reflection of uncertainties in where and when zooplankton are available for aggregation. Oceanographic features capable of aggregating zooplankton can exist without zooplankton present, thus obscuring the link between oceanographic model output and use by whales.

4.2 Feeding behavior in the central Chukchi Sea

Although the importance of the northern Chukotka coast as a feeding area for bowhead whales is well-known (e.g. Moore et al., 1995; Quakenbush et al., 2010; Citta et al., 2015), the central Chukchi Sea has not generally been considered to be an important foraging area (e.g. Quakenbush et al., 2010; Citta et al., 2015; but see Kuletz et al., 2015). Here, however, we show that the central Chukchi can be an important foraging area in some years. Bowhead whales lingered in the central Chukchi in both 2009 and 2012 (Fig. 3), but generally not in 2006, 2007, 2008, or 2010. In 2012, all four whales stopped in the central Chukchi, within Lease Sale Area 193, something we have not observed in any other year. One tag went off the air in October, but the other three whales remained in this area until sea ice began to form in December. By the time these three whales headed south, ice had already formed along the Chukotka coast and these three whales headed directly toward Bering Strait. This behavior would have been notable in a single whale, let alone all four. Unfortunately, we do not have oceanographic model output for 2012.

Close examination of the temperature and salinity maps (Supplemental Material) suggest that feeding in the central Chukchi in 2009 was more likely when northeast winds disrupted the ACC. This can be seen in the plots for 16–31 October and 1–15 November in 2009; note how currents which typically flow northward through Barrow Canyon and eastward across the shelf are reversed. Zooplankton are known to be advected onto shelf waters during periods of east winds. When these winds relax, the ACC traps zooplankton at Barrow (Ashjian et al., 2010; Okkonen et al., 2011). Perhaps whales are finding foraging opportunities on the Chukchi Shelf when east winds persist. East winds that are precursors to zooplankton aggregations at Barrow may also promote aggregations in the north central Chukchi. We have no model output for 2012, the other year where there was substantial lingering in the central Chukchi; however, winds in October and November of 2012 did not appear to be strong enough to disrupt the ACC. Hence, the mechanisms that lead to foraging in the central Chukchi are still unknown.

4.3 Habitat selection in the Russian coastal areas

The fact that habitat use along the Russian coastal areas was related to the strong salinity front was not surprising. As mentioned previously, Moore et al. (1995) documented bowhead whales feeding on large numbers of *T. raschii* along a sharp salinity front associated with the Siberian Coastal Current. Using an earlier version of the oceanographic model used in this study, Berline et al. (2008) modeled particle transport in the Bering and Chukchi seas to determine the most likely source of euphausiids observed near Point Barrow in fall. Although Berline et al. (2008) did not explicitly examine particle transport to the northern coast of Chukotka, many particles, representing euphausiids and copepods, turn west toward Chukotka after passing north of Bering Strait. The locations of landed particles along the northern coast of Chukotka extend from the Wrangel Island to Bering Strait (see Fig. 2 in Berline et al., 2008). Hence, BSAW is expected to deliver zooplankton to much of the Chukotka coast, where aggregation should occur along the front between the Siberian Coastal Current and BSAW (see Fig. 7e, Weingartner et al., 1999).

The probability of lingering along the Russian coast was not related to any of our covariates. Perhaps the microclimates associated with bowhead whale foraging are occurring at smaller scales than are resolved by the ocean model. Alternatively, the entire coast may be conducive for aggregating zooplankton and whales may simply be responding to variations in where and when zooplankton are available.

4.4 Utility of the oceanographic model

Sampling the marine environment at sufficient temporal and spatial resolutions to accurately characterize the entirety of the biophysical environment through which the BCB population of bowhead whales migrates is logistically and economically impossible. In this study, we used an ocean circulation model as a tool to address the logistical limitations of *in situ* sampling. By comparing simulated ocean conditions at and near observed whale locations, we have shown that there are identifiable relationships between ocean conditions and whale behaviors that define aspects of a whale's migration. Moreover, these identifiable relationships indicate that the ocean model itself is effective in simulating the physical environment of the Chukchi region.

Although we advocate collection of data provided by CTD (i.e. Conductivity, Temperature, and Depth) tags attached to animals (e.g. Lydersen et al., 2002), such technology may not provide the kind of data required to examine habitat selection over large scales. CTD data from tags attached to whales will be useful for identifying features that influence the probability a whale stops within its track, yet such data may not be useful for larger scale analyses of habitat selection. For example, we found that bowhead whales preferentially migrated through colder BSAW and PWW, and rarely entered relatively warm ACW or relatively fresh SSW. As such, CTD data collected by whales would show relatively little variation in temperature or salinity. Although this information is important, we also need to know what habitat types or water masses whales are actively avoiding in order to quantify resource selection. In effect, we need to have knowledge of the marine environment where whales are not located. This is also an important consideration for studies that use animals with CTD tags to study oceanography; i.e. studies concerned with oceanography, not animal resource selection. Animals are not random samplers of their environment, so collecting data from the animal alone will be insufficient for understanding the environment or how the animal moves through it. Fortunately, the RASM ocean model provided the temporal and spatial context that helped us understand what marine conditions whales were selecting and, in so doing, more broadly demonstrated the utility of ocean models as analytical tools for studies of the influence of the marine environment on its inhabitants. To be clear, we do not believe that output from oceanographic models are a replacement for empirical data. Rather, we are stating that oceanographic models can be useful and have a role in habitat selection analyses, especially where in situ measurements are lacking. Future resource selection models will clearly benefit by combining model output with empirical data, collected by the oceanographic tows, moorings, gliders, and/or the animals themselves (i.e. with CTD tags).

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Appendix. Supporting information.

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Table 1. Characteristics of bowhead whales used in this analysis. Lengths are estimated visually and are approximate; based upon the work of Koski et al. (1993), we define “mature” whales as those at least 13 m in length and “immature” whales as those less than 13 m in length. Additional information for these whales is presented in Table 1 of Citta et al. (2015). Estimated locations and their associated behavioral state were estimated from the CRW model (see Methods) at 6-hr intervals. The percentage of the September–November study period during which tracking data were available is given for each whale in the last column.

ID	Length (m)	Age	Sex	Tagging location	Deployment date	Behavioral state (# locations) September–November			total 6-hr intervals	% of possible intervals tracked
						Linger	Directed	Unknown		
B06-01	13.7	Mature	M	Barrow, AK	12-May-06	20	68	18	106	29%
B07-10	11	Imm	Unk	Barrow, AK	30-Aug-07	-	42	7	49	14%
B08-01	10.7	Imm	F	Atkinson Point, CAN	12-Aug-08	89	37	57	183	51%
B08-02	12.2	Imm	M	Barrow, AK	10-Sep-08	-	116	4	120	33%
B08-03	14.5	Mature	Unk	Barrow, AK	10-Sep-08	80	94	58	232	64%
B08-06	10	Imm	Unk	Barrow, AK	20-Sep-08	70	70	75	215	60%
B08-07	10	Imm	M	Barrow, AK	21-Sep-08	195	68	60	323	90%
B08-08	10	Imm	Unk	Barrow, AK	23-Sep-08	86	77	34	197	55%
B08-09	9.1	Imm	M	Barrow, AK	23-Sep-08	58	36	35	129	36%
B08-10	10	Imm	M	Barrow, AK	23-Sep-08	103	114	42	259	72%
B08-11	10	Imm	M	Barrow, AK	24-Sep-08	85	91	44	220	61%
B08-13	10	Imm	Unk	Barrow, AK	23-Sep-08	78	44	20	142	39%
B08-14	13.7+	Mature	M	Barrow, AK	23-Sep-08	7	30	16	53	15%

Table 1 continued.

ID	Length (m)	Age	Sex	Tagging location	Deployment date	Behavioral state (# locations) September–November			total 6-hr intervals	% of possible
						Linger	Directed	Unknown		
B09-01	15.2	Mature	F	Barrow, AK	22-Aug-09	30	122	137	289	80%
B09-02	13.7	Mature	Unk	Barrow, AK	22-Aug-09	87	35	26	148	41%
B09-03	12.2	Imm	Unk	Barrow, AK	22-Aug-09	211	83	22	316	88%
B09-04	10	Imm	M	Atkinson Point, CAN	23-Aug-09	42	90	50	182	51%
B09-05	10	Imm	M	Atkinson Point, CAN	23-Aug-09	27	125	31	183	51%
B09-06	12.8	Imm	M	Barrow, AK	24-Aug-09	17	18	3	38	11%
B09-09	13.4	Mature	Unk	Barrow, AK	29-Aug-09	90	78	29	197	55%
B09-12	12.2	Imm	Unk	Atkinson Point, CAN	2-Sep-09	16	16	34	66	18%
B09-13	8.2	Imm	F	Barrow, AK	14-Oct-09	20	-	65	85	24%
B09-15	11.3	Imm	F	Barrow, AK	14-Oct-09	41	57	21	119	33%
B09-16	13.1	Mature	M	Barrow, AK	14-Oct-09	23	65	4	92	26%
B10-01	15.2	Mature	M	Barrow, AK	24-May-10	61	38	27	126	35%
B10-03	13.7	Mature	F	Barrow, AK	24-May-10	18	18	3	39	11%
B10-05	9.1	Imm	Unk	Tuktoyaktuk, CAN	24-Aug-10	2	4	22	28	8%
B10-06	9.1	Imm	Unk	Tuktoyaktuk, CAN	25-Aug-10	16	24	43	83	23%
B10-08	10.7	Imm	Unk	Tuktoyaktuk, CAN	26-Aug-10	34	116	61	211	59%

Table 1 continued.

ID	Length (m)	Age	Sex	Tagging location	Deployment date	Behavioral state (# locations) September–November			total 6-hr intervals	% of possible
						Linger	Directed	Unknown		
B10-09	9.1	Imm	F	Herschel Island, CAN	25-Aug-10	17	8	38	63	18%
B10-11	12.2+	Imm	M	Tuktoyaktuk, CAN	27-Aug-10	74	99	106	279	78%
B10-12	11.4	Imm	F	Tuktoyaktuk, CAN	27-Aug-10	2	88	11	101	28%
B10-13	10.7	Imm	F	Tuktoyaktuk, CAN	28-Aug-10	150	51	20	221	61%
B10-14	12.2	Imm	M	Tuktoyaktuk, CAN	30-Aug-10	57	95	25	177	49%
B10-15	12.2	Imm	F	Tuktoyaktuk, CAN	30-Aug-10	76	86	34	196	54%
B12-01	12.2+	Imm	Unk	Pugughileq, AK	24-Apr-12	201	82	41	324	90%
B12-03	13.7	Mature	Tbd[2]	Barrow, AK	10-Sep-12	122	122	55	299	83%
B12-04	15.2	Mature	Tbd	Barrow, AK	10-Sep-12	94	7	39	140	39%
B12-05	13.7	Mature	Tbd	Barrow, AK	21-Sep-12	62	63	4	129	36%

Figure captions:

Figure 1. Cartoon of the major currents within the Chukchi, northern Bering, and western Beaufort seas. The Alaskan Coastal Current, currents across the Chukchi Shelf, and currents through Bering Strait may reverse under northeast winds. Northeast winds also encourage upwelling along the shelf break in both the Chukchi and Beaufort seas. This map is modified from Citta et al. (2015).

Figure 2. Bowhead whale tracks during the autumn migration across the Chukchi Sea, September–November, 2006–2010 and 2012.

Figure 3. Kernel densities of bowhead whale locations classified as being associated with lingering in the Chukchi Sea, September–November, 2008, 2009, 2010, and 2012. Tagged bowhead whales did not linger in the central Chukchi in 2006 or 2007.

Figure 4. Example of an actual bowhead whale track (red dots) and 25 simulated tracks. Simulated whales share the same step lengths as the actual whale but include a random component in the turn angle (see text). The area boundary is the envelope for all whale locations from September–November and the areas within 75 km of Wrangel Island and along the Chukotka coast are shaded blue.

Figure 5. Example plot of temperature (top) and salinity (bottom), averaged 16–31 October 2009. White arrows denote current vectors. Estimated bowhead whale locations and their behavior classifications overlie temperature and salinity layers. Crosses denote locations

classified as “traveling”, open diamonds are classified as “lingering”, and “x” denotes locations of unknown behavioral state. Plots for all time periods are provided in the Supplementary Material.

Figure 6. The distribution of all bowhead whale locations in temperature-salinity space (a) and the fit models of bowhead whale habitat selection based upon temperature and salinity (b). Tagged whales were most likely to occur in water -1.2 C and 32.75 psu; selection for other temperatures and salinities are scaled relative to this maximum. Blue boxes denote the approximate temperature-salinity signatures of different water masses (see DISCUSSION), including melt water (MW), Alaska Coastal Water (ACW), Bering Summer Water (BSW), Siberian Shelf Water (SSW), Bering Shelf/Anadyr Water (BSAW), Atlantic Water (AW), and Pacific Winter Water (PWW). Water mass boundaries are taken from Esiner et al. (2015), Gong et al. (In press), and Itoh et al. (2015).

Figure 7. Relative selection within the central Chukchi as a function of current gradient while controlling for the effects of salinity (solid line) or temperature (dashed line).

Figure 8. Box plots of the salinity gradient at used and available locations. Center lines are median values, box boundaries are the 25th and 75th percentiles, error bars are the 10th and 90th percentiles, and dots are the 5th and 95th percentiles.

Figure 9. The probability of lingering as a function of the maximum salinity gradient within 20 km. Dotted lines are 95% confidence limits.

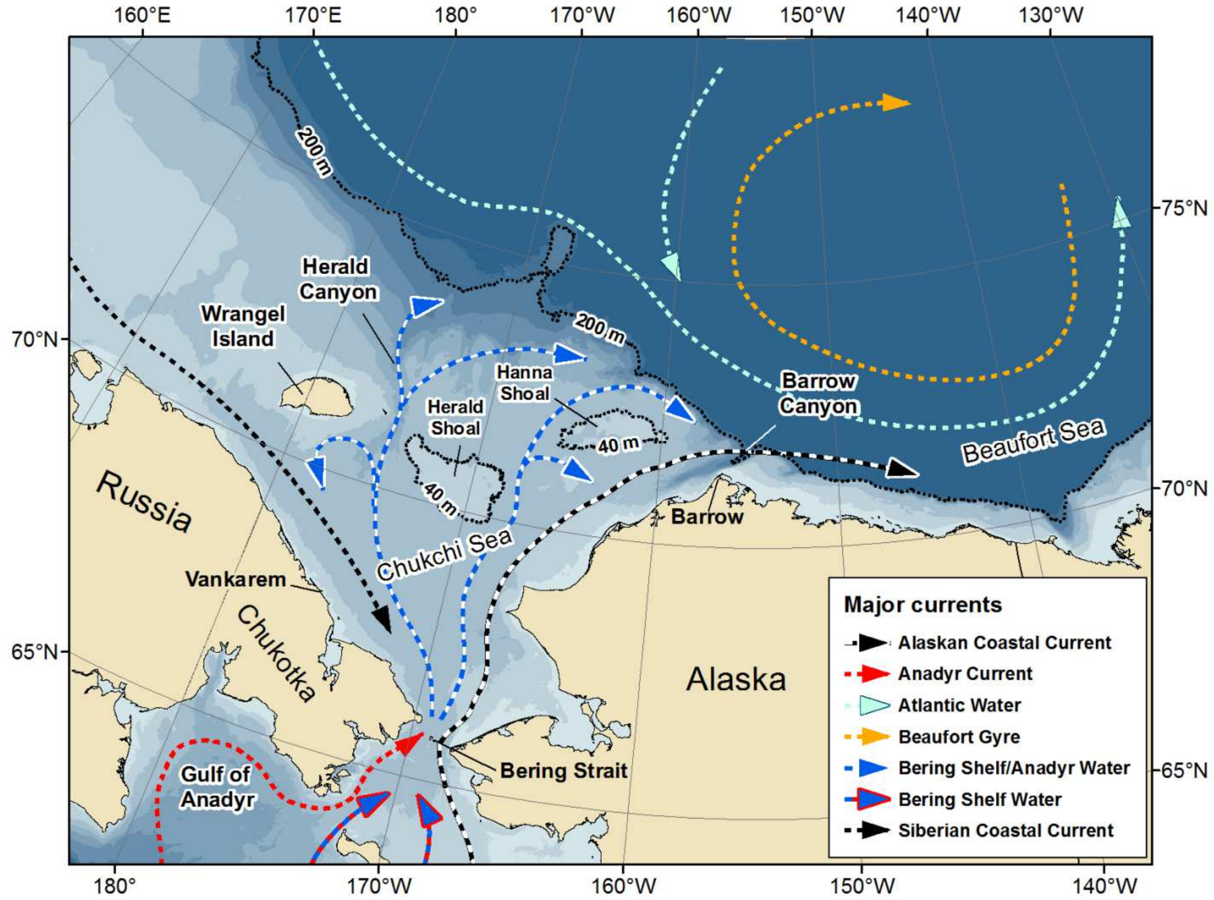

Figure 1. Cartoon of the major currents within the Chukchi, northern Bering, and western Beaufort seas. The Alaskan Coastal Current, currents across the Chukchi Shelf, and currents through Bering Strait may reverse under northeast winds. Northeast winds also encourage upwelling along the shelf break in both the Chukchi and Beaufort seas. This map is modified from Citta et al. (2015).

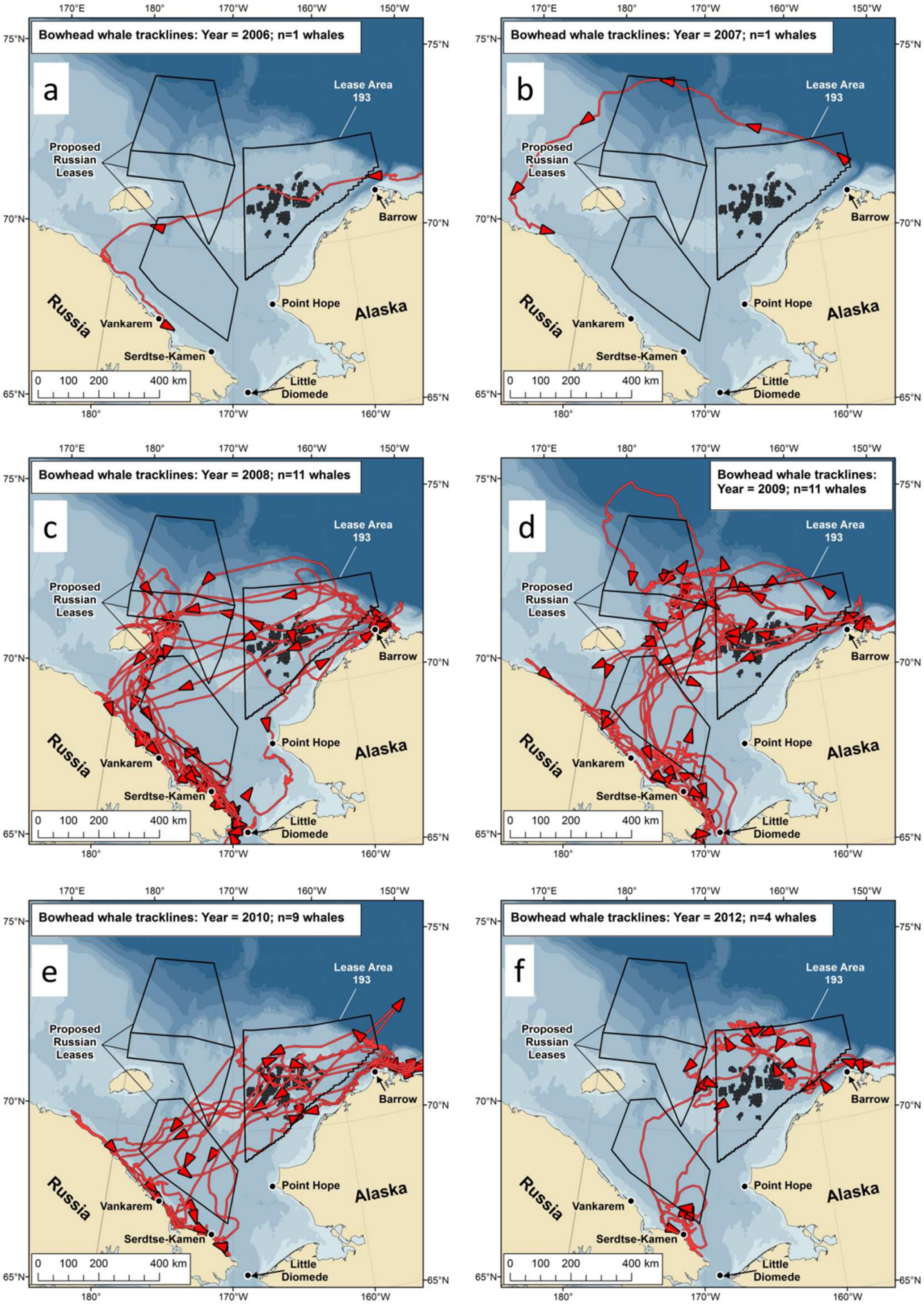

Figure 2. Bowhead whale tracks during the autumn migration across the Chukchi Sea, September–November, 2006–2010 and 2012.

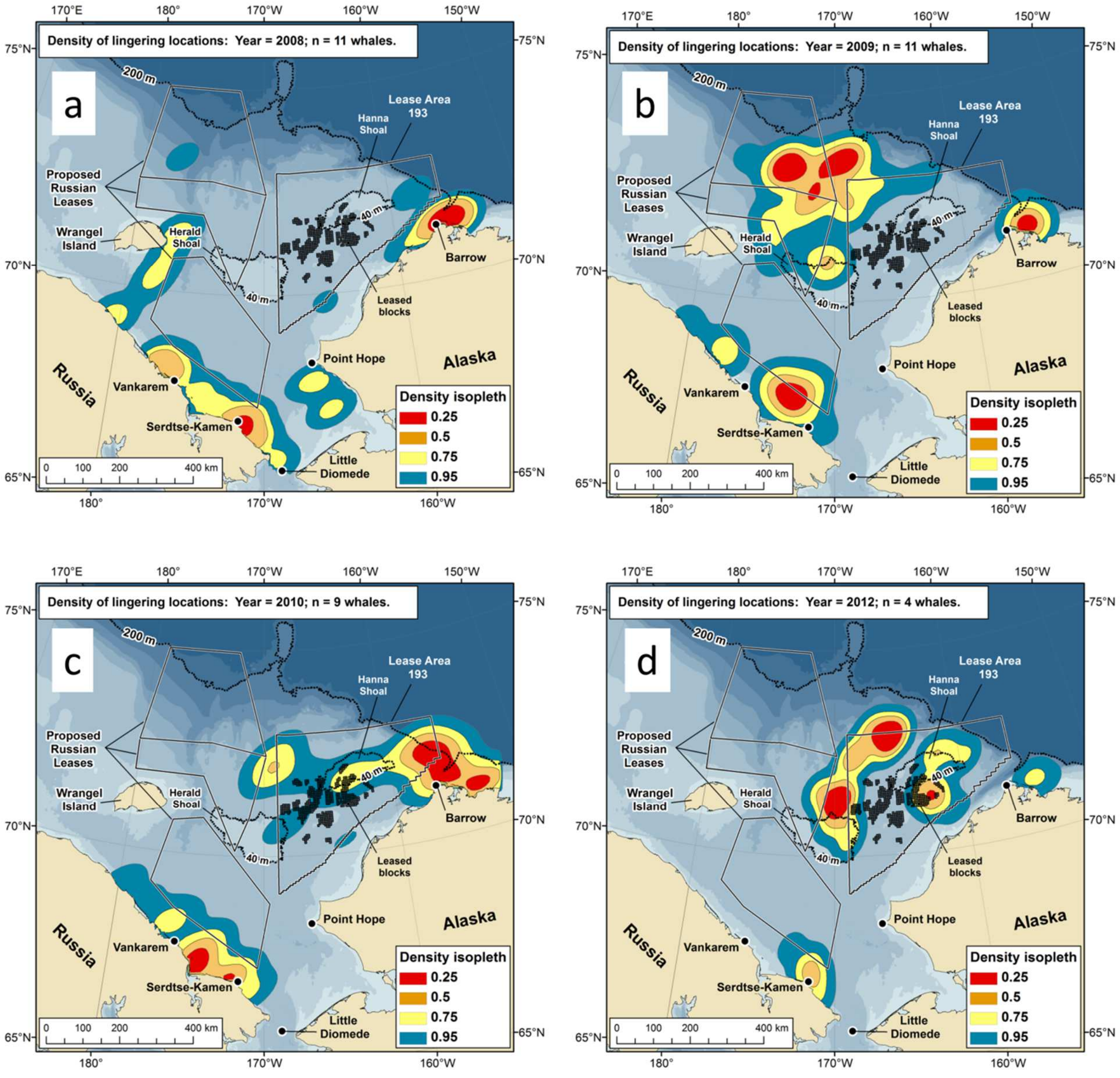

Figure 3. Kernel densities of bowhead whale locations classified as being associated with lingering in the Chukchi Sea, September–November, 2008, 2009, 2010, and 2012. Tagged bowhead whales did not linger in the central Chukchi in 2006 or 2007.

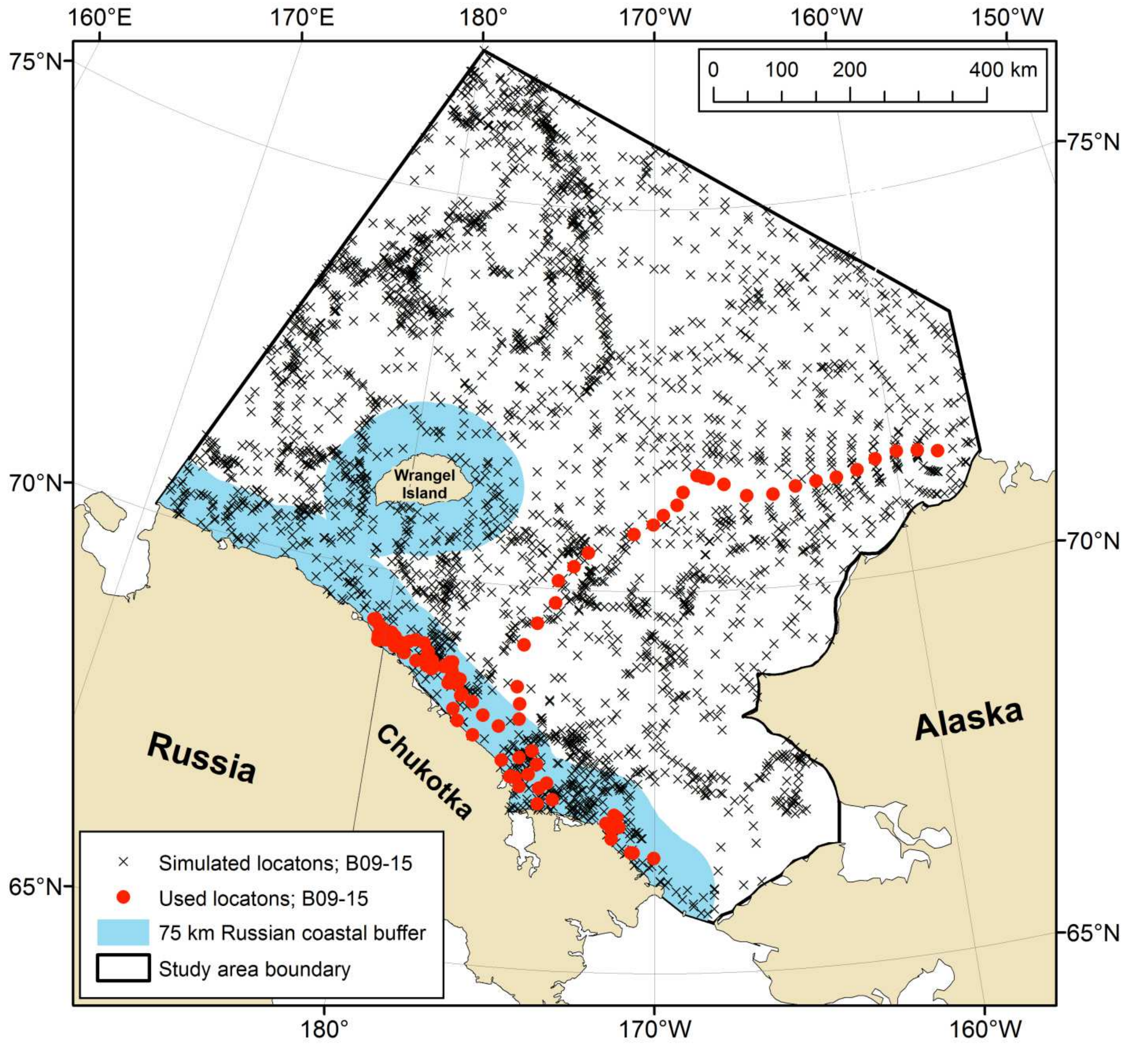

Figure 4. Example of an actual bowhead whale track (red dots) and 25 simulated tracks. Simulated whales share the same step lengths as the actual whale but include a random component in the turn angle (see text). The area boundary is the envelope for all whale locations from September–November and the areas within 75 km of Wrangel Island and along the Chukotka coast are shaded blue.

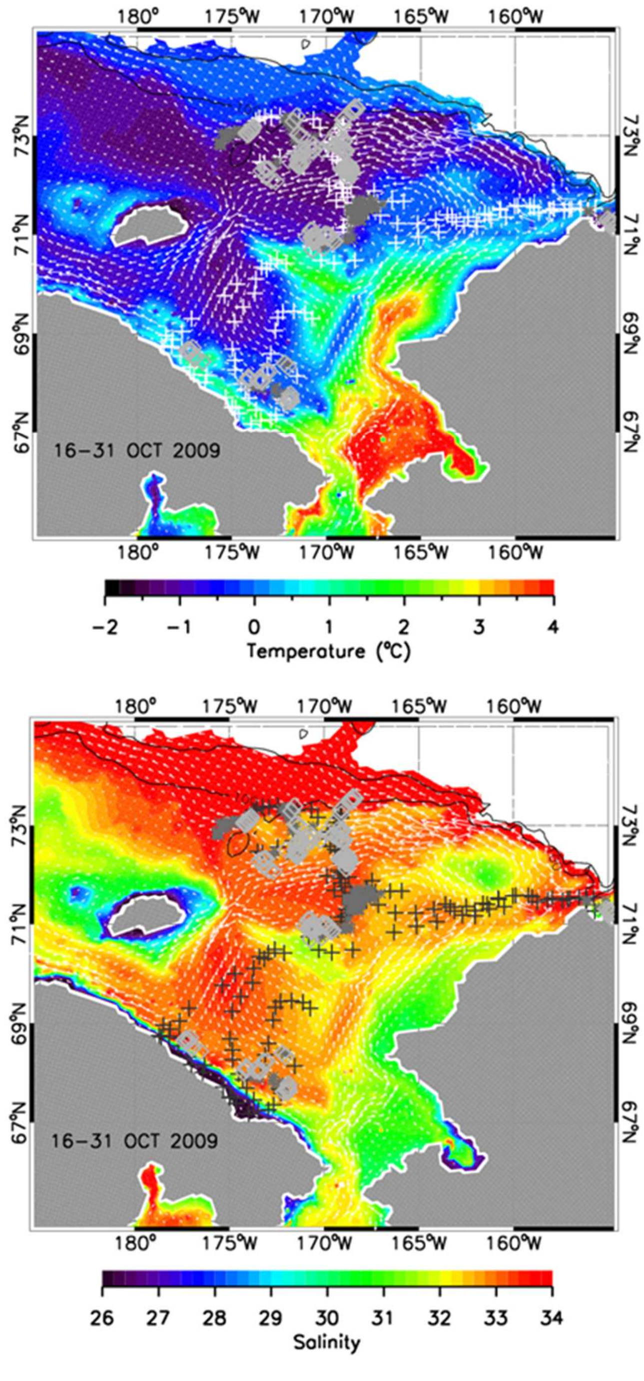

Figure 5. Example plot of temperature and salinity, averaged 16–31 October 2009. White arrows denote current vectors. Estimated bowhead whale locations and their behavior classifications overlie temperature and salinity layers. Crosses denote locations classified as “traveling”, light gray open diamonds are classified as “lingering”, and dark gray “x” denotes locations of unknown behavioral state. Plots for all time periods are provided in the Supplementary Material.

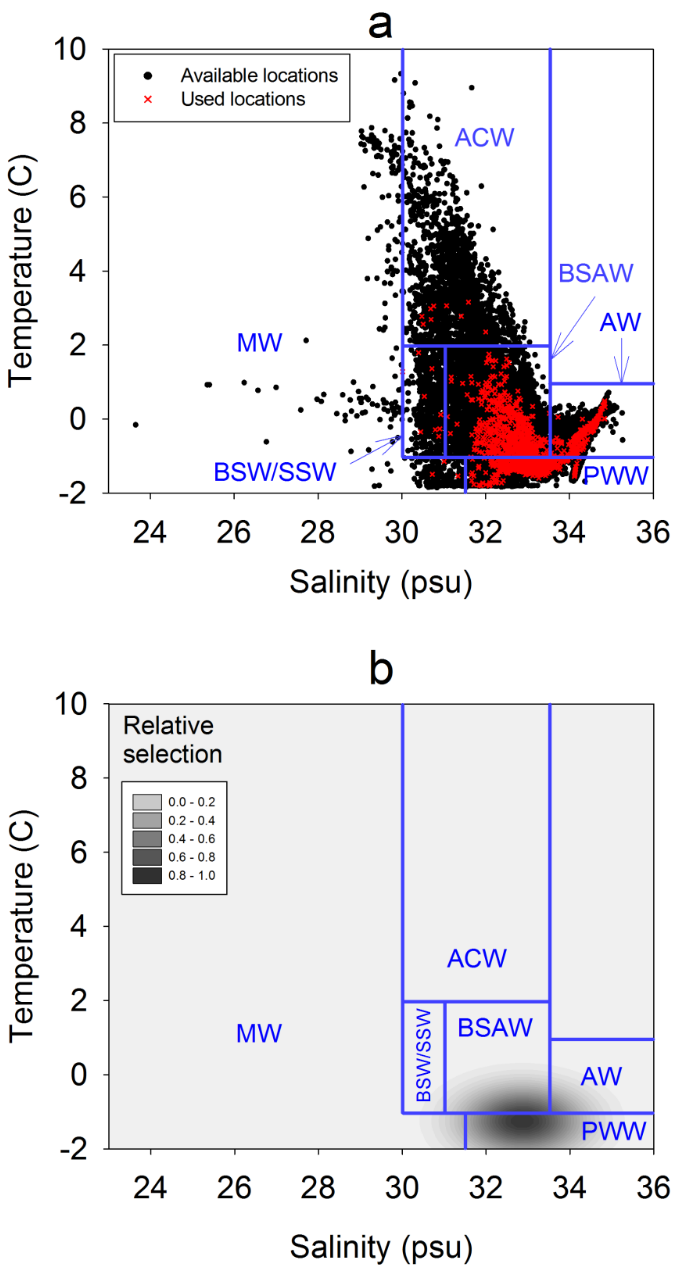

Figure 6. The distribution of all bowhead whale locations in temperature-salinity space (a) and the fit models of bowhead whale habitat selection based upon temperature and salinity (b). Tagged whales were most likely to occur in water -1.2 C and 32.75 psu; selection for other temperatures and salinities are scaled relative to this maximum. Blue boxes denote the approximate temperature-salinity signatures of different water masses (see DISCUSSION), including melt water (MW), Alaskan Coastal Water (ACW), Bering Summer Water (BSW), Siberian Shelf Water (SSW), Bering Shelf/Anadyr Water (BSAW), Atlantic Water (AW), and Pacific Winter Water (PWW). Water mass boundaries are taken from Esiner et al. (2015), Gong et al. (In press), and Itoh et al. (2015).

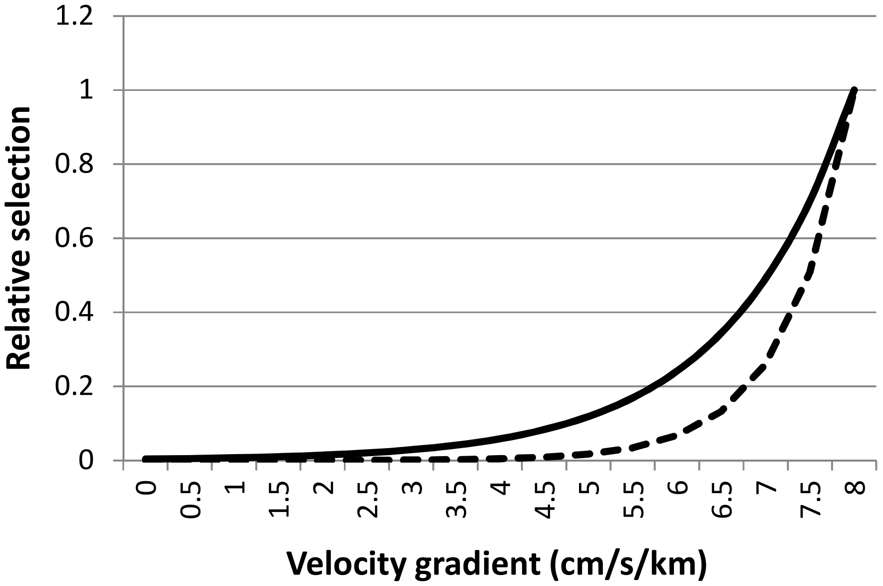

Figure 7. Relative selection within the central Chukchi as a function of current gradient while controlling for the effects of salinity (solid line) or temperature (dashed line).

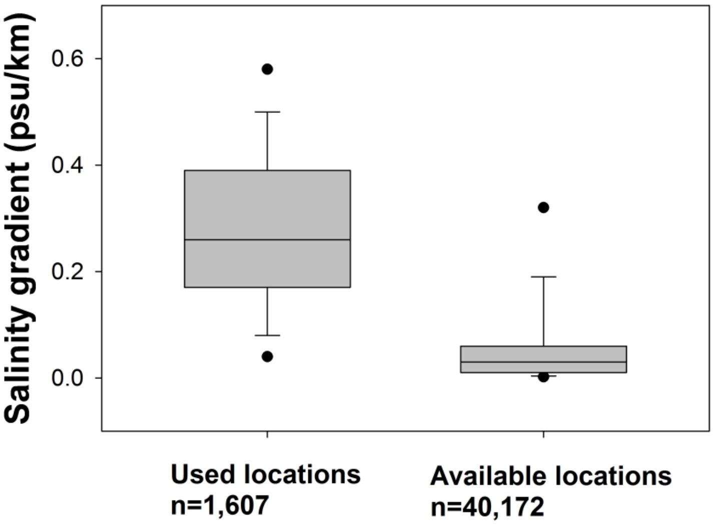

Figure 8. Box plots of the salinity gradient at used and available locations. Center lines are median values, box boundaries are the 25th and 75th percentiles, error bars are the 10th and 90th percentiles, and dots are the 5th and 95th percentiles.

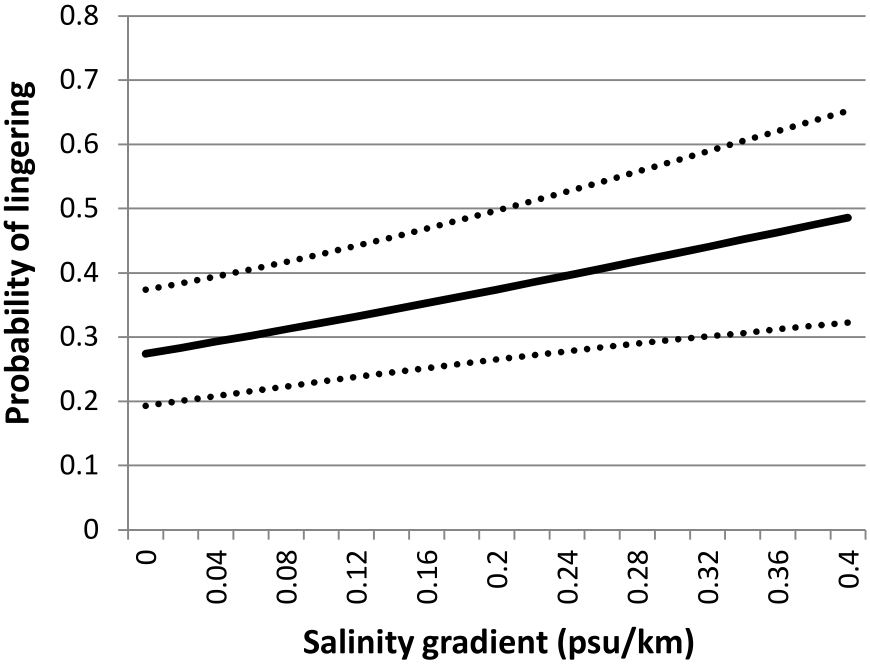

Figure 9. The probability of lingering as a function of the maximum salinity gradient within 20 km. Dotted lines are 95% confidence limits.