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Ecological characteristics of core-use areas used by Bering–Chukchi–Beaufort (BCB) bowhead whales, 2006–2012

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ABSTRACT

The Bering–Chukchi–Beaufort (BCB) population of bowhead whales (*Balaena mysticetus*) ranges across the seasonally ice-covered waters of the Bering, Chukchi, and Beaufort seas. We used locations from 54 bowhead whales, obtained by satellite telemetry between 2006 and 2012, to define areas of concentrated use, termed "core-use areas". We identified six primary core-use areas and describe the timing of use and physical characteristics (oceanography, sea ice, and winds) associated with these areas. In spring, most whales migrated from wintering grounds in the Bering Sea to the Cape Bathurst polynya, Canada (Area 1), and spent the most time in the vicinity of the halocline at depths <75 m, which are within the euphotic zone, where calanoid copepods ascend following winter diapause. Peak use of the polynya occurred between 7 May and 5 July; whales generally left in July, when copepods are expected to descend to deeper depths. Between 12 July and 25 September, most tagged whales were located in shallow shelf waters adjacent to the Tuktoyaktuk Peninsula, Canada (Area 2), where wind-driven upwelling promotes the concentration of calanoid copepods. Between 22 August and 2 November, whales also congregated near Point Barrow, Alaska (Area 3), where east winds promote upwelling that moves zooplankton onto the Beaufort shelf, and subsequent relaxation of these winds promoted zooplankton aggregations. Between 27 October and 8 January, whales congregated along the northern shore of Chukotka, Russia (Area 4), where zooplankton likely concentrated along a coastal front between the southeastward-flowing Siberian Coastal Current and northward-flowing Bering Sea waters. The two remaining core-use areas occurred in the Bering Sea: Anadyr Strait (Area 5), where peak use occurred between 29 November and 20 April, and the Gulf of Anadyr (Area 6), where peak use occurred between 4 December and 1 April; both areas exhibited highly fractured sea ice. Whales near the Gulf of Anadyr spent almost half of their time at depths between 75 and 100 m, usually near the seafloor, where a subsurface front between cold Anadyr Water and warmer Bering Shelf Water presumably aggregates zooplankton. The amount of time whales spent near the seafloor in the Gulf of Anadyr, where copepods (in diapause) and, possibly, euphausiids are expected to aggregate provides strong evidence that bowhead whales are feeding in winter. The timing of bowhead spring migration corresponds with when zooplankton are expected to begin their spring ascent in April. The core-use areas we identified are also generally known from other studies to have high densities of whales and we are confident these areas represent the majority of important feeding areas during the study (2006–2012). Other feeding areas, that we did not detect, likely existed during the study and we expect core-use area boundaries to shift in response to changing hydrographic conditions.

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Introduction

Bowhead whales (*Baelena mysticetus*) of the Bering–Chukchi–Beaufort (BCB) population occupy seasonally ice covered waters of the Bering, Chukchi, and Beaufort seas (Moore and Reeves, 1993). Whales in this population typically winter in the Bering Sea, over the continental shelf and north of the southern boundary of sea ice (Moore and Reeves, 1993; Citta et al., 2012). In April, the majority of whales migrate northward toward the Chukchi Sea and follow the Alaskan coast past Point Barrow and then proceed east through the Alaskan Beaufort Sea to the region near Cape Bathurst in Amundsen Gulf, Canada, where they summer (Quakenbush et al., 2012, 2013). However, upon entering the Chukchi Sea, a few whales migrate westward along the Chukotka coast and remain in the Chukchi Sea all summer (e.g., Melnikov and Zeh, 2007; Citta et al., 2012). Between August and October, whales in the Canadian Beaufort Sea begin to migrate west, following the Alaskan coast back to Point Barrow. From Point Barrow, whales cross the Chukchi Sea to the Chukotka coast and slowly proceed southwards as winter approaches. By the end of December, most bowhead whales have returned to the Bering Sea (Quakenbush et al., 2010; Citta et al., 2012).

Bowhead whales are baleen whales and feed by filtering zooplankton through their exceptionally long 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). Energetic models suggest that bowhead whales need dense aggregations of zooplankton to meet their energetic requirements (see review in Lowry, 1993) and research in Greenland suggests that bowhead whales target dense aggregations of zooplankton (Laidre et al., 2007). Hence, if the density of zooplankton varies spatially and temporally, we expect that variability to influence the spatial and temporal distribution of bowhead whales.

Zooplankton density is known to correlate with areas of high primary productivity (e.g., Springer et al., 1996; Walkusz et al., 2012). Furthermore, although zooplankton are capable of active vertical locomotion, their distribution is affected by advection resulting from currents and wind (e.g., Lane et al., 2008). There is no evidence that euphausiids breed in the Chukchi or Beaufort seas (Niebauer and Schell, 1993; Siegel, 2000; Berline et al., 2008), those found in bowhead whale stomachs near Barrow are thought to be carried on currents from the Bering Sea. In contrast, calanoid copepods are known to reproduce in Arctic waters (Ashjian et al., 2003); upwelling and advection are also known to redistribute and aggregate them (e.g., Ashjian et al., 2010; Walkusz et al., 2012). Seasonal processes within the ice, such as the timing of melt, light intensity, and mixing, affect the timing of phytoplankton blooms and, in turn, also affect seasonal abundance and distribution of zooplankton that feed on them.

The purpose of this paper is to describe areas of concentrated use by bowhead whales, the seasonal progression in the use, and the physical environment within those areas. We use satellite telemetry, collected between 2006 and 2012, to identify areas of concentrated use by bowhead whales in the BCB population. Within core-use areas, we then describe seasonal patterns in ice concentration and wind-driven upwelling, and use a pan-arctic coupled ice-ocean model (Maslowski et al., 2004, 2012) to identify seasonally-occurring frontal features and circulation phenomena that may concentrate bowhead prey. For some areas known to be important bowhead feeding areas, the relevant meteorology and oceanography have been reasonably well-described. For example, upwelling-favorable winds promote favorable feeding conditions on the shallow shelves near Tuktoyaktuk (Walkusz et al., 2012) and Point Barrow (Ashjian et al., 2010). In contrast, downwelling-favorable winds promote favorable feeding conditions along the Chukotka coast (Moore et al., 1995; Weingartner et al., 1999). Where applicable, we interpret the results of the oceanographic model in light of these empirical studies to verify that model results reasonably simulate observed oceanographic features and phenomena that promote the aggregation of zooplankton and use by bowhead whales.

Methods

Tagging

We used the satellite-linked transmitter attachment and deployment system developed by the Greenland Institute of Natural Resources (Heide-Jørgensen et al., 2001, 2003) to deploy tags on bowhead whales, and the Argos system of satellites to obtain data from the tags. 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). All tags recorded location data; SPLASH, Mk10, and CTD tags also recorded dive and oceanographic data.

Tags were attached to whales by researchers and 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 during tag deployment. Skin biopsies were used to determine sex of whales using the polymerase chain reaction to amplify 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 Native whalers at the time of tagging. Due to permitting requirements, calves less than 1 year of age and cows with calves were avoided.

Location processing

Transmitter locations were estimated using signals received by Argos satellites when whales were at the surface. Location error is estimated by the Argos system and characterized by "location classes" (see the Argos User's Manual for a complete description; available from argos-system.org/manual/). Location classes are only an approximation of location accuracy (e.g., Vincent et al., 2002). Instead of using only the locations representing the highest accuracy (2 or 3), we chose to use all available location classes (B, A, 0, 1, 2, 3) and a filter developed by Freitas et al. (2008) in R (R Core Team, 2013) to remove less accurate locations. Locations that resulted in swim velocities of >1.94 m/s (>6.98 km/h) were removed unless they were ⩽5 km from the previous location. The threshold velocity of 1.94 m/s is the maximum observed migration speed of bowheads not fleeing vessels or assisted by currents (e.g., Zeh et al., 1993). Locations ⩽5 km from the previous location were filtered using angular thresholds because velocity thresholds remove many good-quality locations for which high swim speeds are simply due to locations being recorded close in time. For locations collected close in time, low-quality ones often fall far from the line of travel, forming acute angles between adjacent locations (e.g., Freitas et al., 2008; Keating, 1994). We used default settings to define the angular components of the Freitas et al. (2008) filter; within 2.5 km of the track line, locations resulting in angles <15 degrees were removed and locations between 2.5 and 5 km of the track line were removed if they resulted in angles <25 degrees. We then removed locations that fell on land to establish the final set of locations used in our analyses. This study includes locations used for prior studies of whale movements (Quakenbush et al.,

2010; Heide-Jørgensen et al., 2011; Citta et al., 2012) and additional location data not previously considered.

Identifying bowhead whale core-use areas

We calculated utilization distributions (i.e., probability densities) from our sample of bowhead locations to identify core-use areas. Utilization distributions were calculated using the lattice-based approach of Barry and McIntyre (2011). Most kernel methods estimate probability density in unconstrained space, not accounting for areas in which animals cannot enter. When locations cluster along shorelines or in rivers, use often occurs in areas that should have no use, such as land. Typical approaches to estimating kernel densities first estimate location density in unconstrained space, clip areas that are unavailable to the animal, and then renormalize the density surface so it sums to one. The approach of Barry and McIntyre (2011) starts with a grid of evenly spaced nodes; nodes are connected to adjacent nodes to form a spatial lattice. Location density is estimated using a random walk process, where the length of the random walk, k, and the probability that the random walk moves to a neighboring node, M, controls the smoothness of the density. Specifically, location density is estimated as the probability density of the length-k random walk on the lattice. At $k = 0$, the probability density is equal to the original observations. As k increases, probability density diffuses from node to node. An obvious advantage to this model is that density must follow linkages between nodes and, therefore, is not allowed to fall on land or cross impassable barriers, such as peninsulas. As a smoothing parameter, k is analogous to the bandwidth of kernel methods (e.g., Worton, 1989) and, as with kernel methods, cross-validation can be used to estimate k. We used Package "latticeDensity" (Barry and McIntyre, 2011) in R (R Core Team, 2013) to estimate k with

cross-validation and to estimate lattice-based densities of bowhead whale locations. Smoothing is fine-tuned by M, which was manually set by Barry and McIntyre (2011). We used the movements of whales to approximate M, the probability that a random walk remains at the same node (or within the same grid cell) in one time step. Using average daily locations for whales, we calculated M as the proportion of locations found in the same grid cell on sequential days. Choosing the spacing between nodes is a tradeoff between computational efficiency and the ability for the lattice to fit complicated coastlines. We used a node spacing of 15 km, which is sufficient for delineating the coastlines and for identifying large islands.

Most whales were tagged near Barrow, Alaska, or Tuktoyaktuk, Canada (Fig. 1) and tags have a finite life-span (Table 1). This resulted in large differences in the number of locations that occur in each sea (Bering, Chukchi, Beaufort). For example, the largest sample sizes occur in the Chukchi Sea, because many whales were tagged as they passed Point Barrow during the autumn migration. To account for these differences, we estimated separate probability densities for the Bering, Chukchi, and Beaufort seas and then combined the resulting probability density functions to generate a single map, where each sea is equally weighted. Whale core-use areas were defined as occurring within the 25% density contour.

Dive behavior

We used data from SPLASH tags to identify characteristics of whales' dive histories. SPLASH tags sampled pressure (i.e., depth) every 10 s. Because this was too much data to process through the Argos system, tags had software onboard that summarized dive information into histograms. Histograms covered 6-h intervals and were stored onboard the tag until they could be transmitted to a satellite. In this study, we consider the Time-At-Depth (TAD)
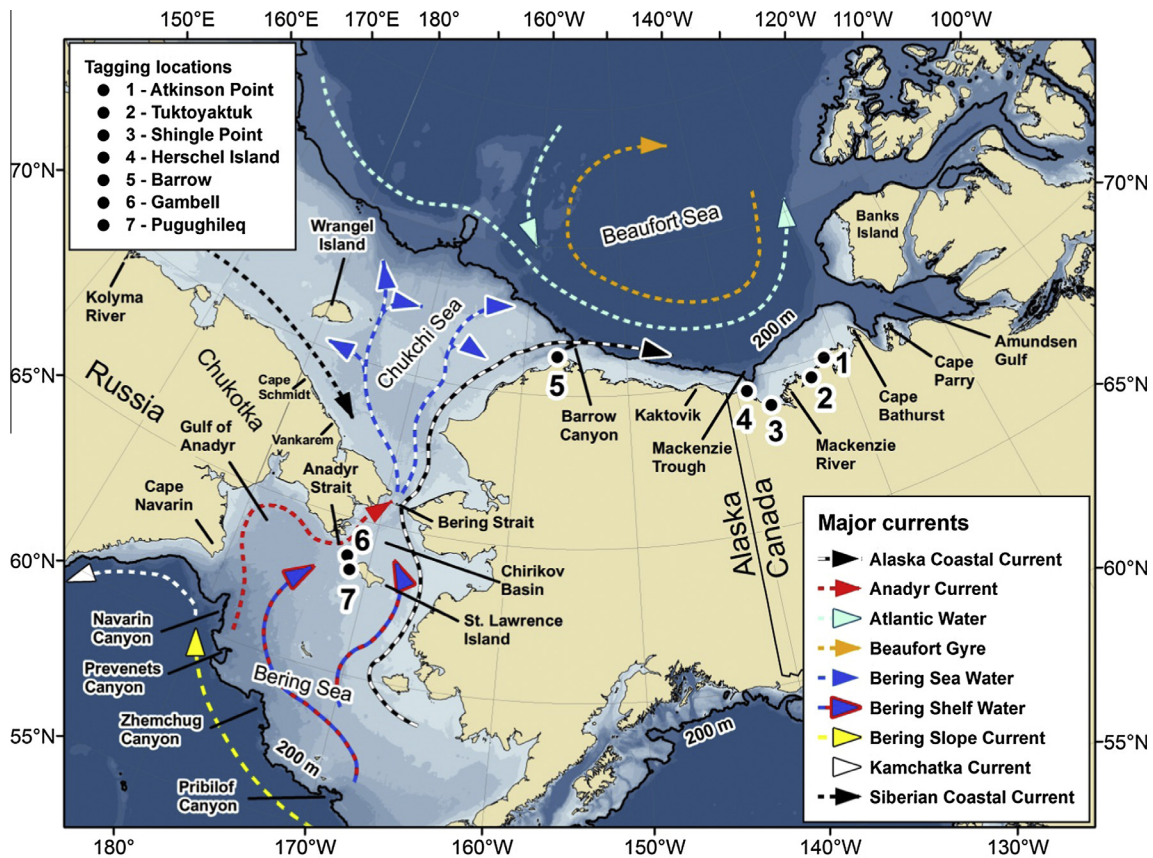

Fig. 1. Tagging locations, stylized currents, and submarine canyons within the study area.

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. "Dive data?" indicates if dive data were used from this whale in these analyses.

ID	Length (m)	Age	Sex	Dive data?	Location	Deployment (UTC)	Last transmission (UTC)	Days with transmissions	Tagger/boat driver
B06-01	13.7	Mature	Male	N	Barrow, AK	12-May-06	10-Nov-06	182	M. Jensen/From ice edge
B06-03	10.6	Imm	Unk[a]	N	Barrow, AK	21-Sep-06	21-Nov-06	6	M. Jensen/J. George
B07-01	9.1	Imm	Male	N	Barrow, AK	25-Apr-07	29-Apr-07	4	L. Brower/From ice edge
B07-02	10.1	Imm	Male	N	Barrow, AK	26-Apr-07	18-Jul-07	6	L. Brower/From ice edge
B07-06	9.7	Imm	Male	N	Shingle Point, CAN	25-Aug-07	5-Sep-07	10	G. Tagarook/L. Arey
B07-08	13.7	Mature	Female	N	Barrow, AK	30-Aug-07	3-Sep-07	5	C. George/L. Brower
B07-09	11.5	Imm	Female	N	Barrow, AK	30-Aug-07	31-Aug-07	2	C. George/L. Brower
B07-10	11	Imm	Unk	N	Barrow, AK	30-Aug-07	14-Sep-07	16	C. George/L. Brower
B08-01	10.7	Imm	Female	Y	Atkinson Point, CAN	12-Aug-08	18-Aug-09	241	A. Jensen/D. Arey
B08-02	12.2	Imm	Male	Y	Barrow, AK	10-Sep-08	16-Oct-08	35	B. Adams/F. Suvlu
B08-03	14.5	Mature	Unk	Y	Barrow, AK	10-Sep-08	22-Nov-08	73	H. Brower/B. Adams
B08-04	11.9	Imm	Unk	N	Barrow, AK	20-Sep-08	21-Sep-08	2	L. Brower/N. Arey
B08-05	10.7	Imm	Female	N	Barrow, AK	20-Sep-08	23-Sep-08	4	L. Brower/N. Arey
B08-06	10	Imm	Unk	Y	Barrow, AK	20-Sep-08	12-Mar-09	170	H. Brower/B. Adams
B08-07	10	Imm	Male	Y	Barrow, AK	21-Sep-08	19-Oct-09	365	H. Brower/B. Adams
B08-08	10	Imm	Unk	Y	Barrow, AK	23-Sep-08	3-Jul-09	267	H. Brower/B. Adams
B08-09	9.1	Imm	Male	N	Barrow, AK	23-Sep-08	6-Jul-09	216	L. Brower/M. Donovan
B08-10	10	Imm	Male	N	Barrow, AK	23-Sep-08	16-Apr-09	204	H. Brower/B. Adams
B08-11	10	Imm	Male	N	Barrow, AK	24-Sep-08	16-Apr-09	202	L. Brower/M. Donovan
B08-12	9.1+	Imm	Male	N	Barrow, AK	23-Sep-08	31-Aug-09	268	H. Brower/B. Adams
B08-13	10	Imm	Unk	N	Barrow, AK	23-Sep-08	12-Mar-09	149	L. Brower/M. Donovan
B08-14	13.7+	Mature	Male	N	Barrow, AK	23-Sep-08	24-Jul-09	254	H. Brower/B. Adams
B09-01	15.2	Mature	Female	Y	Barrow, AK	22-Aug-09	21-Dec-09	122	H. Brower III/B. Adams
B09-02	13.7	Mature	Unk	Y	Barrow, AK	22-Aug-09	30-Jan-10	138	H. Adams/B. Adams
B09-03	12.2	Imm	Unk	Y	Barrow, AK	22-Aug-09	4-Dec-09	105	L. Brower/M. Donovan
B09-04	10	Imm	Male	Y	Atkinson Point, CAN	23-Aug-09	31-Jul-10	311	J. Pokiak/D. Arey
B09-05	10	Imm	Male	Y	Atkinson Point, CAN	23-Aug-09	3-Sep-10	340	J. Pokiak/C. Pokiak
B09-06	12.8	Imm	Male	Y	Barrow, AK	24-Aug-09	14-Sep-09	22	L. Brower/P. Anashuak
B09-07	11.3	Imm	Male	Y	Barrow, AK	29-Aug-09	5-Sep-09	8	L. Brower/D. Pikok
B09-08	13.7	Mature	Male	N	Barrow, AK	29-Aug-09	4-Mar-10	28	B. Adams/J. Aiken
B09-09	13.4	Mature	Unk	Y	Barrow, AK	29-Aug-09	23-Aug-10	311	L. Brower/D. Pikok
B09-12	12.2	Imm	Unk	N	Atkinson Point, CAN	02-Sep-09	4-Nov-09	60	A. Jensen/D. Arey
B09-13	8.2	Imm	Female	Y	Barrow, AK	14-Oct-09	15-Nov-10	350	H. Brower/J. George
B09-14	13.7	Mature	Male	N	Barrow, AK	14-Oct-09	15-Oct-09	2	H. Brower/J. George
B09-15	11.3	Imm	Female	Y	Barrow, AK	14-Oct-09	2-Sep-10	261	L. Brower/W. Williams
B09-16	13.1	Mature	Male	N	Barrow, AK	14-Oct-09	27-May-10	164	J. George/H. Brower
B10-01	15.2	Mature	Male	Y	Barrow, AK	24-May-10	17-Nov-10	175	A. Kippi/C. Kippi
B10-03	13.7	Mature	Female	Y	Barrow, AK	24-May-10	6-Aug-10	75	C. Kippi/J. Sage
B10-04	16.8	Mature	Female	N	Barrow, AK	25-May-10	11-Sep-10	18	A. Kippi/M. Adams
B10-05	9.1	Imm	Unk	Y	Tuktoyaktuk, CAN	24-Aug-10	25-Sep-10	31	J. Pokiak/C. Pokiak
B10-06	9.1	Imm	Unk	Y	Tuktoyaktuk, CAN	25-Aug-10	6-Oct-10	31	J. Pokiak/C. Pokiak
B10-07	9.9	Imm	Unk	Y	Tuktoyaktuk, CAN	26-Aug-10	4-Sep-10	6	J. Pokiak/C. Pokiak
B10-08	10.7	Imm	Unk	Y	Tuktoyaktuk, CAN	26-Aug-10	16-Sep-11	281	J. Pokiak/C. Pokiak
B10-09	9.1	Imm	Female	N	Herschel Island, CAN	25-Aug-10	8-Mar-11	66	A. Jensen/D. Arey
B10-11	12.2+	Imm	Male	Y	Tuktoyaktuk, CAN	27-Aug-10	25-Jun-11	155	J. Pokiak/C. Pokiak
B10-12	11.4	Imm	Female	Y	Tuktoyaktuk, CAN	27-Aug-10	16-Feb-11	118	J. Pokiak/C. Pokiak
B10-13	10.7	Imm	Female	Y	Tuktoyaktuk, CAN	28-Aug-10	14-Nov-10	79	J. Pokiak/C. Pokiak
B10-14	12.2	Imm	Male	Y	Tuktoyaktuk, CAN	30-Aug-10	13-Jul-11	255	J. Pokiak/C. Pokiak
B10-15	12.2	Imm	Female	Y	Tuktoyaktuk, CAN	30-Aug-10	13-Sep-11	336	J. Pokiak/C. Pokiak
B12-01	12.2+	Imm	Unk	Y	Savoonga, AK	24-Apr-12	12-Dec-12	225	Travis Akeya/Tom Akeya
B12-02	13.7	Mature	Unk	N	Gambell, AK	30-Apr-12	13-Oct-12	83	C. Iworrigan/C. Irrigoo
B12-03	13.7	Mature	Tbd[b]	Y	Barrow, AK	10-Sep-12	31-Jan-13	123	B. Adams/J. Kippi
B12-04	15.2	Mature	Tbd	Y	Barrow, AK	10-Sep-12	27-Nov-12	38	I. Leavitt/H. Brower
B12-05	13.7	Mature	Tbd	N	Barrow, AK	21-Sep-12	24-Oct-12	34	J. George/ I. Leavitt

[a] Unknown; no skin sample was collected for sex identification.
[b] To be determined.

histograms. TAD histograms measure the proportion of depth readings that occur in histogram bins during a 6-h interval. As such, the TAD histograms indicate the depth intervals where whales spend the most time. The upper threshold of histogram bins are user specified before the tag is deployed. Our threshold depths were 2, 10, 20, 30, 40, 50, 75, 100, 150, 200, 250, 300, 350, and >350 m. The final bin included all data on dives deeper than 350 m. When presenting data summaries for each core-use area, we considered the variability between whales to be more important than the variability within whales. Hence, ranges in time-at-depth are the range in means for individual whales and the population mean is the mean of individual means.

Upwelling-favorable winds

NCEP/NCAR Reanalysis 1 (National Center for Environmental Prediction/National Center for Atmospheric Research) gridded dataset (http://www.esrl.noaa.gov/psd/) wind velocities were used to calculate the number of days per month with upwelling-favorable (from the eastern quadrant and parallel to the coast) wind stresses within whale core-use areas. Based upon prior studies of the relationship between wind-driven upwelling and bowhead feeding near Point Barrow, Alaska (Ashjian et al., 2010) and Cape Bathurst, Canada (Walkusz et al., 2012), we defined a threshold for upwelling-favorable wind stresses as greater or equal to

0.05 Pa. A wind stress of this magnitude is associated with a wind speed of ~5.3 m/s.

Sea ice

Ice concentration data, which were used to determine the daily percentages of open water within the whale core-use areas, were derived from satellite-based passive microwave datasets of brightness temperature. The data originate from the consecutive missions of the Special Sensor Microwave Imager (SSM/I) and Special Sensor Microwave Imager/Sounder (SSMIS) and were processed using the NASA Team algorithm (Comiso et al., 1997). The processed daily SSM/I and SSMIS data were accessed from the National Snow and Ice Data Center and obtained for years 2006 and 2007–2012, respectively. These binary array data were converted to grids in ArcGIS. Individual polygons of the core-use areas were then used as masks to extract the desired data for the respective regions.

Physical model

The oceanographic model we used is a version of the Regional Arctic System Model (RASM; Maslowski et al., 2012), which in the 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 used a subset of the RASM model, where the atmospheric and land models are replaced with prescribed realistic atmospheric reanalyzed data from the Common Ocean Reference Experiment version 2 (CORE2) 1948–2009 reanalysis. This approach allows direct comparison of model results with observations as well as investigation of the importance of mesoscale ocean and sea ice processes and interactions among them.

The ocean and sea ice models are configured on the same rotated spherical 1/12-degree and 45-level grid, with eight levels in the upper 50 m. The model domain covers the entire Northern Hemisphere marine cryosphere and extends south 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 realistic exchanges between the Arctic and the lower latitude oceans.

We identified frontal features using gradients in salinity, because strata typically have different origins with characteristic salinity signatures. For each area of high whale use, we summarized salinity gradients near the seafloor and also along cross-sections. Where appropriate, we also examined temperature gradients and current velocities. Model output was available for four years (2006–2009) of the six year study period (2006–2012).

Results

From 2006 to 2010 and 2012, satellite tags provided location data from 54 bowhead whales, and dive data from 28 whales (Table 1). Of the 54 whales, 39 (72%) were tagged in Alaskan waters, mostly near Barrow (69% of the total sample) (Fig. 1). Fifteen of the 54 whales (28%) were tagged in Canadian waters, mostly near Tuktoyaktuk (17% of the total sample). Sex was determined for 34 whales; 13 (38%) were female and 21 (62%) were male. Seventeen of the 54 whales (32%) were ⩾13 m and considered mature. No cows with dependent calves were tagged.
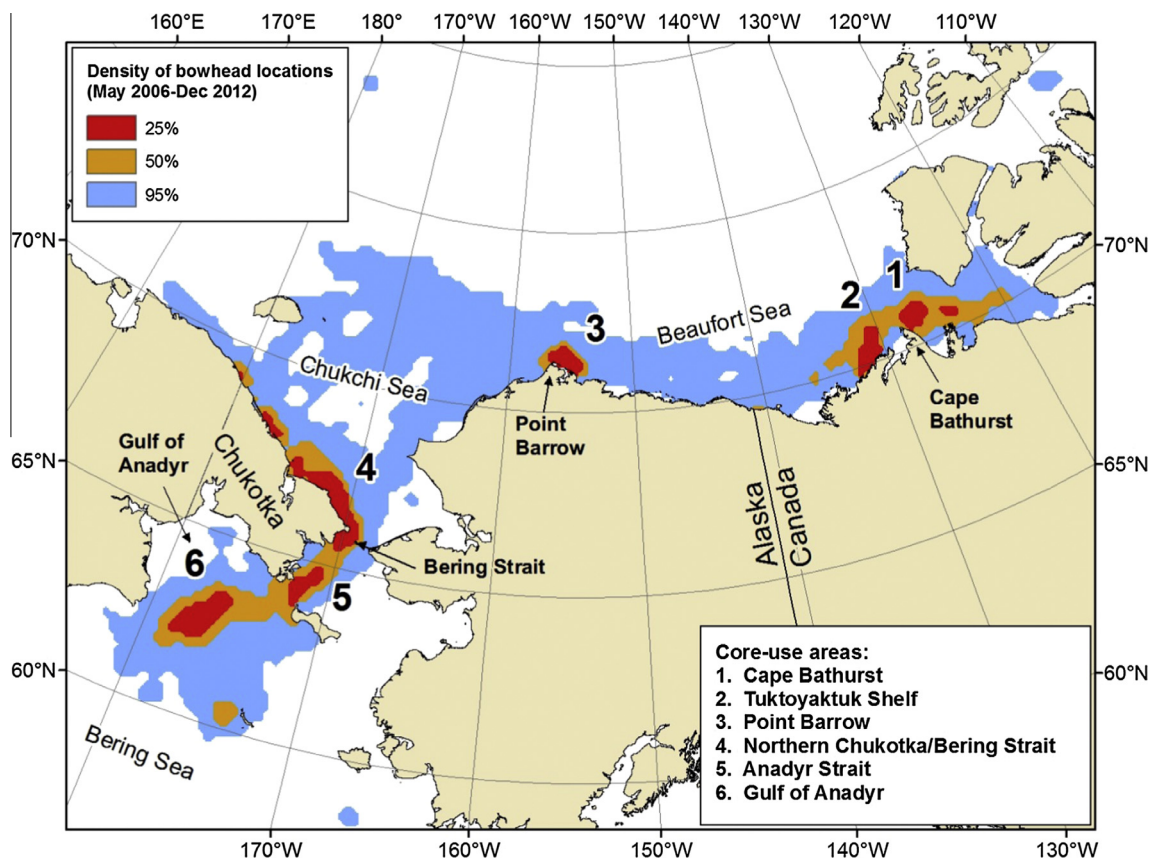

Fig. 2. Utilization distribution of BCB bowhead whales with satellite tags, 2006–2011. Core-use areas were defined as lying within the 25% density contours of satellite locations. Six primary core-use areas were identified.

Using the 25% utilization contours, we identified six primary core-use areas which we refer to as: (1) Cape Bathurst; (2) Tuktoyaktuk Shelf, (3) Point Barrow; (4) Northern Chukotka/Bering Strait, (5) Anadyr Strait; and (6) Gulf of Anadyr (Fig. 2). We discuss each area in turn, starting with Cape Bathurst, the core-use area whales migrate to in spring, and ending with the Gulf of Anadyr core-use area, where whales typically end the autumn/winter migration.

Cape Bathurst core-use area

Of the six core-use areas, the Cape Bathurst core-use area (Area 1; Fig. 2) in Amundsen Gulf has the deepest waters (range

∼60–400 m; mean depth ∼250 m). Tagged whales were present between 3 May and 14 August; however, peak use occurred between 7 May and 5 July (Fig. 3a). Whales arrived at Cape Bathurst while this core-use area was largely ice covered (Fig. 3b) and bounded by consolidated pack ice which restricts the eastward movement of whales (Fig. 4). During the study period, an average of 11% of the core-use area was ice-free on 7 May, ranging from near 0% in 2006 and 2011 to 24% in 2008 and 2012. The Cape Bathurst core-use area is largely defined by the location of the Cape Bathurst polynya (Arrigo and van Dijken, 2004). The amount of open water and the variation in how much open water was present increased between 7 May and 5 July; by 5 July, 87% of the core-use area was ice-free on average, ranging from 33% in 2006 to 85–100% in all other years.
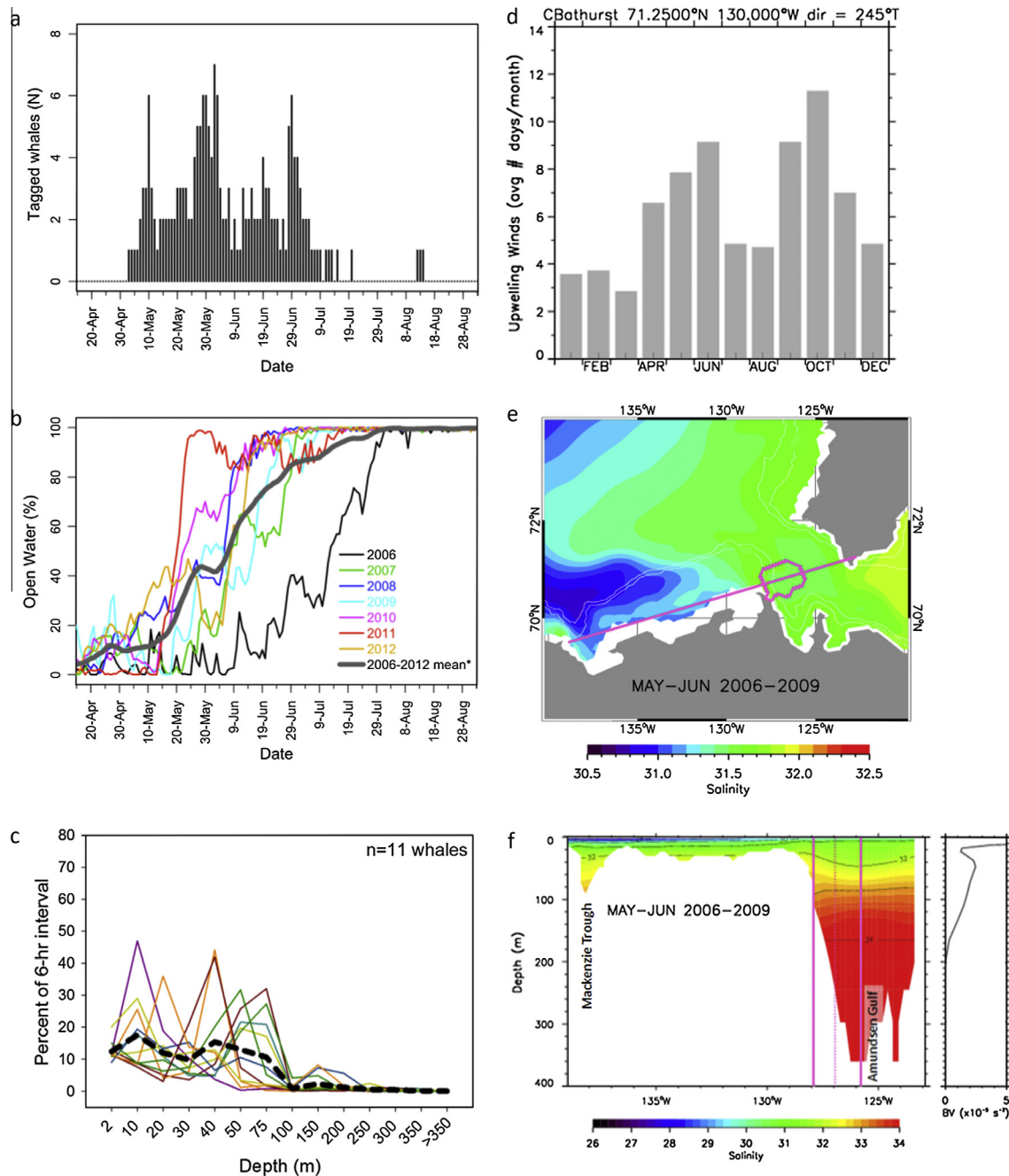
Fig. 3. Characteristics of whale use and the physical environment for the Cape Bathurst core-use area, including (a) timing of occupancy (tagging data), (b) sea ice concentration (SSM/I and SSMIS data), (c) time-at-depth (tagging data), (d) average number of days with upwelling wind (NCEP data), (e) map of bottom salinity with core-use area outline and cross-section line (RASM model data), and (f) salinity cross-section with the core-use area boundaries shown as vertical lines (RASM model data).
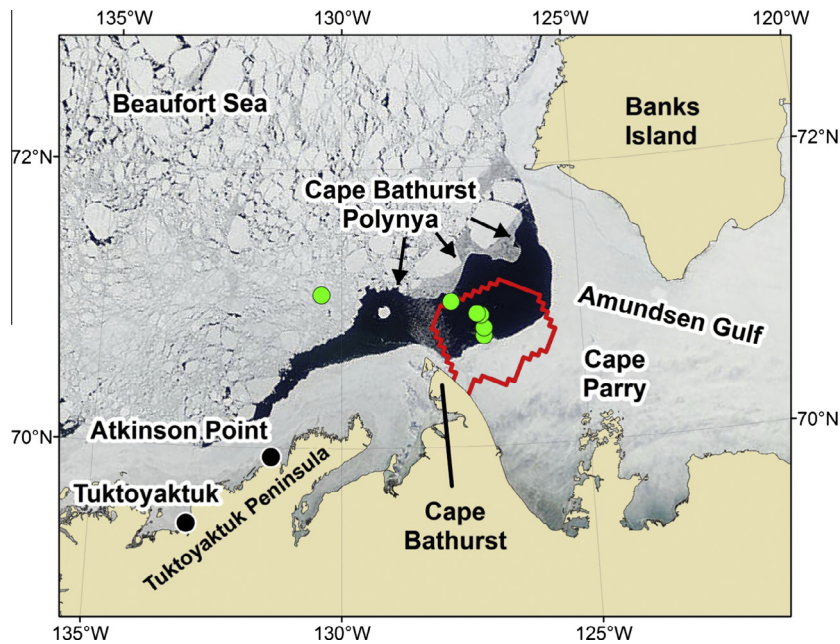
Fig. 4. Position of the Cape Bathurst core-use area (red outline) relative to the Cape Bathurst polynya on 30 May 2009. Green circles are the locations of six bowhead whales on 30 May 2009; MODIS image also taken on 30 May 2009.

Dive histories for 11 tagged whales within the Cape Bathurst core-use area were recorded. Time-at-Depth (TAD) histogram data indicated that they spent most of their time at depths less than 100 m (Fig. 3c). TAD histograms averaged over the study period are bimodal (black dotted line in Fig. 3c), with one mode near the surface in the 2–10 m bin and another occurring between 30 and 75 m bins. The whales generally did not dive to the bottom. On average, the maximum depth of dives at whale locations included the seafloor in 17% of 6-h dive histograms (range of means = 0–46% by whale). On average, whales only spent more time at the bottom than at other depths in 3% of 6-h dive histograms (range of means = 0–13% by whale). Most dives were to depths ⩽75 m, yet all 11 whales occasionally dove to depths >200 m. These dives were rare; of 12,486 dives, only 189 (1.5%) were to depths >200 m. Of these 189 TAD histograms, whales visited the seafloor in 44 (66%) of them but never spent more time there than at other depths.

During the study period, winds over the Cape Bathurst core-use area in the peak use months of May and June were, on average, upwelling-favorable eight and nine days per month, respectively (Fig. 3d). However, the presence of consolidated pack ice and relatively little open water reduce the effectiveness of winds in driving an upwelling response. The absence of a well-defined upwelling response is evident in the map showing the mean modeled salinity in the 15–20 m layer (Fig. 3e), which depicts only a gradual east-west salinity gradient largely attributable to fresher water associated with Mackenzie River discharge. The presence of up-warped isohalines in the upper 80 m near 127–128°W of the corresponding salinity cross section (Fig. 3f) does indicate upwelling within the core-use area, although weak when compared to late summer conditions (cf. Fig. 5d–f). The companion plot of the vertical salinity gradient (right panel of Fig. 3f) within the core-use area indicates a stratification maximum near the surface and a subsurface stratification layer with a local maximum at 40–60 m depth. The correspondence between the mean bowhead dive profile and mean stratification profile suggests that the whales are preferentially spending time and assumed to be feeding within these layers.

Tuktoyaktuk Shelf core-use area

The Tuktoyaktuk Shelf core-use area (Area 2; Fig. 2), approximately 130 km west of Cape Bathurst, is entirely on the continental shelf with depths less than 60 m. Tagged whales were present within the Tuktoyaktuk Shelf core-use area between 5 May and 16 October; however, peak use occurred between 12 July and 25 September (Fig. 5a). The large spike in the histogram near the end of August is largely due to nine whales tagged near Tuktoyaktuk in 2010. If whales tagged near Tuktoyaktuk or Atkinson Point are removed from the analysis for the year in which they are tagged, peak use is similar, occurring between 9 July and 25 September. By the time whales are present within this core-use area, sea ice has largely retreated (Fig. 5b). During the study period, an average of 13% of the core-use area was ice-free on 5 May, ranging from 0% in 2011 to 47% in 2008. On 12 July, when peak use began, 87% of the core-use area was ice-free, ranging from 47% in 2006 to above 95% in all other years, except 2009 at 74%. Most whales left this core-use area in September, prior to ice formation (Fig. 5b).

Dive information from 15 whales within the Tuktoyaktuk Shelf core-use area was collected. TAD histograms averaged over the study period had a dominant mode comprising the 2–20 m bins (Fig. 5c). On average, the maximum depth of dives included the seafloor in 89% of 6-h dive histograms (range of means = 77–100% by whale). Whales often spent more time near the bottom than at other depths (average across whales = 66%; range of means = 23–100% by whale).

For 2006–2012, winds over the Tuktoyaktuk Shelf core-use area during the peak use months of July to September were, on average, upwelling-favorable slightly less than five to more than nine days per month (Fig. 5d). The general absence of sea ice during the July–September time period allows efficient transfer of wind energy to the ocean and leads to a stronger upwelling response than during the ice covered months. This strong upwelling response is evident in the map showing the mean (July–September, 2006–2009) modeled salinity in the 10–15 m layer (Fig. 5e) which shows a locus of higher salinity water on the shelf to the north and west of Cape Bathurst (i.e., the Cape Bathurst upwelling; e.g., Walkusz et al.,
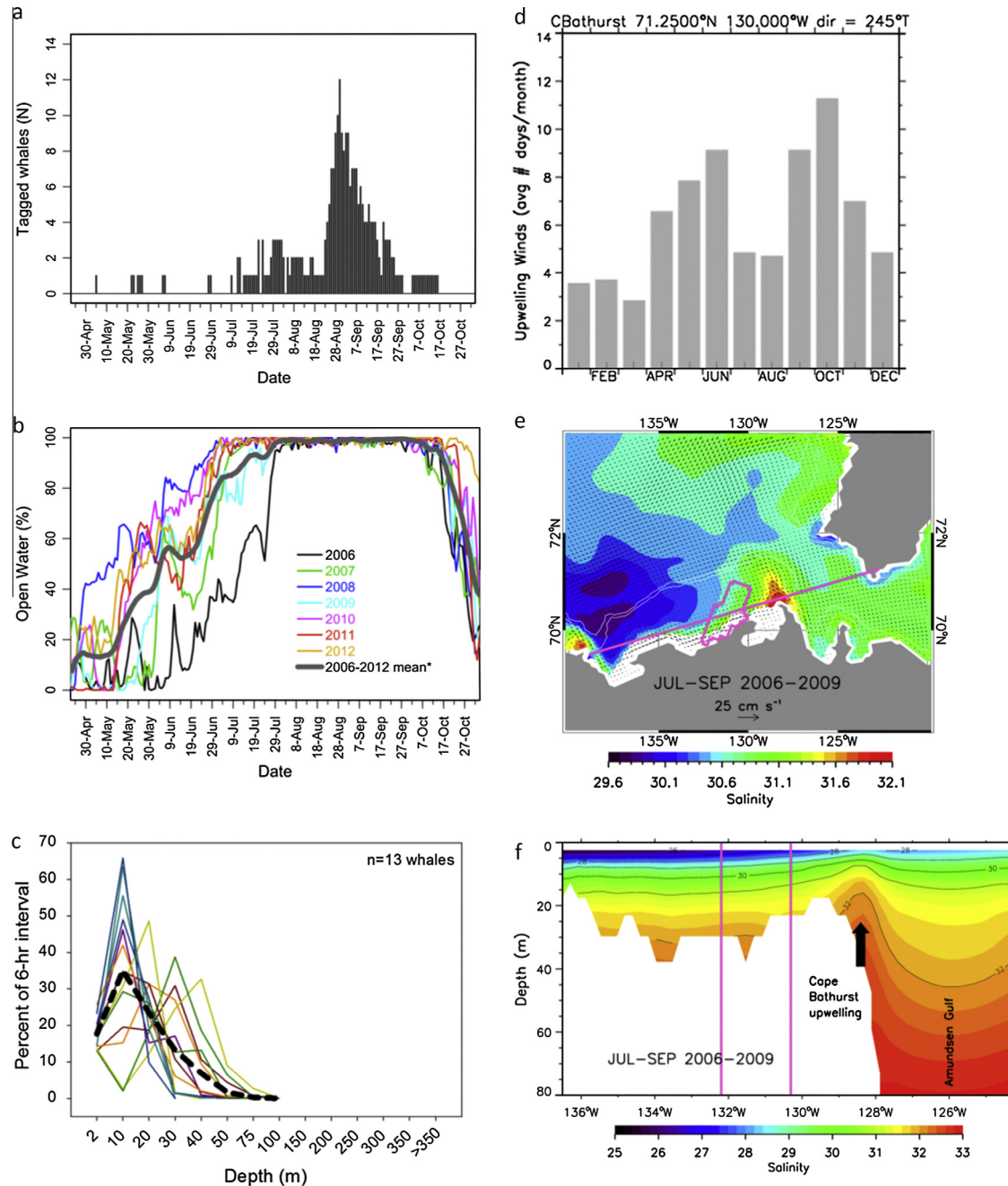
Fig. 5. Characteristics of whale use and the physical environment for the Tuktoyaktuk Shelf core-use area, including (a) timing of occupancy (tagging data), (b) sea ice concentration (SSM/I and SSMIS data), (c) time-at-depth (tagging data), (d) average number of days with upwelling wind (NCEP data), (e) map of bottom salinity with core-use area outline and cross-section line in pink (RASM model data), and (f) salinity cross-section with the core-use area boundaries shown as vertical pink lines (RASM model data).

2012). As a consequence, the overall west–east salinity gradient was stronger from July–September than from May–June (cf. Fig. 3e). This core-use area is located between the Cape Bathurst upwelling (Fig. 3e and f) and an intrusion of fresh water from the Mackenzie River (i.e., the Mackenzie Plume; Carmack and Macdonald, 2002). The circulation model did not indicate significant upwelling along the shelf edge, west of the Cape Bathurst upwelling.

Point Barrow core-use area

Tagged whales were present within the Point Barrow core-use area (Area 3, Fig. 2) between 17 April and 4 November; however,

use was low in late spring and early-to-mid summer (Fig. 6a). Most BCB bowhead whales migrate past Point Barrow, toward Cape Bathurst, in spring. Whales within the core-use area between 17 April and 25 May were migrating and did not remain within the core-use area on consecutive days. Whales were also documented migrating into the Alaskan Beaufort and Chukchi seas in summer, prior to the autumn migration (e.g., Quakenbush et al., 2013; Christman et al., 2013). The record of a whale on 21 July (Fig. 6a) is of an individual that migrated early from the Canadian Beaufort to the Chukchi Sea in 2010. Tagged whales did not linger in the Point Barrow core-use area other than during the autumn migration; peak use of the area was between 22 August and 2 November (Fig. 6a). Most whales were tagged near Point Barrow; as such, the
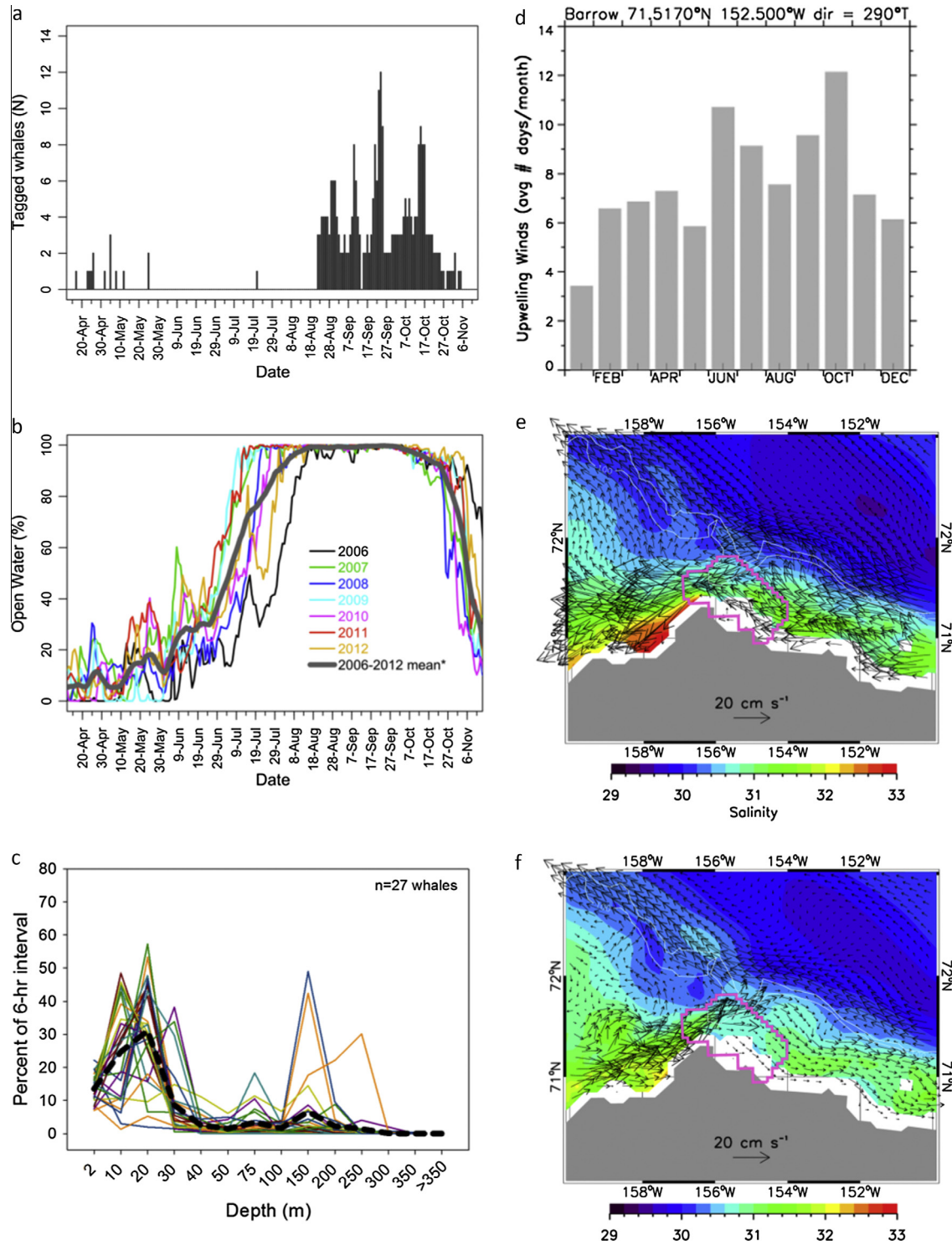
Fig. 6. Characteristics of whale use and the physical environment for the Point Barrow core-use area, including (a) timing of occupancy (tagging data), (b) sea ice concentration (SSM/I and SSMIS data), (c) time-at-depth (tagging data), (d) average number of days with upwelling wind (NCEP data), (e) map of bottom salinity and velocity when east winds predominate, core-use area outline shown in pink (RASM model data), and (f) map of bottom salinity and velocity when west or weak winds predominate, core-use area outline shown in pink (RASM model data).

span of occupancy is more important than the actual number of whales in Fig. 6a. However, removing whales that were tagged near Point Barrow from the year and season in which they were tagged only shortens the peak use period by seven days (29 August–2 November; $n = 23$ whales).

From 2006 to 2012, the Point Barrow core-use area was generally ice free during the beginning of the peak use period on 22

August (Fig. 6b). The end of the peak use period on 2 November correlated with when sea ice began to form; on 2 November an average of 71% of the core-use area was ice-free (range = 28–94% by year).

Dive information was collected from 27 tagged whales within the Point Barrow core-use area during the autumn migration. The average bottom depth at whale locations within this area
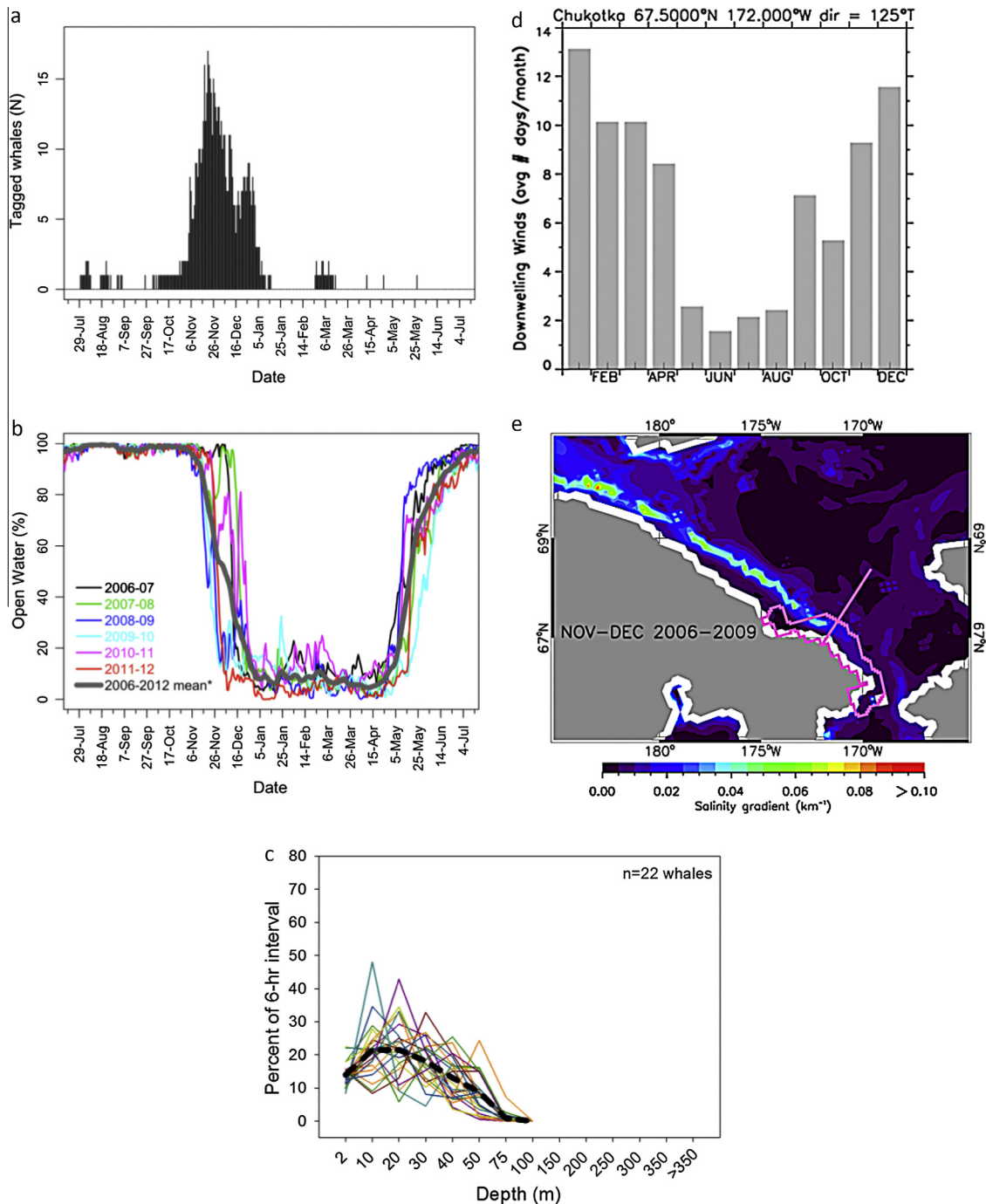
Fig. 7. Characteristics of whale use and the physical environment for the Northern Chukotka/Bering Strait core-use area, including (a) timing of occupancy (tagging data), (b) sea ice concentration (SSM/I and SSMIS data), (c) time-at-depth (tagging data), (d) average number of days with downwelling-favorable (NCEP data), and (e) map of bottom salinity gradient with core-use area outline and cross-section line shown in pink (RASM model data).

was 43 m and ranged from 3 m on the continental shelf to 300 m in Barrow Canyon (Fig. 1). Dives to the 300–350 m dive bin occurred within Barrow Canyon, yet whales generally spent the most time at shallow depths (Fig. 6c). On average, whales spent 78% of each 6-h dive histogram within 30 m of the surface (range of means = 18–99% by whale; median of means = 87% by whale) and the maximum depth of dives included the seafloor in 91% of 6-h dive histograms (range of means = 50–100% by whale). Whales spent more time near the bottom than at other depths in 59% of 6-h dive histograms (range of means = 0–100% by whale).

With the exception of August, winds were favorable for upwelling for more than nine days per month from June through October during the study period (Fig. 6d). During the peak months of the autumn migration past Point Barrow, there were, on average, ~9 days with upwelling-favorable winds in September and ~12 days with upwelling-favorable winds in October. Modeled currents driven by upwelling-favorable winds indicate that zooplankton on the shallow Alaskan Beaufort shelf were exported from the shelf by strong northwestward-flowing shelf currents to the deeper waters of Barrow Canyon (Fig. 6e). After the

upwelling-favorable winds relax and turn downwelling-favorable, average currents on the shelf in the Barrow core-use area weakened and reversed to the southeast; conditions that were conducive to the retention and aggregation of krill on the shelf (Fig. 6f).

Northern Chukotka/Bering Strait core-use area

Peak use of the northern Chukotka/Bering Strait core-use area (Area 4; Fig. 2) occurred between 27 October and 8 January (Fig. 7a); however, some whales likely use the area year-round when ice conditions allow. Observations in April are from whales migrating to the Canadian Beaufort. All observations in May and some in July and August are from a whale that migrated up the Chukotka coast in spring 2010, rather than to the Canadian Beaufort (B09-09, Table 1; Citta et al., 2012). Some observations in July and August are also from a whale that migrated to the Canadian Beaufort in spring and then traveled to this area in the summer of 2010 (B10-13, Table 1). Waters were ice-free when most whales arrived (Fig. 7b). Sea ice gradually formed while whales were present. By the time most whales leave the area and move south (8 January), only 8% of the core-use area was ice-free on average (range = 0–17% by year). Some open water was present all winter and whales were present in the area in February and March (Fig. 7a and b).

Dive data were collected for 21 tagged whales within the Northern Chukotka/Bering Strait core-use area. This core-use area is located on the continental shelf and average depth at whale locations was 36 m (range = 1–56 m). TAD histogram data indicated that whales spent the most time in the 10–30 m bins, but distributed their time across all depths (Fig. 7c). Whales often dove to the bottom; on average, the maximum depth of dives at whale locations included the seafloor in 93% of 6-h dive histograms (range of means = 82–100% by whale). Whales spent more time at the bottom than at other depths in 44% of 6-h dive histograms (range of means = 0–88% by whale).

During the peak use months of November and December, the prevailing winds were downwelling-favorable, occurring on average, about nine and twelve days per month, respectively (Fig. 7d). Weingartner et al. (1999) showed that downwelling-favorable winds from the northwest promote the maintenance of the front between the cold, fresh southeastward-flowing Siberian Coastal Current and warmer, saltier waters of Bering Sea origin and that upwelling-favorable winds weaken this front. Model results show that the Northern Chukotka/Bering Strait core-use area is co-located with this salinity front (Fig. 7e). The salinity front is well-established in October, but weakens by December, as Siberian rivers freeze-up and freshwater discharges decline (Fig. 8).

Anadyr Strait core-use area

Whales were located within the Anadyr Strait core-use area (Area 5; Fig. 2) between 26 November and 23 May. However, peak use occurred between 29 November and 20 April (Fig. 9a). Waters were generally ice free when whales first arrived, but began to freeze soon thereafter (Fig. 9b). The percentage of open water within the core-use area averaged 83% (range = 41–100% by year) at the beginning of peak use on 29 November. Open water was available to whales all winter; during the study period, open water averaged 57% in December, 21% in January, and 17% in February. On 20 April, when peak use ended, open water averaged 43%, ranging from 15% in 2010 to 72% in 2009 and 2011). Because this area was largely ice-covered while whales were present, we did not determine how often winds promoted upwelling.

Dive data were collected for 16 whales within the Anadyr Strait core-use area. Average depth at whale locations was 43 m (range = 5–62 m). TAD histogram data indicated that whales used the entire water column (Fig. 9c). On average, the maximum depth
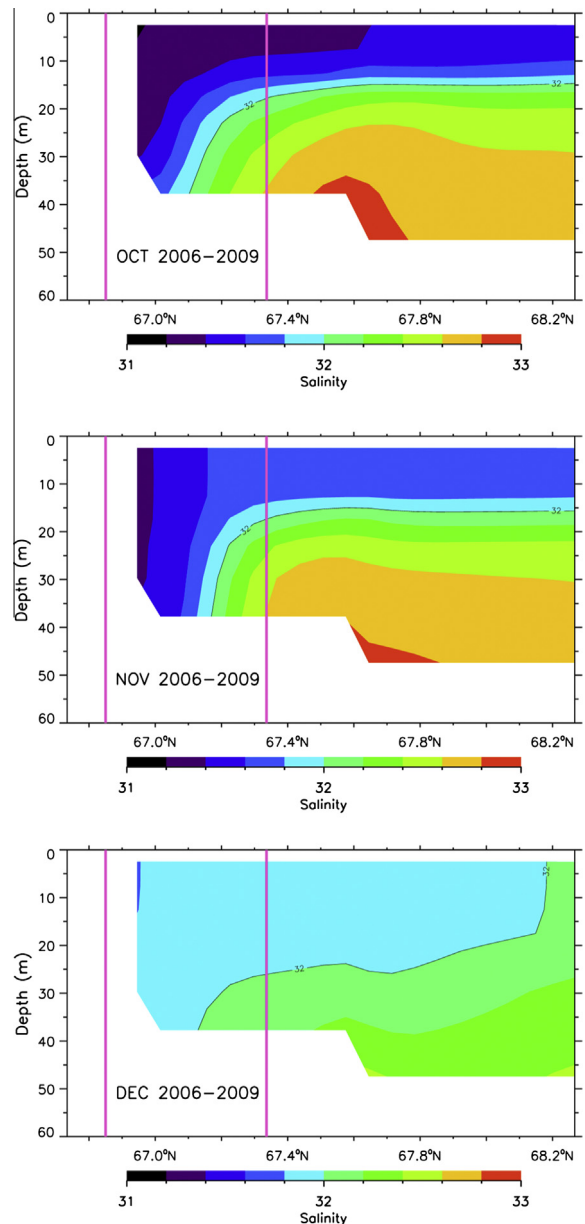

Fig. 8. Monthly average salinity cross-section in the Northern Chukotka/Bering Strait core-use area. Core-use area boundaries are shown as vertical pink lines. Salinity fronts are strongest in October and weaken as rivers freeze.

of dives included the seafloor in 90% of 6-h dive histograms (range of means = 50–100% by whale). Whales spent more time at the bottom than at other depths in 39% of 6-h dive histograms (range or means = 0–100% by whale). The Anadyr Strait core-use area is co-located with an intrusion of relatively high salinity water (>32.5) originating in the Bering slope region and extends to the northern shore of the Gulf of Anadyr (Fig. 9d). This water occurs near the bottom in Anadyr Strait (Fig. 9e) and current vectors show that the Anadyr Strait core-use area is within the principal advective pathway for northward transport from the Bering Sea and the Chirikov Basin (Fig. 9d).

Gulf of Anadyr core-use area

Whales were located within the Gulf of Anadyr core-use area (Area 6; Fig. 2) between 4 December and 18 April, although
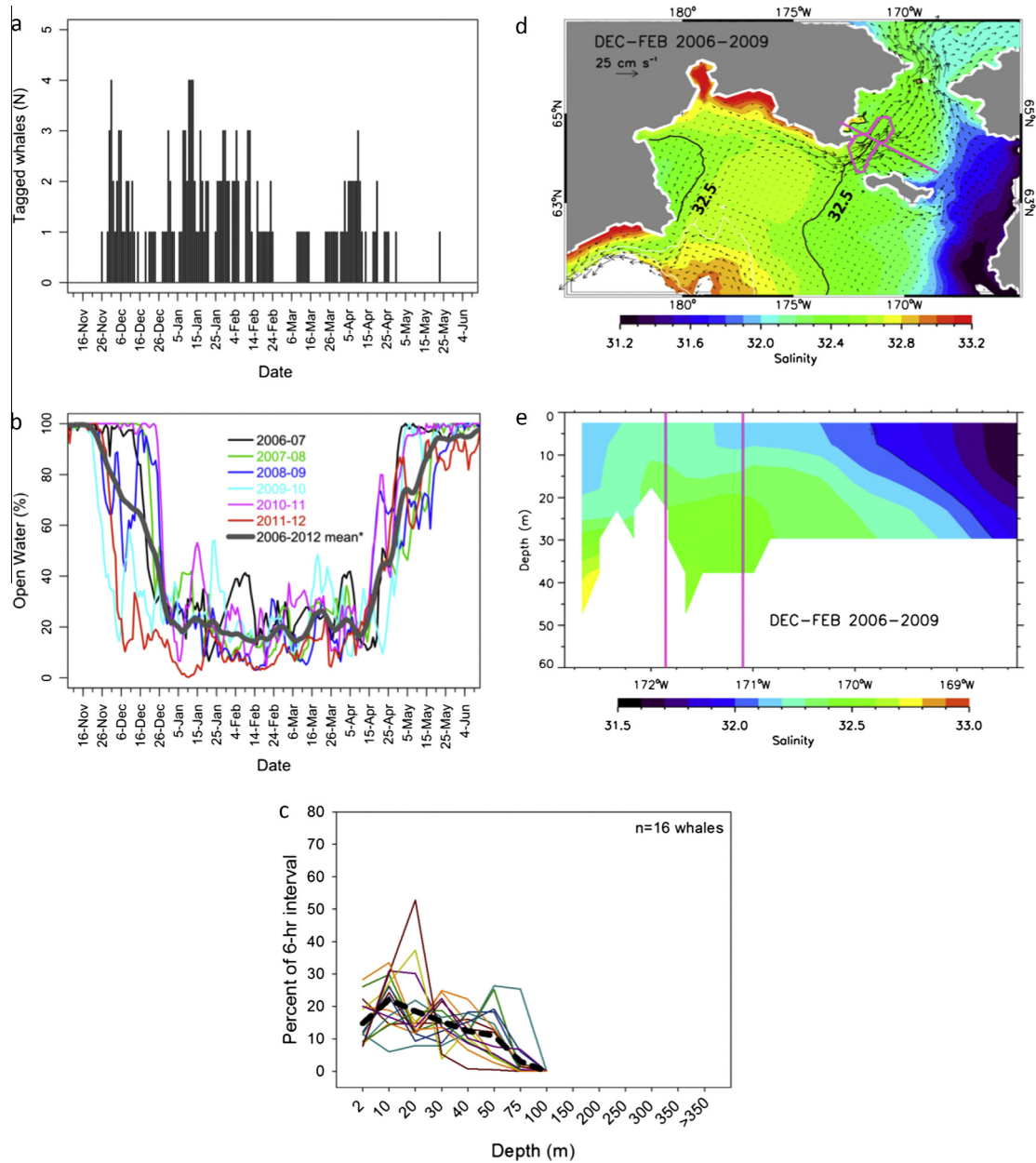
Fig. 9. Characteristics of whale use and the physical environment for the Anadyr Strait core-use area, including (a) timing of occupancy (tagging data), (b) sea ice concentration (SSM/I and SSMIS data), (c) time-at-depth (tagging data), (d) map of bottom salinity gradient with core-use area outline and cross-section line shown in pink (RASM model data; 200 m limit), and (e) salinity cross-section with core-use area boundaries shown as vertical pink lines.

most left the area by 1 April (Fig. 10a). Waters generally began to freeze as whales arrived (Fig. 10b). Open water within the core-use area averaged 99% (range = 95–100% by year) when whales first arrived on 4 December. Open water is available to whales all winter; during the study period, open water averaged 90% in December, 29% in January, and 15% in February. Whales generally began migrating north before the sea ice retreated. On 18 April, when the last whale departed, an average of only 18% of the core-use area was ice-free (range = 3–36% by year). Because this area was largely ice-covered while whales are present, we did not determine how often winds promoted upwelling.

Dive data from 10 whales were collected within the Anadyr Gulf core-use area. Average depth at whale locations was 94 m (range = 77–118 m). TAD histogram data indicated 9 of 10 whales

spent the majority of time within the 75–100 m depth bin (Fig. 10c). Individual whales spent 26–69% of each 6-h histogram within the 75–100 m depth bin. Dive data from tags also indicated that whales typically dove to the bottom. The maximum depth of dives included the seafloor in 100% of dive histograms (range of means = 99–100% by whale). Whales spent more time at the bottom than at other depths in 82% of dive histograms (range of means = 46–100% by whale).

The core-use area was roughly in the middle of a region characterized by bottom salinities >32.5 and exhibiting continuity between the Bering slope and Anadyr Strait (Fig. 10d), within the trough at the head of Navarin Canyon (Fig. 10e). While currents were generally weak on the shelf, the core-use area was characterized by weaker currents than what occurred to the north, south, and west (see vectors in Fig. 10d). Because the bottom salinity
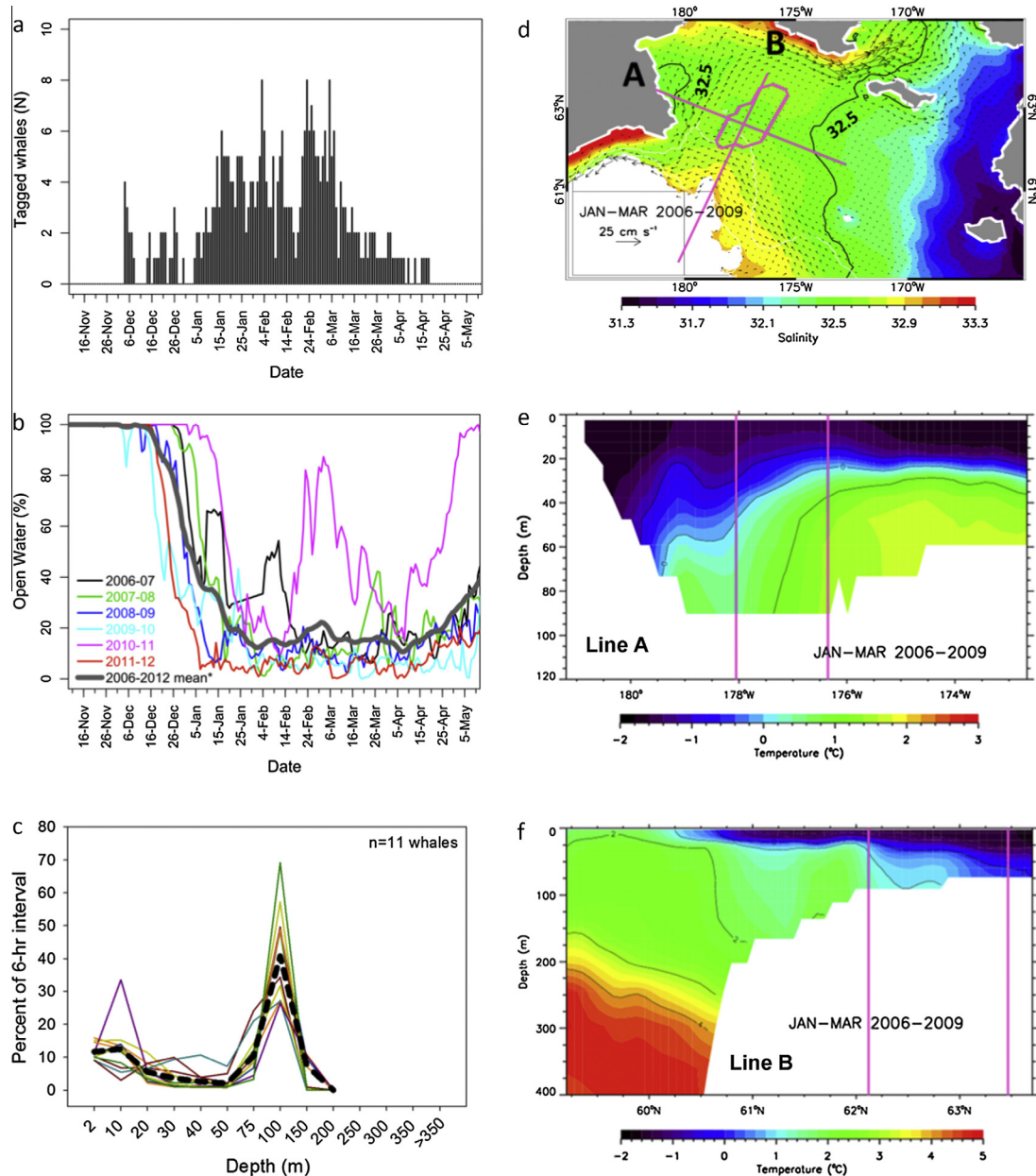
Fig. 10. Characteristics of whale use and the physical environment for the Gulf of Anadyr core-use area, including (a) timing of occupancy (tagging data), (b) sea ice concentration (SSM/I and SSMIS data), (c) time-at-depth (tagging data), (d) map of bottom salinity gradient with core-use area outline and cross-section line shown in pink (RASM model data; 200 m limit), (e) temperature cross-section for Line A, with core-use area boundaries shown as vertical pink lines, and (f) temperature cross-section for Line B, with core-use area boundaries shown as vertical pink lines.

gradient was very weak, it was instructive to also consider temperature sections through the core-use area.

Section A (Fig. 10e) depicts a thermally stratified water column, with the core-use area lying between warmer (>1 °C) Bering Shelf waters to the south and east and colder (<0 °C) Anadyr Waters to the north and west. The cross-shelf section (Fig. 10f) shows that the relatively warm Bering Shelf water originated seaward of the shelf-break. While these data were modeled rather than empirical, we have paired depth, temperature, and location readings for a whale located southwest of this core-use area, near Navarin Canyon. Although the whale was tagged in 2013, after both the 2006–2012 study period and the 2006–2009 model simulation period, data from this whale documented the presence of a thermocline located between 75 and 100 m in March (Fig. 11).

Discussion

Limitations to inference

We focused on general patterns of whale distribution and characterized how core-use areas were related to features known to aggregate zooplankton (i.e., sea ice, wind, and physical oceanography). While our generalizations largely ignore annual variability, they provide an overview of ecological patterns that can be further examined with focused studies. More detailed interpretations of these data are not appropriate because our inference is limited by a number of factors. Although the core-use areas we identified are generally known to have large numbers of bowhead whales based on other studies (e.g., Brueggeman et al., 1984, 1987;
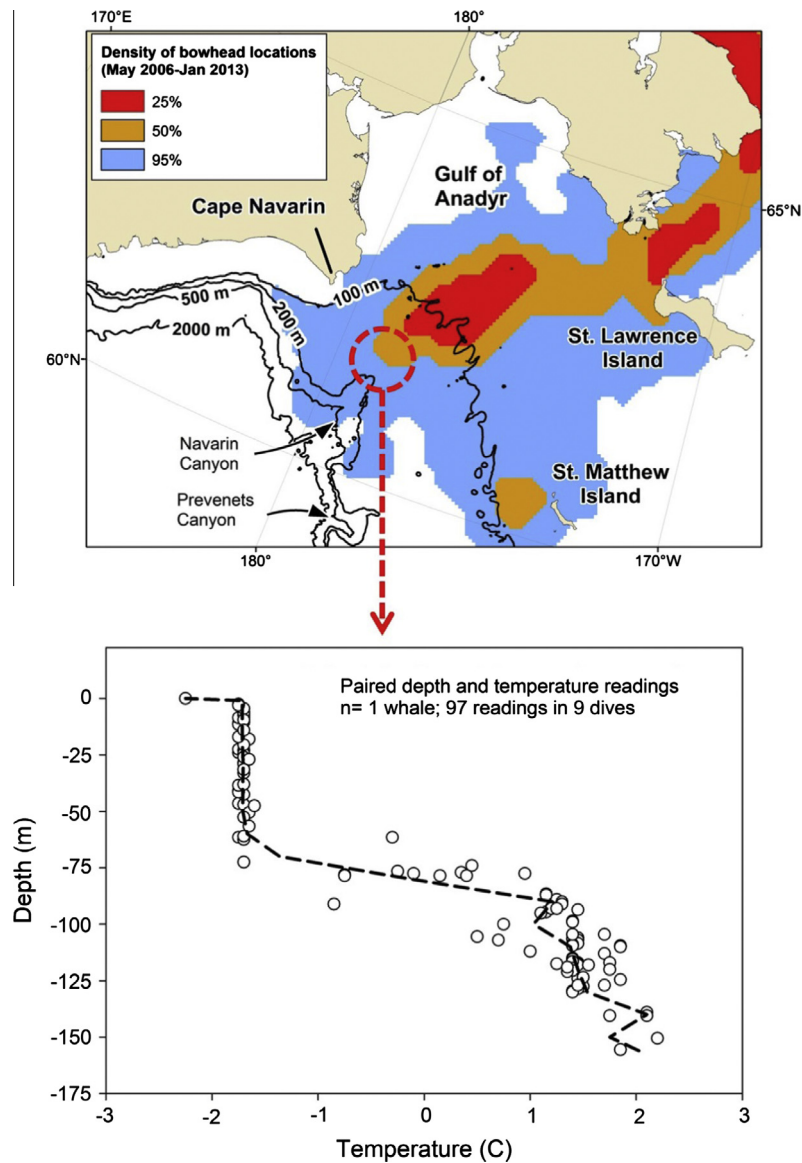
Fig. 11. Paired depth and temperature readings for one whale near the Gulf of Anadyr core-use area in March 2013.

Burns, 1993; Moore and Reeves, 1993; Moore et al., 1995, 2010; Harwood et al., 2010; Walkusz et al., 2012), our inference is limited by the study design and the duration of the bowhead tagging study. We tagged 54 whales out of a population >16,000 (Givens et al., 2013), the majority of whales were tagged near Point Barrow, Alaska, and we did not tag cows with calves. Hence, our data may under-represent or not include some segments of the population. In particular, there is concern that a segment of the population summers in the Chukchi Sea and may never enter the Beaufort Sea. However, whales tagged near St. Lawrence Island made similar movements as whales tagged at Point Barrow or in the Canadian Beaufort. Furthermore, one whale tagged at Point Barrow in 2009, spent the following summer in the Chukchi Sea without returning to where it was tagged. Although we clearly have not tagged enough whales to know the actual proportion of the population that summers in the Chukchi Sea, we think it is unlikely that we have missed a large segment of the population that summers there.

Although it is likely that we identified the major feeding areas used during the study period (2006–2012), other areas we did not identify may also be important, at least in some years. For

example, aerial surveys in the Canadian Beaufort in August and September, 1980–1984, found higher numbers of whales near Herschel Island than on the shelf near Tuktoyaktuk in 1982, 1983, and 1984 (see summary in Moore and Reeves, 1993). Aerial surveys conducted between 2007 and 2009 also found higher numbers of whales near Herschel Island (Harwood et al., 2010). As such, we cannot conclude that areas outside of the core-use areas are unimportant, especially if past studies have characterized these areas as having high densities of bowhead whales. Our sample of tagged whales also did not include cows with calves. Aerial surveys conducted in the 1980s found that larger whales were more likely to be found in Amundsen Gulf in late summer and that smaller whales and cows with calves were more likely to be found on the shelf near Tuktoyaktuk (Koski et al., 1988). As such, reproductive status and maturity will also be important factors to consider in future studies.

The eastern Alaskan Beaufort sea, near Kaktovik (Fig. 1), deserves special mention. Because of petroleum exploration in this area, the U.S. Minerals Management Service (now Bureau of Ocean Energy Management) funded numerous studies that have tried to address the importance of the eastern Alaskan Beaufort for bowhead whales

(see Richardson and Thompson, 2002). Whalers typically harvest 2–3 whales near Kaktovik every autumn, usually in September (Suydam and George, 2004; Koski et al., 2005). Between 1998 and 2000, whales were commonly observed feeding near Kaktovik (Würsig et al., 2002) and the examination of stomach contents from whales harvested between 1997 and 2000 indicated that 83% of whales had recently fed (Lowry and Sheffield, 2002). Hence, the presence and feeding of whales is well documented for the area surrounding Kaktovik. However, based upon short residence times and calculations of the energetic requirements of whales, Richardson and Thompson (2002) concluded that whales did not acquire a significant amount of their annual energy within the eastern Alaskan Beaufort. Detailed comparisons of our data with the studies reported in Richardson and Thompson (2002) are outside the scope of this manuscript; however, we clearly did not observe tagged whales lingering in the eastern Alaskan Beaufort during our study.

Inference is also limited by how we estimated the utilization distribution and delineated core-use areas. The boundaries of core-use areas will depend upon what statistical method is used to estimate the utilization distribution and how the distribution is smoothed. Furthermore, because our sampling was not evenly distributed, we estimated utilization distributions for each sea (Bering, Chukchi, and Beaufort) separately and then combined the distributions such that data from each sea were weighted equally. Most whales were tagged near Point Barrow in the autumn, before they migrated across the Chukchi Sea. This resulted in the Chukchi having more locations than the Bering or Beaufort seas. By weighting each sea equally, we prevented the majority of the use, indexed by the density of whale locations, from "piling-up" in the Chukchi Sea. As a consequence of equal weighting, we cannot comment on the relative importance of core-use areas among seasons, nor delineate the exact boundaries of core-use areas.

We arbitrarily chose the 25% density contour to define core-use areas. While this may initially seem to limit inference, the oceanographic factors that focus density within the core-use areas likely apply to larger areas. For example, the salinity front along the northern coast of Chukotka extends far to the northwest, outside of the core-use area we describe, and this front is co-located with higher whale density along the coast (compare Figs. 2 and 7e). Likewise, intrusion of relatively salty water of Bering slope origin was co-located with a higher density of whale locations throughout the western Bering Sea. Hence, our inferences on why whales may aggregate in these areas (see below) are not limited by how we defined core-use areas.

Last, we are relating our core-use areas to results from an oceanographic model. While model results have compared favorably to empirical data (e.g., Clement et al., 2005), the model run extends only through 2009. Additionally, representation of frontal locations and the degree of stratification are somewhat dependent upon the horizontal and vertical resolution of the model. For example, the model identified a thermocline in the Gulf of Anadyr at approximately 25–50 m, where −2 °C water near the surface transitioned into +3 °C water (Fig. 10e and f). Paired depth and temperature data from a whale tag in the general area indicated that there was indeed a vertical stratification in temperature, but the thermocline was positioned at approximately 75 m (Fig. 11). Direct comparisons are difficult, because we averaged model results across years to identify larger patterns and no model results are available for March of 2010, when the empirical data were obtained from a tagged whale. Averaged results were generally useful for identifying features known to aggregate zooplankton on the shelf near Tuktoyaktuk and along the northern coast of Chukotka; however, averaged results were not useful for identifying the krill trap at Point Barrow (see Section 'Tuktoyaktuk Shelf core-use area'). Hence, while comparing the distribution of bowhead whales with model results was a worthwhile exercise, our conclusions are best interpreted as hypotheses to be tested with empirical data.

Cape Bathurst core-use area

The Cape Bathurst core-use area is co-located with the Cape Bathurst polynya (Fig. 4), an enlarged flaw lead that forms when easterly winds push the more broken Beaufort Sea pack ice away from the more stable pack ice in Amundsen Gulf (Arrigo and van Dijken, 2004; Williams and Carmack, 2008). The lead system extends from Cape Bathurst into Amundsen Gulf and along the western coast of Banks Island. The size of the polynya is variable and in some years extends east of Cape Parry (see Fig. 1 in Arrigo and Van Dijken, 2004; Fig. 1). Polynyas generally have enhanced primary and secondary production relative to adjacent ice-covered waters. In the Arctic, winter days with limited daylight and thick ice restrict phytoplankton blooms to a short period in summer following ice melt. In contrast, phytoplankton blooms within polynyas begins as soon as the polar night ends, typically in April or May, thereby extending the growing season (Tremblay et al., 2002; Arrigo and van Dijken, 2004; Simpson et al., 2013). As a consequence, phytoplankton are typically found at higher densities within polynyas than in surrounding waters, as are zooplankton grazers, such as calanoid copepods (Ringuette et al., 2002).

Zooplankton communities in the Arctic are often dominated by calanoid copepods; indeed, *Calanus glacialis* and *C. hyperboreus* make up ∼70% of the zooplankton biomass in the south-eastern Beaufort Sea (Darnis et al., 2008). Studies conducted in Amundsen Gulf indicate that *C. glacialis* is found throughout the gulf, while *C. hyperboreus* is more common over deeper waters and within the polynya (e.g., Darnis et al., 2008; Hop et al., 2011). As such, we expect the Cape Bathurst core-use area to have high densities of both *C. glacialis* and *C. hyperboreus* (see Fig. 8 in Darnis et al., 2008). Both species are omnivorous and feed upon phytoplankton and microzooplankton depending upon relative availability (Campbell et al., 2009). In spring, they feed primarily upon ice algae and phytoplankton (Forest et al., 2011a) and are believed to enter diapause sometime in late summer–early autumn when food is less available (e.g., Smith and Schnack-Schiel, 1990; Falk-Petersen et al., 2009). Diapause ends sometime in late winter and individuals ascend, usually in April, to take advantage of ice algal and phytoplankton blooms. In Amundsen Gulf, the bloom of ice algae begins in mid-March, peaks in April, and declines in May (Daase et al., 2013). The pelagic phytoplankton bloom occurs later, beginning in April and peaking in May (see Fig. 2d in Daase et al., 2013). *C. glacialis* and *C. hyperboreus* time their reproduction and ascent to take advantage of these blooms, albeit differently. *C. glacialis* ascends in April and feeds upon ice algae to fuel molting, maturation, and reproduction (Daase et al., 2013). In contrast, *C. hyperboreus* spawns at depth between February and April, using lipid stores to fuel reproduction (e.g., Conover, 1988; Conover and Huntley, 1991; Hirche and Niehoff, 1996). Eggs of *C. hyperboreus* mature as they rise to the surface and reproduction is timed such that the naupliar stages can feed upon ice algae at the ice–water interface (Conover, 1988; Conover and Huntley, 1991).

While there is no direct evidence that whales are feeding within the polynya in May and June, the co-location of copepods and bowhead whales at similar depths in combination with the fact that bowheads leave the productive Bering Sea area and migrate directly to the Cape Bathurst core-use area, is highly is suggestive of feeding. Tagged bowhead whales were present within the Cape Bathurst core-use area in May and June, and spent the majority of time at depths ⩽75 m (Fig. 3c). The lower boundary of the euphotic zone occurs at ∼80 m in Amundsen Gulf (Forest et al., 2011b) and waters are relatively stable at this time of year with little upwelling (Fig. 3f). As such, most phytoplankton are distributed within

80 m of the surface in May and June (see Fig. 2d in Forest et al., 2011b) and this is where zooplankton are expected to aggregate. At this time, the highest abundance of *C. glacialis* and *C. hyperboreus* are typically found in the upper 25–50 m of water (Ashjian et al., 2003; Wold et al., 2011; Daase et al., 2013; Darnis and Fortier, 2014). However, copepods must be large enough to be filtered by baleen and copepods found in bowhead stomachs are generally >2.4 mm (Lowry, 1993). Hence, bowhead whales are expected to feed mainly on larger copepodite stages, such as CIV, CV, and adults. These stages may be found at a greater range of depths, ranging from the surface to approximately 200 m (Darnis and Fortier, 2014) and this generally corresponds to the depths to which we recorded whales diving (Fig. 3c).

The circulation model indicated that waters within the Cape Bathurst core-use area were highly stratified near the surface due to melt water and/or freshwater from the Mackenzie River. Another stratified layer began at 40 m and peaked between 40 and 60 m; this secondary stratification declined with increasing depth and became indiscernible at approximately 200 m (Fig. 3f, side panel). This pattern of stratification generally agreed with empirical observations of temperature and salinity from other studies (e.g., Martin et al., 2010; Forest et al., 2011b; Hop et al., 2011). Phytoplankton are more concentrated at pycnoclines, both because sinking of diatoms (copepod food) is reduced and because nutrient availability may be greater there, which promotes phytoplankton growth if the pycnocline is within the euphotic zone. Copepods in turn will concentrate at the pycnocline to feed upon the elevated concentrations of phytoplankton. Whales preferentially dove to the depths of the stratification (Fig. 3c), presumably to feed on patches of copepods that are expected there.

Why all whales occasionally dove to 200–400 m in May and June is unclear. Such dives were relatively rare (1.5% of all dives) and whales typically spent little time below 200 m (~1.9% of each 6-h histogram). However, they sometimes spend significant amounts of time at depth. For example, bowhead B10-15, an immature female, spent 50% of a 6-h interval within the 250–300 m histogram bin (seafloor depth ~335 m), suggesting that sometimes whales find prey at depth.

The movement of whales out of the Cape Bathurst core-use area in July corresponds to the initial descent of some of the large copepods to deeper depths (e.g., Wold et al., 2011; Daase et al., 2013; Darnis and Fortier, 2014). Although the timing of diapause for copepods is not well understood in Amundsen Gulf, much of the population of *C. glacialis* and *C. hyperboreus* is found at deeper depths in July. This movement may correspond to a shift in chlorophyll maxima from the surface to the lower euphotic zone. For example, Forest et al. (2011a) found the chlorophyll maximum descended from ~20 m in April to ~50 m in August. Because diatoms are present as late as September in the lower euphotic zone (Martin et al., 2010), Daase et al. (2013) suggest that the initial downward migration of *C. glacialis* in July may be in response to the location of the chlorophyll maxima and that diapause may occur sometime after September.

Tuktoyaktuk Shelf core-use area

The movement of whales into the Tuktoyaktuk Shelf core-use area in July corresponded with the clearing of sea ice (Fig. 5b) and the beginning of upwelling at Cape Bathurst (Walkusz et al., 2012). Williams and Carmack (2008) provide a detailed description of the Cape Bathurst upwelling. In summary, winds from the east create a flaw lead by pushing broken Beaufort Sea pack ice west, away from land-fast ice at Cape Bathurst, and along the western shore of Banks Island, and also away from the more consolidated pack ice in Amundsen Gulf. Wind stress within the lead results in upwelling at Cape Bathurst and, to a lesser extent, along the

shelf break, drawing nutrient-rich water from as deep as 110 m in Amundsen Gulf onto the shelf near Tuktoyaktuk (Williams and Carmack, 2008). While the upwelling is wind-driven and may occur at any time of year, the circulation model indicated that the upwelling was (on average) weak in May and June (Fig. 3e and f), but well developed while whales were present between July and September (Fig. 5e and f). Within and adjacent to the area we identified as the Tuktoyaktuk Shelf core-use area, Walkusz et al. (2012) found dense aggregations of copepods, mostly *C. glacialis* and *C. hyperboreus*, where bowhead whales were feeding. These copepods were concentrated near the seafloor in water with an upwelling signature. Walkusz et al. (2012) speculated that the copepods were 'likely in a resting phase' prior to diapause and were concentrated near the seafloor because they were avoiding light. We found that whales spent more time near the seafloor than at other depths in 66% of dive histograms, likely feeding on aggregations of copepods as described by Walkusz et al. (2012).

Also, there are known beds of benthic amphipods (*Ampelisca*) on the shelf adjacent to Tuktoyaktuk (Conlan et al., 2008, 2013) that might provide additional prey for the bowhead whales. Although bowhead whales in the Beaufort Sea are thought to feed primarily on copepods, based on analysis of stomach contents, feeding on amphipods has been documented with the proportion of amphipods occasionally being substantial (Lowry, 1993; Lowry et al., 2004; Pomerleau et al., 2011). The availability of benthic amphipods is unlikely to be seasonally or sea-ice dependent, because they would be present year round. By contrast, calanoid copepods undergo ontogenetic migrations in late summer and fall to depth (~200 m) in the slope-basin region (e.g., Dawson, 1978; Conover, 1988; Ashjian et al., 2003; Falk-Petersen et al., 2009; Daase et al., 2013) and would be less available to be upwelled onto the shelf at that time. The timing of reduced availability of upwelled copepods generally corresponds with onset of the fall migration of the bowheads to the west, supporting the assumption that calanoid copepods are the primary food source for the bowheads on the shelf near Tuktoyaktuk.

The Tuktoyaktuk Shelf core-use area was bounded on the west by the brackish water plume of the Mackenzie River (Fig. 5e). Brackish waters associated with the Mackenzie Plume are known to have concentrations of *Limnocalanus macrurus* (Walkusz et al., 2010). Large quantities of *L. macrurus* were found in the stomach of a whale harvested at Shingle Point (Fig. 1), west of the plume, in 1996 (Pomerleau et al., 2011). However, we do not think bowhead whales within the Tuktoyaktuk Shelf core-use area were targeting brackish plume waters. The core-use area was located east of the plume (Fig. 5e) and did not follow its edge. Whales spent more time at the bottom than at other depths in 66% of dive histograms and this is where water is known to have an upwelling signature (Walkusz et al., 2012). Rather, it is likely that zooplankton were upwelled onto the shelf at Cape Bathurst and drifted west with currents, and that plume waters form a barrier to westward transport of these zooplankton, effectively defining the western edge of the Tuktoyaktuk Shelf core-use area.

The location of what we define as the Tuktoyaktuk Shelf core-use generally corresponds with where aerial surveys find high numbers of bowhead whales. In August 2007, Harwood et al. (2010) estimated that approximately 50% of the population was located between Cape Bathurst and the Alaskan border, mostly within shallow shelf waters north of Atkinson Point. However, in some years significant numbers of whales are observed closer to Cape Bathurst or in Canadian waters west of Herschel Island (Harwood et al., 2010). While our 50% density contour covers the area from Cape Bathurst west to the Mackenzie Delta (Fig. 2), tagged whales generally did not linger in Canadian waters west of Herschel Island. The mechanism aggregating zooplankton that we describe applies to the shelf waters adjacent to Tuktoyaktuk, east of the Mackenzie freshwater plume. Aggregations of bowhead

whales near Herschel Island may be related to a separate upwelling near the Mackenzie Trough (Fig. 5e).

What determines when whales leave the Tuktoyaktuk Shelf core-use area is speculative. Sea ice is expected to limit the capacity for wind-induced upwelling. While the formation of sea ice correlates with when the last whales migrated west, most whales left the area prior to ice formation. Rather than migration being due to ice formation, we suspect that copepods finally enter diapause and descend to depths too deep (>100 m) for upwelling at Cape Bathurst and along the shelf to result in dense aggregations of copepods on the shelf. Zooplankton surveys in October and November will be required to verify this hypothesis.

Point Barrow core-use area

While bowhead whales are thought to feed primarily upon calanoid copepods in the Canadian Beaufort, their diet is thought to shift toward euphausiids (krill), predominately *Thysanoessa inermis* and *T. rachii*, as whales migrate west toward Point Barrow, Alaska (Lowry, 1993; Lowry et al., 2004). Euphausiids probably do not reproduce in the Chukchi or Beaufort seas (Niebauer and Schell, 1993; Siegel, 2000; Berline et al., 2008) and those found in bowhead stomachs at Barrow are thought to be carried there by currents from the Bering Sea. The process by which krill (and copepods) aggregate near Point Barrow is described by Ashjian et al. (2010) and Okkonen et al. (2011). Briefly, krill are carried northeast in the Alaska Coastal Current (Fig. 1) and copepods near the shelf break are upwelled onto the shelf northeast of Point Barrow 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) refer to this as the "krill trap".

The core-use area we identified using bowhead tag locations (Fig. 2) closely corresponded with the area identified by Ashjian et al. (2010) as having a high density of krill (see Fig. 9 in Ashjian et al., 2010) and a high density of whale sightings (see Fig. 13 in Ashjian et al., 2010 and Fig. 5a and b in Okkonen et al., 2011). However, the krill trap was difficult to identify with the oceanographic model because of its episodic nature and how we were summarizing (averaging) model results. Zooplankton must first be available to seed the shelf. East winds are then necessary to advect zooplankton onto the shelf and then must relax to trap zooplankton. If east winds do not relax, zooplankton exit the shelf to the northwest. This process was impossible to identify using salinity or temperature gradients because we averaged model results across years while whales were present. Instead, we illustrated the krill trap by plotting velocity under different wind regimes (Fig. 6e and f). We could only do so because we knew what pattern we were trying to identify; hence, the oceanographic model, as we applied it, was generally not useful for identifying features that may aggregate zooplankton near Point Barrow over shorter time frames.

Although upwelling-favorable winds are present year round near Barrow (Fig. 6d), the peak number of days per month with upwelling-favorable winds occurs in October. Such winds diminish in November, coincident with the formation of sea ice there (Fig. 6b) and the migration of the whales away from Point Barrow. Fewer days with upwelling-favorable winds reduces the frequency of upwelling while greater sea ice reduces the effectiveness of upwelling, both of which likely contribute to lower availability of bowhead prey and the whales' exit from the Barrow region by early November.

Northern Chukotka coast/Bering Strait core-use area

While copepods occur on the Chukchi Shelf and are advected onto the shelf from deeper waters in the Arctic Basin (Ashjian

et al., 2003), much of the biomass of zooplankton in the Chukchi Sea may originate in the Bering Sea and then travel north with currents (e.g., Springer et al., 1989; Hopcroft et al., 2010). The Bering Slope Current (Schumacher and Reed, 1992) flows westward along the shelf break (Fig. 1) and, upon reaching Cape Navarin, most flows south as the Kamchatka Current. A northern branch, the Anadyr Current, flows northward into the Gulf of Anadyr and passes through Anadyr and Bering straits (Overland et al., 1996). Shelf break waters are characterized by periodic eddies and upwelling (e.g., Stabeno and Van Meurs, 1999), which moves nutrient rich waters into the euphotic zone in the vicinity of the shelf break. These nutrient rich waters result in a "green-belt" of high primary and secondary productivity that extends along the Bering Sea shelf break toward Russia and northwards through Anadyr and Bering straits (Springer et al., 1996). CTD deployments and zooplankton sampling in the northern Bering and southern Chukchi seas in September show that combined Bering Shelf/Anadyr Waters (BSAW) carry a higher abundance of large calanoid copepods and euphausiids than Alaska Coastal Water, especially where BSAW occurs near the seafloor (Eisner et al., 2013).

Using the same oceanographic model we did, 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 autumn. While 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 extends from the area south of Wrangel Island to Bering Strait and largely corresponds to where we found high densities of whale locations (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 salinity gradient formed between the Siberian Coastal Current and BSAW (Fig. 7e, Weingartner et al., 1999). Bowhead whales were observed along the Chukotka coast in September–October 1990 (See Fig. 18.6 in Burns, 1993) and in October of 1992 and 1993 (Moore et al., 1995). Moore et al. (1995) documented bowhead whales feeding at a sharp salinity gradient between the Siberian Coastal Current and water of Bering Sea origin, where there were high densities of *T. rachii*.

While some whales summer along the coast of Chukotka (Melnikov and Zeh, 2007; Citta et al., 2012), peak use of the core-use area occurred between 27 October and 8 January. Typically, whales first arrive on the coast of Chukotka farther north, near Cape Schmidt, prior to 27 October and gradually move southwards (Quakenbush et al., 2010). Within the core-use area, we found that the salinity front was strongest in October and November and becomes non-existent in December as rivers freeze and outflow is reduced (Fig. 8). Currents through Bering Strait also weaken at this time; mean monthly northward transport though Bering Strait is highest in July ($\sim 1.4 \times 10^6$ m³/s) and lowest in December ($\sim 0.3 \times 10^6$ m³/s) (Stabeno et al., 1999). Hence, it is likely that the transport of zooplankton slows down at the same time that the salinity gradient, which helps aggregate bowhead prey, becomes less pronounced. Due to shifting sea ice, there is typically some open water north of Bering Strait (Fig. 7b) and bowhead whales could remain there all winter if foraging conditions were favorable.

Anadyr Strait/Gulf of Anadyr core-use areas

Tagged whales were present in the Anadyr Strait and Gulf of Anadyr core-use areas concurrently between late November and April when the Bering Sea was largely ice covered north of the shelf break (see Figs. 10 and 11; Citta et al., 2012). While some studies have documented frontal features in this area in summer (e.g.,

Hunt, 1997; Russell et al., 1999), little is known about currents in the western Bering Sea in winter. The oceanographic model indicated that both core-use areas in the Bering Sea were co-located with an intrusion of relatively high salinity (>32.5) water near the seafloor that was of Bering Slope origin. Relatively warm Bering Shelf water originates from south of the shelf-break, where between December and March warmer water occurs at depth (Fig. 10f). This pattern was verified with paired-depth and temperature data from a single whale (Fig. 11). The intrusion is narrow and largely restricted to the seafloor within Anadyr Strait. South of St. Lawrence Island the intrusion is relatively wide, and while this area roughly corresponds with 95% density contour for whale locations in the Bering Sea (Fig. 2), salinity alone does not explain why the Gulf of Anadyr core-use area is located where it is within the intrusion. The core-use area is co-located with a number of additional hydrographic characteristics which may promote the aggregation of zooplankton. First, the core-use area is located within a trough at the head of Navarin Canyon (Fig. 1). Second, while most of the Bering shelf region is characterized by weak currents in winter, the core-use area is bounded by stronger currents to the north, south, and west (Fig. 10d). Third, the core-use area is bounded on the west and north by cold Anadyr Water (Fig. 10e and f) which may act as a barrier to the transport of zooplankton.

Interestingly, whales within the Gulf of Anadyr core-use area spent more time at the bottom than at other depths in 82% of dive histograms (range of means = 46–100% by whale) and spent the most time in the 75–100 m depth bin (Fig. 10c). This depth corresponds to that at which the paired depth and temperature data identified a thermocline between colder surface waters, likely Anadyr Water, and warmer waters at depth, likely Bering Shelf Water or water from the slope. Hence, we think it highly likely that whales are foraging on prey near the bottom. Bowhead whales are known to feed in or near all other core-use areas we identified (e.g., Lowry and Burns, 1980; Würsig et al., 1985; Carroll et al., 1987; Moore et al., 1995; Noongwook et al., 2007; Walkusz et al., 2012). However, little is known about feeding behavior south of St. Lawrence Island. Opportunities to observe winter feeding behavior or examine stomach contents are limited as there are no whaling villages nearby and the area is remote and ice-covered. Aerial surveys documented whales wintering in this area in the 1980s (e.g., Brueggeman et al., 1984, 1987); however, feeding behavior was not observed. Isotope studies concluded that the majority of feeding occurs somewhere in the Bering and Chukchi seas (e.g., Schell et al., 1989; Schell and Saupe, 1993; Lee et al., 2005) but could not pinpoint where or exactly when whales were feeding.

While we are relatively sure that whales are feeding in winter, we do not know what they are consuming. Possible prey include euphausids (T. inermis and T. rachii) and calanoid copepods (C. marshallae/glacialis, Neocalanus flemingeri/plumchrus or N. cristatus). Both T. inermis and T. rachii are known to make strong vertical migrations in summer and autumn, migrating toward the seafloor during the day (e.g., Ponomareva, 1966; Coyle et al., 1992; Zhou et al., 2005); however, their winter movements are not well understood. Unlike copepods, euphausiids are thought to be active all winter. High latitude populations of T. rachii are generally not thought to have enough lipid reserves to survive the winter without feeding and supplement their lipid reserves by feeding on detrital particulate material of planktonic origin and upon copepods in winter (Ponomareva, 1966; Sargent and Falk-Petersen, 1981; Falk-Petersen et al., 2000). In high latitude populations of T. inermis, summer lipid reserves are thought to be large enough to sustain them through the winter and to fuel reproduction prior to the spring bloom of phytoplankton. As such, high latitude populations of T. inermis are not thought to forage much in winter (Falk-Petersen et al., 2000). While few studies focus on euphausiid

ecology in the Gulf of Anadyr, Ponomareva (1966) states that there are large populations of both T. rachii and T. inermis in the eastern Gulf of Anadyr and that both species descend to the seafloor in winter when there is little suspended forage. We also expect C. marshallae/glacialis to occur near the seafloor during their winter diapause and other, subarctic species of copepods may be available in winter (see review in Hunt, 1997). The large Neocalanus spp. have been observed in Anadyr Strait in summer (Springer et al., 1989) and to the NW of St. Lawrence Island in November (C.J. Ashjian, R.G. Campbell, S.R. Okkonen, pers. comm.) as well as in water of Pacific Origin in the Chukchi Sea (e.g., Hopcroft et al., 2010; Eisner et al., 2013). They overwinter at depth (>250 m) south of the shelf in the Bering Sea (e.g., Miller et al., 1984; Miller and Clemons, 1988) and could provide an alternative high-value food source for bowhead whales in the Gulf of Anadyr if upwelled into the head of Navarin Canyon. While winter diet is unknown, stomachs from whales harvested near St. Lawerence Island in late autumn (November) and in spring (April–May) typically contain C. marshallae. Other, less common, prey includes amphipods, cumaceans, polychaetes, and clams, all indicative of benthic feeding, but no euphausiids (Hazard and Lowry, 1984; Sheffield et al., 2008).

Studies have shown that bowhead whales in other populations also feed at or near the bottom, usually on copepods. Finley (1990) reported bowhead whales feeding over two deep troughs (>200 m) in late autumn (September) at Isabella Bay, Baffin Island. Although diving behavior of the whales was unknown, the correlation of feeding whales with the position of the troughs suggests that whales may have been feeding on copepods in diapause. In Disko Bay, West Greenland, Laidre et al. (2007) found that bowhead whales targeted the bottom where pre-ascension copepods, primarily C. finmarchicus, occurred in dense layers in April. In the same area, Heide-Jørgensen et al. (2013) documented bowhead whales feeding on dense layers of calanoid copepods near the seafloor (100–400 m) in late winter (March). When copepods began their spring ascent in April, bowhead whales transitioned to feeding near the surface, but left the area before peak densities of copepods aggregated near the surface. They speculated that whales left the area because the density of ascending copepods was too low, the quality of copepods may be too low by spring, when lipid reserves are expended, or that the whales had simply met their energetic needs and were satiated. Similarly, we found that bowhead whales left the Bering Sea when copepods and euphausiids were expected to begin their spring ascent to forage on ice algae and phytoplankton.

It is unknown if foraging conditions in May and June are better for bowhead whales at their destination within the Cape Bathurst polynya than they would be if they remained in the Bering Sea. Diving behavior of whales in the polynya did not indicate zooplankton were concentrated immediately near the surface, rather whales used the entire euphotic layer (upper ~80 m). Whales may simply be staging in the polynya while they wait for ice to clear from the shelf waters near Tuktoyaktuk. However, whales migrated to the Cape Bathurst polynya almost two months prior to when they moved to the shelf near Tuktoyaktuk. If whale behavior is adaptive, it is more likely that foraging is somehow better in the polynya than in the Bering Sea in spring. Perhaps the density of zooplankton near the surface is more concentrated within the polynya than within the Bering Sea.

Why bowhead whales do not remain in the Bering Sea year-round is also unknown. They summered in the Bering and Chukchi seas when Yankee whalers first arrived in 1848 and stable isotope studies indicate that the majority of what bowhead whales consume comes from the Bering and Chukchi seas (Schell et al., 1989; Schell and Saupe, 1993). Also using stable isotopes, Lee et al. (2005) estimated that only 13.7% of the diet of subadults

and 4.6% of the diet of adults were derived from the Beaufort Sea. However, isotope studies must be interpreted cautiously. Krill thought to be of Bering Sea origin are found in the stomachs of bowhead whales near Point Barrow and Kaktovik. Hence whales may feed in the Alaskan Beaufort Sea on prey that have isotopic ratios consistent with the Bering or Chukchi seas. Furthermore, whales harvested at Point Barrow in autumn, when returning from the Canadian Beaufort, have better body condition than whales harvested in spring, when returning from the Bering Sea (J.C. George, pers. comm.). While we cannot explain the discrepancy between studies of isotopes and body condition, our study suggests that bowhead whale movements from wintering areas in the Bering Sea, where they appear to be feeding, are to spring core-use areas in the Cape Bathurst area where whales also appear to be feeding. Numerous studies have also observed summer feeding in Canadian Beaufort Sea (e.g., Würsig et al., 1985; Walkusz et al., 2012).

The interpretation of movement patterns is complicated by the history of commercial whaling and whale behavior. Although Yankee whalers found bowhead whales summering in the Bering and Chukchi seas in 1848, by 1853 this segment of the population was either extirpated or displaced to summering grounds in the Canadian Beaufort Sea (Bockstoce and Botkin, 1983; Bockstoce et al., 2005). As such, bowhead whales may simply migrate to the Canadian Beaufort Sea each spring because they have become behaviorally entrained to do so. Bowhead whales have life-spans in excess of 100 years (George et al., 1999). Indeed, the recovery of fragments from whale bombs, likely deployed in the 1880s, and of stone and ivory whaling tools from contemporary whale harvests (George and Bockstoce, 2008) indicates that some whales currently alive survived the Yankee whaling period (1848–1914) because they migrated to the Canadian Beaufort Sea in spring and were spared from intense whaling in the Bering and Chukchi seas.

Conclusions

We used satellite-linked transmitters on bowhead whales to identify areas of concentrated use throughout their annual range. While most of these areas were known to be important prior to this study (e.g., Carroll et al., 1987; Moore et al., 1995; Harwood et al., 2010; Walkusz et al., 2012), there was an incomplete understanding of the timing and sequence of whale movements between areas where information was collected. Observations near whaling communities and aerial surveys are essentially "snapshots" of movements or behavior at a particular point in time and space. While these methods allowed a general description of whale movements to be developed, satellite telemetry was necessary to fit the pieces together. This was especially true for areas in Russian waters, such as the northern coast of Chukotka, and in winter, when whales occupy ice-covered waters, also largely within Russian waters.

The model of movements that has emerged indicates that bowhead whales largely move from one foraging location to another. Whales appear to have an annual "circuit" of known locations where food is seasonally abundant. Most whales migrate to the Cape Bathurst polynya in Canadian Beaufort Sea and the timing of the migration corresponds to when zooplankton seasonally ascend into the euphotic zone. When zooplankton descend in July, most whales move to the shallow shelf waters adjacent to the Tuktoyaktuk Peninsula (and/or Herschel Island), where upwelling is expected to aggregate copepods. The autumn migration may correspond to when copepods finally descend to depths too deep for the upwelling to carry them onto the shelf. In late summer/early autumn, whales are known to pause their migration and feed near Point Barrow when the "krill trap" actively aggregates zooplankton (Ashjian et al., 2010). From the Point Barrow area, whales typically migrate to the northern coast of Chukotka, where a salinity front within the Siberian Coastal Current likely aggregates prey coming north in Anadyr/Bering Shelf waters. This front disappears in December, as rivers freeze and freshwater outflow is reduced. At the same time, currents flowing northwards through Bering Strait weaken (Stabeno et al., 1999), likely reducing zooplankton advection into the Chukchi Sea. Whales then move into the Bering Sea, where they spend time in an intrusion near the seafloor of relatively salty (>32.5) water originating from the Bering Sea slope region. In the Bering Sea, especially near the Gulf of Anadyr, whales spent much of their time at or near the seafloor, providing strong evidence of winter feeding. As such, whales of the BCB population likely forage year-round, although it is unclear how much energy is obtained in each core-use area or how their reproductive status or age may affect movements or foraging.

These explanations for the timing of whale movements among core-use areas are speculative; more detailed examinations of our existing data are warranted, as is the collection of empirical data within whale core-use areas. While collecting empirical data on oceanographic features and zooplankton associated with whale use areas (e.g., Laidre et al., 2007; Walkusz et al., 2012) provides the most reliable inference, such opportunities are limited in Russian and/or ice-covered waters. As such, we expect advances in our knowledge to derive mainly from advances in how the ocean environment is remotely sampled using gliders (e.g., Baumgartner et al., 2013) and/or innovative tags on the whales themselves (e.g., Lydersen et al., 2002). However, much more can be accomplished with our existing dataset. Future analyses need to link and statistically model whale movements using time-specific model results, focusing how best to explain the variation in movements among individual whales and over time.

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