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Bowhead Whale (*Balaena mysticetus*) Migration and Calling Behaviour in the Alaskan Beaufort Sea, Autumn 2001–04: An Acoustic Localization Study

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ABSTRACT. The westward migration of bowhead whales (Bering Sea stock) was studied during autumn 2001–04 as part of an oil industry monitoring program. An array of Directional Autonomous Seafloor Acoustic Recorders (DASARs) was deployed northeast of the Northstar oil production island near Prudhoe Bay, Alaska. Underwater sounds were recorded continuously for 24–35 days per year, mainly in September. More than 130 000 bowhead calls were detected, and the directional capability of DASARs allowed triangulation of whale position for ~93 500 calls. The migration pathway was closer to shore in 2003–04 than in 2001–02. Calls were clumped in space and time, and there was significantly more calling at night than by day. From 65% to 82% of calls were simple frequency-modulated calls, and the percentage of complex calls was positively related to the daily number of calls. No songs were detected, but in 2004 there were numerous call sequences consisting of repeated identical calls in series and generally lasting up to a few minutes. The DASAR methodology provides detailed information on the temporal and spatial distribution of calling whales and on their acoustic repertoire.

Key words: Alaska, autumn, *Balaena mysticetus*, Beaufort Sea, bowhead whale, calls, diel pattern, migration

RÉSUMÉ. La migration à l'ouest de la baleine boréale (population de la mer de Béring) a été étudiée durant quatre automnes (2001-2004) dans le cadre d'un programme d'étude de l'industrie pétrolière. Un réseau d'enregistreurs sous-marins autonomes et directionnels (DASAR) a été déployé au nord-est de Northstar, une île artificielle d'exploitation pétrolière près de Prudhoe Bay en Alaska. Des enregistrements sous-marins continus ont été récoltés pendant 24 à 35 jours chaque année, principalement pendant le mois de septembre. Plus de 130 000 appels de baleines ont été enregistrés et la capacité directionnelle des DASAR a permis de déterminer par triangulation la position des baleines pour ~ 93 500 de ces appels. Le corridor de migration s'est avéré plus proche de la côte en 2003-2004 qu'en 2001-2002. Les appels des baleines étaient groupés dans le temps et l'espace et il y avait significativement plus d'appels la nuit que le jour. Soixante-cinq à 82 % des appels appartenaient au type dit « simple », et le pourcentage d'appels du type « complexe » était positivement corrélé au nombre journalier d'appels. Aucun chant n'a été détecté, mais les enregistrements de 2004 contenaient de nombreuses séquences d'appels composées de séries d'appels identiques répétés pendant 30 minutes et plus. L'utilisation des DASAR a permis d'obtenir des renseignements détaillés sur la distribution spatiale et temporelle de baleines boréales vocalisant ainsi que sur leur répertoire acoustique.

Mots clés : Alaska, automne, *Balaena mysticetus*, mer de Beaufort, baleine boréale, appels, diel, migration

Реферат. Исследовали западную миграцию беринговоморской популяции гренландских китов в осенний период в 2001-2004 гг. Это исследование является частью программы мониторинга, финансируемой нефтяными компаниями. Сеть направленных автономных донных акустических приемников (АДАП) была размещена к северо-востоку от искусственного нефтепроизводящего острова "Нортстар" около зал. Прудо на Аляске. Подводные акустические сигналы записывали непрерывно в течение 24-35 дней в год, в основном в сентябре. Были зафиксированы более 130 000 сигналов гренландских китов, а направленные датчики позволили триангулировать местонахождение кита для 93 500 сигналов. Путь миграции китов в 2003-2004 гг был ближе к берегу, чем в 2001-2002 гг. Сигналы были агрегированы в пространстве и времени, и их было значительно больше ночью, чем днем. Простые частотно-модулированные сигналы составляли 65-82% всех сигналов, а процент сложных сигналов был позитивно коррелирован с числом сигналов за день. "Песни" не были отмечены, но в 2004 г. были зафиксированы многочисленные последовательности, состоящие из повторяющихся идентичных сигналов в сериях длительностью до нескольких минут. Методология использования АДАП дает детальную информацию о распределении акустических сигналов китов в пространстве и времени и о характере этих сигналов.

Ключевые слова: Аляска, осень, *Balaena mysticetus*, море Бофорта, гренландский кит, вокализация, циркадные ритмы, миграция

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INTRODUCTION

The Bering Sea stock of bowhead whales, *Balaena mysticetus*, undertakes an annual migration from summering areas in the central and eastern Beaufort Sea and Amundsen Gulf to wintering areas in the Bering Sea. During this migration, whales pass offshore of Alaska's Prudhoe Bay oilfields in late August through late October en route westward towards the Chukchi Sea (Moore and Reeves, 1993). Off northern Alaska, most of the whales travel over the continental shelf, mainly in waters 20–50 m deep (Moore et al., 1989b; Moore and Reeves, 1993; Treacy, 2002), i.e., generally 20–60 km offshore (Treacy, 2002; Monnett and Treacy, 2005; Treacy et al., 2006). During autumn migration bowheads may migrate steadily across the Beaufort Sea, at swimming speeds of 4–5 km/h (Koski et al., 2002), or they may mill or feed along the way (Ljungblad et al., 1986a; Moore et al., 1989b; Würsig and Clark, 1993; Treacy, 2002; Lowry et al., 2004).

The sounds of bowhead whales have been described in several earlier studies (Braham et al., 1980; Ljungblad et al., 1980, 1982; Clark and Johnson, 1984; Cummings and Holliday, 1985, 1987; Moore et al., 1989a; Würsig and Clark, 1993). Bowhead sounds are mainly frequency-modulated (FM) calls at low (< 400 Hz) frequencies ("moans"), but the repertoire also includes a variety of amplitude-modulated (AM) and pulsed calls at frequencies up to at least 4 kHz (Cummings and Holliday, 1987; Würsig and Clark, 1993). Spring recordings include complex songs (Clark and Johnson, 1984; Cummings and Holliday, 1987), which differ from one year to the next (C.W. Clark, pers. comm. 2006). Source levels for both calls and songs have been estimated (during spring) at up to 189 dB re 1 µPa-m (Cummings and Holliday, 1985, 1987), and calls have often been detected from bowheads 10 km or more away (Cummings and Holliday, 1985; Ko et al., 1986; Clark et al., 1996). Bowhead calls may be slightly directional, i.e., stronger ahead than astern, but evidence for this is inconclusive (Clark et al., 1986a). Functions of bowhead calls are not well documented, but calls might be used to maintain social cohesion in groups during migration, feeding, etc. (Würsig et al., 1983; Ljungblad et al., 1986b; Würsig and Clark, 1993). Bowhead whales might also use echoes or reverberation from low-frequency calls to help navigate through ice (Ellison et al., 1987; George et al., 1988b).

Northstar is a man-made oil production island constructed by BP Exploration (Alaska) in 2000 and located in nearshore waters of the Alaskan Beaufort Sea, northwest of Prudhoe Bay (Fig. 1). Located 5 km offshore, Northstar is close to the southern edge of the fall migration corridor. Since 2001, we have been conducting a long-term acoustic monitoring program near the Northstar oil development. This program has provided information on the occurrence, characteristics, and (usually) locations of more than 130 000 bowhead calls over four autumn migrations. We have used these recordings to examine bowhead migration behaviour as evidenced by timing and distribution of calls, and to compare call types, call detection rates, and diel patterns with those described in other studies and at other times of the year.

METHODS

Instrumentation

This study relied on an array of Directional Autonomous Seafloor Acoustic Recorders (DASARs, described in Greene et al., 2004) to localize and record bowhead whale calls. DASARs were deployed at 10 locations 6.5–21.5 km northeast of the Northstar oil production island in late August of each year 2001–04 (Fig. 1). All DASARs were retrieved around 30 September (Table 1), before freeze-up, even though it was known that the bowhead migration in the Prudhoe Bay area continues until mid- or late October (Moore and Reeves, 1993). Thus, this study includes only data from the early and middle part of the bowhead migration season.

The DASARs were placed on the seafloor (depth range 12–24 m) at the vertices of equilateral triangles with 5 km sides, collectively forming two overlapping hexagons (Fig. 1). In 2003 and 2004, a DASAR was also deployed ~500 m north of the island. DASARs recorded continuously at a 1 kHz sampling rate for the duration of the deployments, allowing sounds at frequencies up to ~500 Hz to be detected. Once a week, a compass and clock calibration of the DASARs was performed by playing a calibration sound (a combination of low-frequency tones and sweeps) at specific locations within and outside the DASAR array (Greene et al., 2004). In 2002–04, we did not analyze whale calls recorded when the boat conducting the calibration work was more than 2 km seaward of Northstar. (In 2001 we knew the dates, but not the exact times during which the acoustic vessel was in the DASAR array.) No adjustments were made for other vessel traffic known to occur in the array, which includes whale hunters based on Cross Island, slightly east of the map shown in Figure 1. Hunting took place every year for 1–3 weeks starting around 1 September.

Call Classification

Trained staff classified each call manually by listening to recordings and examining spectrograms. The lead analyst performed regular checks for consistency among analysts. Most calls were detected by more than one DASAR, but each call was classified and tallied only once. Reception of a call at more than one DASAR allowed for triangulation of the call's estimated position, according to a method described in Greene et al. (2004). Calls were classified into three major categories, ***simple calls***, ***complex calls***, and ***call sequences***, on the basis of call descriptions by Clark and Johnson (1984) and Würsig and Clark (1993). ***Simple calls*** were FM tonal calls or "moans" in the

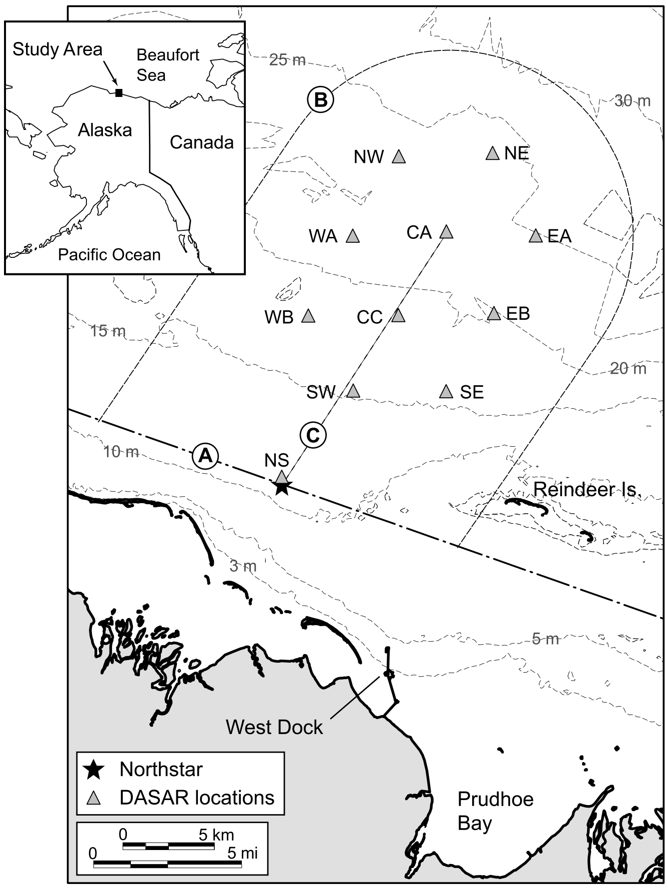

FIG. 1. Map of study area showing DASAR locations (grey triangles) in relation to Northstar (black star). DASAR locations were the same in 2001–04 except (1) that there were two recorders at location CA in 2001–03 (the second was a backup, and its data were not analyzed) and (2) DASAR NS (near Northstar) was present only in 2003 and 2004. (A) = baseline, (B) = edge of analysis area, (C) = central axis (see text for explanations).

50–300 Hz range. We distinguished (1) ascending or "up" calls, "/"; (2) descending or "down" calls, "\"; (3) constant calls, "–"; and (4) inflected calls, "∪" and "∩". ***Complex calls*** were infinitely varied and included pulsed sounds, squeals, growl-type sounds with abundant harmonic content, and combinations of two or more simple and complex segments. Subcategories of complex calls could not be consistently discerned, so all subcategories were pooled. ***Call sequences*** were repeated utterances, usually every 2–5 s, of a simple or complex call. Sequence duration ranged from less than 1 min to many minutes. Call sequences were detected only in 2004. Call sequences were not included in the analysis of the frequencies of call types.

Except for a few "barks," possibly produced by ringed seals (*Phoca hispida*), we did not identify any sounds that could be attributed to other marine mammals, such as bearded seals (*Erignathus barbatus*) or gray whales (*Eschrichtius robustus*).

Defining the Analysis Area

The DASARs' ability to detect a call varied with the call's source level, the distance from the whale to the

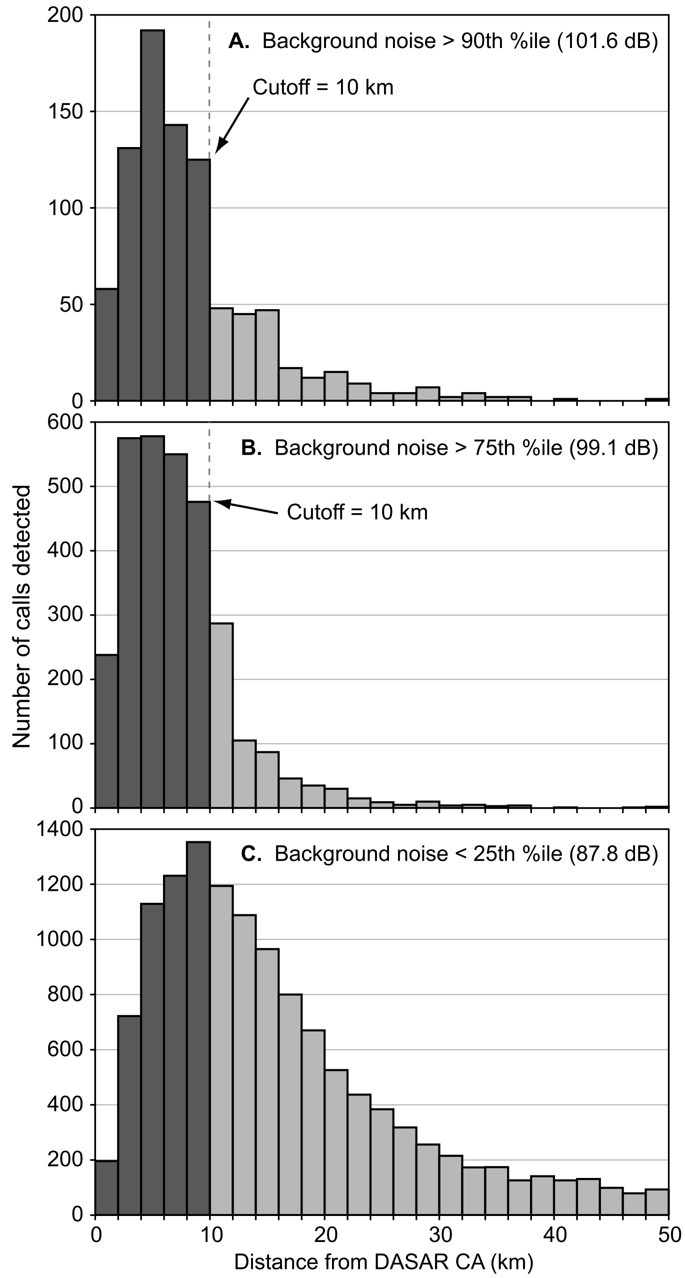

FIG. 2. Distances from estimated locations of calling whales to DASAR CA during (A) very high, (B) high, and (C) low background noise conditions in 2003. Note that the y-axis ranges are different in the three plots. A cutoff distance of 10 km was established at the "shoulder" evident in (A) and (B). Background noise was measured at the NE DASAR in the 10–500 Hz band (one 1-min measure every 4.37 min, or ~330 times per 24-hour day). Values in dB re 1 μPa. See Greene et al. (2004) for corresponding 2002 graph.

DASAR, and ambient noise levels. To minimize potential biases associated with ambient noise, we defined an analysis area in which all (or nearly all) calls would be heard by one or several DASARs even when ambient noise levels were high. To define the analysis area, we first calculated the distance from a central location within the DASAR array (point CA on Fig. 1) to each call location. Figure 2 summarizes these distances for 2003, distinguishing times with varying levels of ambient noise, as measured in the 10–500 Hz band at DASAR NE, the farthest from Northstar.

TABLE 1. Dates of operation and numbers of detected calls meeting various criteria during the four years of study. To get a position estimate, a call had to be detected by at least two DASARs; therefore, a position estimate is not available for all calls. The 5th percentile of offshore distances (i.e., distances from the baseline) for all calls with a position estimate, including those outside the analysis area, is also given for each year.

	2001	2002	2003	2004
Dates of operation (beginning – end)	29 August – 3 October	30 August – 23 September[1]	29 August – 28 September	30 August – 1 October
# of days	35	24	30	32
Total calls detected	10 738	10 576	45 622	66 232
Mean calls per day	307	441	1521	2070
Total calls with position estimate	3446	7922	32 938	49 270
5th percentile of offshore distances (km)	13.8	14.2	8.4	10.1
Total calls with position estimate inside analysis area	1114	2056	16 379	26 369
Mean calls per day	32	86	546	824

[1] Monitoring terminated early because a storm disrupted the DASARs.

Very high, high, and low noise levels at that DASAR were defined as those above the 90th, above the 75th, and below the 25th percentile, respectively. A cutoff distance was established at the distance where the number of calls detected under high ambient noise conditions dropped appreciably. A 10 km cutoff distance was chosen for 2003 on the basis of the "shoulder" at 10 km in Figure 2. The same 10 km shoulders were apparent in 2001 and 2002 (Greene et al., 2004). In 2004, the cutoff distance was arguably closer to 8 km than to 10 km, but we used 10 km for consistency among years.

Using this 10 km cutoff distance, we defined calls as being inside the analysis area if they were within 10 km from the "central axis" of the DASAR array. That axis was the straight line from CA to Northstar (Fig. 1). Thus, the analysis area was a 20 × 26.6 km silo-shaped area shown in Figure 1. Unless stated otherwise, we considered only the calls that were inside this area in our analyses. However, some figures also show calls outside the analysis area for comparative purposes.

The line forming the inshore edge of the analysis area was the "baseline" (see Fig. 1). Offshore distances of whale calls were calculated perpendicular to this line. The baseline runs through Northstar Island approximately parallel to the Beaufort Sea coast, with an orientation from 108˚ to 288˚ True. The most appropriate baseline orientation for assessing the offshore distance of calls depends on the length of coastline considered, whether the barrier islands are taken into account, and whether only the coastline is considered or also the bathymetric contours. We chose a baseline appropriate in relation to the section of coast from 146˚ W to 150.5˚ W, a distance of about 180 km. This was the same region and orientation used in the analyses of Miller et al. (1999).

RESULTS

Call Numbers and Locations

The total numbers of calls (a) detected, (b) with an estimated position (i.e., detected by more than two DASARs), and (c) located inside the analysis area are summarized in Table 1. Because the duration of monitoring varied among years, the number of whale calls is also expressed as a mean number of calls per monitoring day. This number increased every year from 2001 to 2004.

The locations of calls with known positions are shown in Figure 3. The 5th percentile of offshore distances for all calls with a known position, including those beyond the analysis area, was about 14 km in 2001 and 2002 (Table 1). In 2003 and 2004, the migration corridor was closer to shore (Fig. 3), with 5th percentiles of offshore distances close to 10 km (Table 1).

There was year-to-year variation in the uncertainty of whale call localizations. Over all years, for calls in the analysis area, the lengths of the long and short axes of the 90% confidence ellipses were as follows: for the long axis, 75th percentile = 656 m, 95th percentile = 1266 m, median = 374 m; for the short axis, 75th percentile = 212 m, 95th percentile = 303 m, median = 142 m. In general, the long axis of confidence ellipses was oriented radially in relation to the centre of the DASAR array, but less so inside the array, where a higher proportion of bearings tended to intersect at roughly right angles. Outside the analysis area, the long-axis lengths of the 90% confidence ellipses increased rapidly, reaching 2.5–5 km within 20 km from the centre of the array (see Greene et al., 2004; Blackwell et al., 2004). Some calls were from whales less than 20 km offshore, but more than 20 km from the array, i.e., well to the east or west; their positions are quite uncertain. The greater uncertainty about the locations of distant calling whales was another reason for considering only calls in the analysis area during our analyses.

The number of calls detected per hour varied widely, fluctuating between 0 and over 600 calls per hour (Fig. 4). The day with the highest number of detected calls was early in the season in 2001 (6 September) and towards the end of our sampling season in 2002–04 (20, 21, and 21 September, respectively). Peak hourly call-detection rates in the four years were on 13, 21, 19, and 21 September, respectively (Fig. 4).

Ambient sound levels (which vary with the amount of wind) affected our ability to detect calls. Generally, call

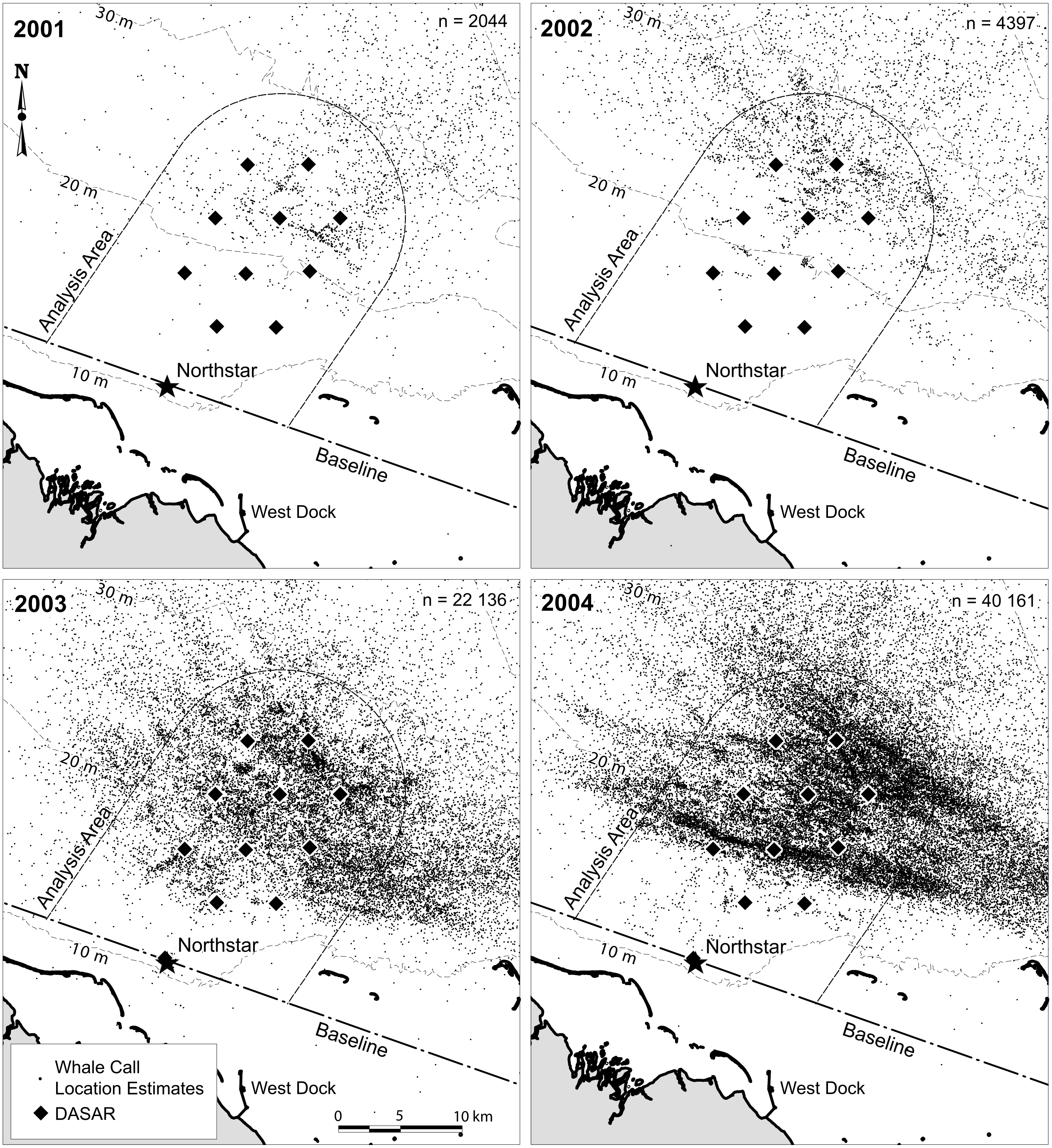

FIG. 3. Maps of whale call locations within and near the silo-shaped analysis area in 2001–04. Northstar is shown as a black star, and the DASARs are shown as black diamonds. The "baseline" is parallel to the general trend of the coast (see text for details). Sample sizes on plots are for geographical area shown.

detection rates on windy days with higher background noise levels tended to be lower, whereas calm days included times with both high and low calling rates (Fig. 4). Even when restricting our analyses to the analysis area, the hourly rate of call detection decreased with increasing background sound levels in three out of four years (Spearman's rank correlation: 2001, r_s = –0.076; 2003, r_s = -0.173; 2004, r_s = -0.319; $p < 0.01$ except for 2001 where $p < 0.05$). In this comparison we used background sound levels from DASAR NE, the DASAR farthest from Northstar and therefore the least influenced by anthropogenic sounds. In 2002, the number of detectable calls

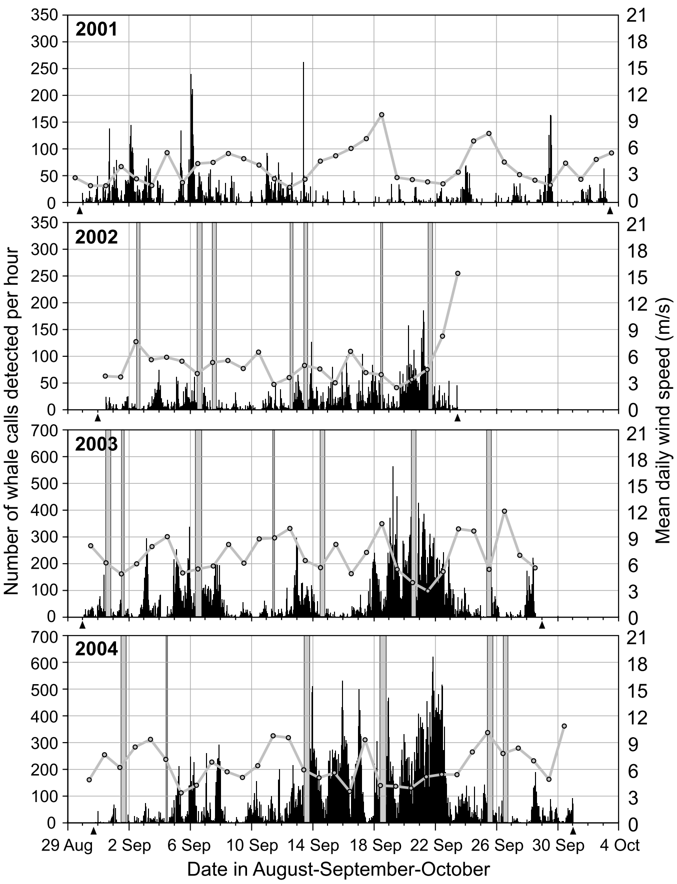

FIG. 4. Number of whale calls detected each hour and mean daily wind speed over the 2001–04 monitoring seasons. The y-axis range for 2001 and 2002 is half that for 2003 and 2004. Wind speed data are daily averages of hourly means from the Northstar weather station (see http://www.resdat.com/mms). Black triangles below x-axes show the beginning and end dates of data analyzed. Grey areas in the 2002–04 plots delimit times excluded from the analysis because the service vessel was in the DASAR array. (In 2001 such times were retained in the analysis.) This figure includes all detected calls, with or without a position estimate.

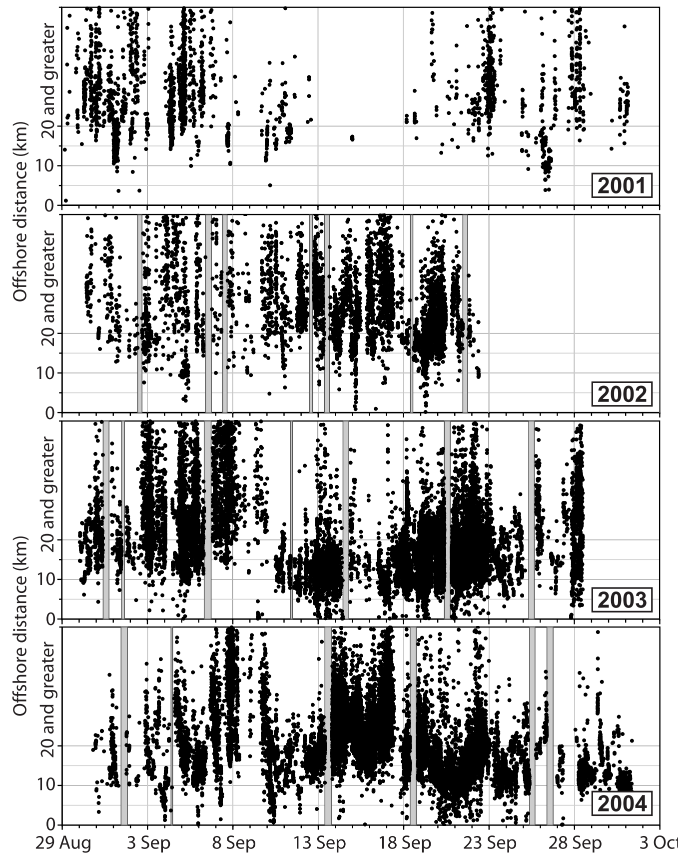

FIG. 5. Offshore distance for each whale call with a location estimate, as a function of date, for all four monitoring seasons. Calls both inside and outside the analysis area are included. Note that distances greater than 20 km from the central axis of the array have large associated errors; those locations should be used only as an index of the frequency of whale calls at great distances from the island. Grey areas in the 2002–04 plots delimit times excluded from the analysis because the service vessel was in the DASAR array. Date labels appear at the start of each day (00:00 AKDT).

tended to increase with broadband levels at NE ($r_s = 0.241$; $p < 0.01$).

Calls were detected in "pulses," both in time (as shown in Fig. 4) and in space. This pattern is evident in plots of offshore distance to whale call locations as a function of date (Fig. 5). For example, most calls were detected 15 km or more seaward of the baseline through Northstar on 17 September 2004, but three days later, on 20 September, numerous calls were detected very close to shore.

Diel Patterns

Figure 6 shows diel patterns in call detection rates for all monitoring seasons. Only complete monitoring days, starting and ending at midnight, were included; this excludes days in all four years when the acoustic vessel was in the DASAR array. Each year there was some variation in call detection rates with time of day, but there was no consistent pattern of hour-to-hour change that applied in all years. However, during all years the two-hour bin with the most calls was during nighttime or around dawn, between 22:00 and 06:00 Alaska Daylight Time (AKDT). Also, in all four years the average call detection rate was significantly ($p < 0.05$) higher at night than in daytime, as shown by Wilcoxon matched-pairs signed-ranks tests (2001, $T = 119$, $n = 27$; 2002, $T = 15$, $n = 15$; 2003, $T = 32$, $n = 22$; 2004, $T = 71$, $n = 25$). For this analysis, average call detection rates were calculated, in calls/h, for each day and each night in all four years, using the same dataset as in Figure 6. For each 24-hour period, "night" was defined as the time from midnight to 30 min before sunrise and from 30 min after sunset until midnight, and "day" was defined as the period starting 30 min after sunrise and ending 30 min before sunset. Mean daytime and nighttime call detection rates for all four years of the study are presented in Table 2.

Daytime and nighttime mean wind speeds and mean broadband levels of sound at DASAR NE were analyzed in the same way as the call detection rates, for all four years. Neither analysis showed any significant differences between day and night. This suggests that the day-night difference in call detection rates was not an artefact of a diel pattern in wind speed or background noise levels.

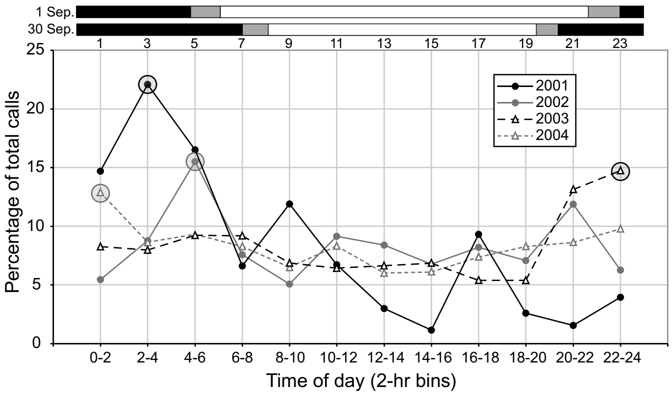

FIG. 6. Diel patterns of calling within the analysis area, expressed as a percentage of total calls included in each of 12 two-hour bins, 2001–04 (the 12 values for a given year add up to 100%). Circles indicate the two-hour bin with the highest percentage of calls for each year. The two horizontal bars at the top of the figure show the change in the length of day (white), night (black), and twilight (grey) between 1 September (top) and 30 September (bottom), as defined by the times (AKDT) of sunrise, sunset, and civil twilight.

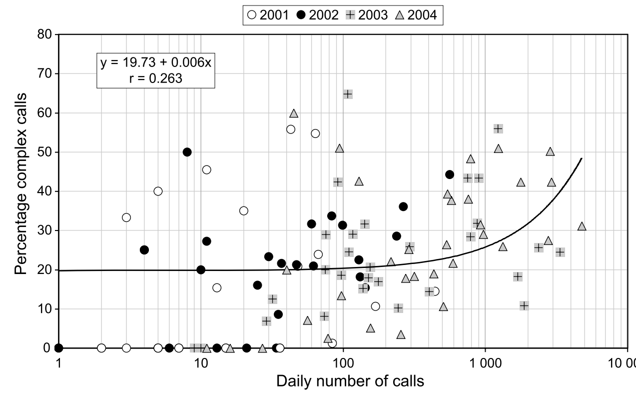

FIG. 7. Percentage of calls that were complex as a function of the daily number of whale calls detected inside the analysis area (used as an index of whale density), for all four years. A linear regression was applied to the combined data sets, but the x-axis is plotted on a logarithmic scale because of the spread of values.

TABLE 2. Average call detection rates within the analysis area during daytime and nighttime for 2001–04. Sample sizes (# calls) are smaller than in Table 1 because days when the acoustic vessel was in the DASAR array were excluded, as were calls occurring during the day/night transition (2h/day). See text for details, and for definition of “day” and “night.”

	Night (calls/h)	Day (calls/h)	# calls
2001	2.6	1.0	930
2002	5.4	3.0	1330
2003	32.8	20.0	12 460
2004	45.8	33.6	21 294

TABLE 3. Percentages of different call types during all four field seasons. Only calls inside the analysis area were considered. Sample size for 2004 is lower than in Table 1 (26 369) because it does not include call sequences.

	2001	2002	2003	2004
Up call “/”	30.6	20.0	21.7	28.5
Down call “\”	27.6	17.3	11.3	10.8
Constant call “–“	7.5	14.0	27.1	10.4
Inflected “∪”	10.1	13.0	7.9	10.0
Inflected “∩”	6.4	5.4	5.1	4.8
Simple calls (sum of the above)	82.1	69.8	73.2	64.5
Complex calls	17.9	30.2	26.8	35.5
Sample size	1114	2056	16 379	25 709

Call Types

Yearly percentages of the different call types inside the analysis area are shown in Table 3. The overall percentages of calls that were simple, based on annual samples of 1114–25 709 calls, were 82% in 2001, 70% in 2002, 73% in 2003, and 65% in 2004. In 2002, 2004, and all four years combined (Fig. 7), the daily proportions of calls that were complex were significantly related to the daily number of calls (product-moment correlation $r = 0.49$, 0.38, and 0.26, respectively; d.f. = 23, 32, and 114; $p < 0.01$, $p < 0.05$, and $p < 0.01$). Assuming that the number of calls detected inside the analysis area is an index of the number of whales passing by, then the correlation indicates a positive relationship between the number (i.e., density) of whales and the use of complex calls. The trend seems particularly well defined for daily call counts above ~150 (Fig. 7).

We investigated whether the proportions of the different call types detected within the analysis area changed over the course of our field seasons. We calculated the percentage of each call type for each 24-hour period (midnight to midnight) each year. We then tested the relationship between the daily percentage of each call type and Julian date, using Spearman’s rank correlation. Days with fewer than 20 calls (of all types) were excluded. There was little consistency from one year to the next (Table 4). The proportional frequency of “up” calls was not strongly related to date in three of four years, but decreased significantly with date in 2004 and overall (Table 4). In contrast, the frequency of “down” calls increased significantly with date in 2004, but not in the other three years. When all four years of data were pooled, only the frequency of “up” calls was correlated with Julian date, but this result was largely determined by the 2004 trend (Table 4).

Call Sequences

We defined a call sequence as a series of repeated identical or similar calls, presumably produced by one individual whale or an interacting group of whales. Call sequences were evident only in the 2004 data set, in which over 650 sequences were identified. Of those, 65 were systematically chosen (by selecting about every 10th identified call sequence) and analyzed in more detail. Call sequences generally lasted from ~14 s to 5.5 min, with a median duration of 73 s. However, among the 65 analyzed sequences there were two notable extremes—sequences that lasted over 30 and 50 min, both occurring between 23:30 on 18 September and 01:00 on 19 September. Inter-

TABLE 4. Spearman's rank correlation between daily percentage of each call type versus Julian date, for each of the four study years and all years combined. Only calls within the analysis area were considered.* and ** indicate that the correlation is significant at the 0.05 or 0.01 level, respectively.

	n	Up calls	Down calls	Constant calls	∪-shaped undulation	∩-shaped undulation	Complex calls
2001	10	- 0.176	- 0.300	- 0.468	- 0.657*	- 0.091	0.345
2002	17	- 0.103	- 0.017	- 0.348	0.358	- 0.146	0.131
2003	27	0.170	- 0.274	0.293	- 0.436*	0.229	- 0.149
2004	31	- 0.579**	0.706**	0.190	0.294	0.384*	- 0.044
All	85	- 0.247*	0.100	0.133	- 0.010	0.101	0.084

call interval was generally 2–5 s, but occasionally up to ~15 s and more. Therefore the durations of the sequences are somewhat subjective, as durations depended on the maximum inter-call interval that we considered to be part of the same sequence. We generally defined a sequence as having ended if the inter-call interval exceeded 20 s.

Like other bowhead calls, sequences generally appeared in clusters. The call sequences analyzed were nearly always detectable simultaneously via several DASARs—85% of call sequences were recorded by at least five DASARs and 15% were recorded by all the DASARs, including the one close to Northstar. This indicates that individual calls within sequences were commonly detectable over distances of 5 km and sometimes up to 15 km or more.

Calls within sequences were repeated regularly but with some variation over time. The calling rate could slow down or speed up, and calls were sometimes skipped or slightly modified. The frequency range with most of the call's energy could also shift over time, particularly at the beginning and end of a sequence. A sample call sequence is shown in Figure 8A. This 4 min section was extracted from the first of the two long call sequences, recorded by DASAR EB a little before midnight on 18 September 2004.

Seventy-seven percent of the call sequences contained one specific call type: an owl-like "ou," sometimes varying to "eu" or "en." This was expressed one to four times in rapid succession ("ou," "ou-ou," etc.), followed by a gap of (typically) 1–5 s, and then repeated (e.g., Fig. 8C). One "ou" sound was generally 0.3–0.5 s in duration. The frequency range with most of the call's energy was variable, but usually 150–250 Hz as shown in Figure 8C, or 350–450 Hz, sometimes both simultaneously. The call sequence shown in Figure 8C can be transcribed as "ou-ou, ou-ou, ou, ou."

Another 20% of the sequences were made up of a stereotypical broadband call that can be described as a double (rarely triple) grunt lasting ~0.6–1.2 s. This type of call is shown in Figure 8A and is enlarged in Figure 8B. The frequency content of the grunts was usually inflected, the most common pattern being a decreasing inflection on the first grunt and an increasing inflection on the second grunt (Fig. 8B). More rarely, the second grunt was also inflected downward or had a constant frequency. Both of the exceptionally long call sequences (see above) were made up of this "double grunt" call.

Finally, "up" calls constituted the third and least common (3%) type of call found in call sequences during 2004.

Throughout the two exceptionally long call sequences there were regular periods during which the calls were weaker, i.e., "washed out" on a spectrogram—especially at the lower frequencies. Three such periods are visible in Figure 8A, starting near times 0, 80, and 180 s. The median duration of these "weak periods" was ~20 s (range 8–50 s, n = 42) and the median amount of time between two weak periods was 106 s (range 35–230 s, n = 42). Weak periods were also present in a few of the shorter call sequences.

Occasionally two call types would alternate during a sequence of a few calls. These alternating sequences usually lasted less than 10 s. Often, the involvement of more than one whale could be confirmed by examining the bearings to the two types of alternating calls as provided by a nearby DASAR. The alternating sequence of call types then corresponded to an alternating sequence of bearings.

We also used the DASAR directional capability to track the vocalizing whale(s) during the two exceptionally long call sequences mentioned above. These occurred consecutively, the first one ending at 23:59:05 and the second one starting at 23:59:45 on 18 September 2004. We obtained a position for one call about every 2 min, using bearings from at least three DASARs. The resulting positions and tracks are plotted in Figure 9, which shows an area of 3 × 3 km close to DASAR EB, in the eastern part of the DASAR array (see Fig. 1). Taking the errors in estimated positions into account (see Greene et al., 2004, and above), the vocalizing whale was relatively stationary during the first call sequence. During the second call sequence the vocalizing animal moved about 2 km towards the southeast at a rate of ~2.2 km/h or 0.6 m/s, away from the general direction of the migration. Given the proximity in time and space between the end of the first sequence and the beginning of the second (Fig. 9) and the fact that both sequences contained the same type of call, these two sequences may have been produced by the same animal.

DISCUSSION

Placing an array of seafloor acoustic recorders within the southern (nearshore) part of the autumn migration path of bowhead whales yielded many data on the timing, locations, and characteristics of calling activity. These data complement and extend available aerial survey data on the timing and route of bowhead migration past the

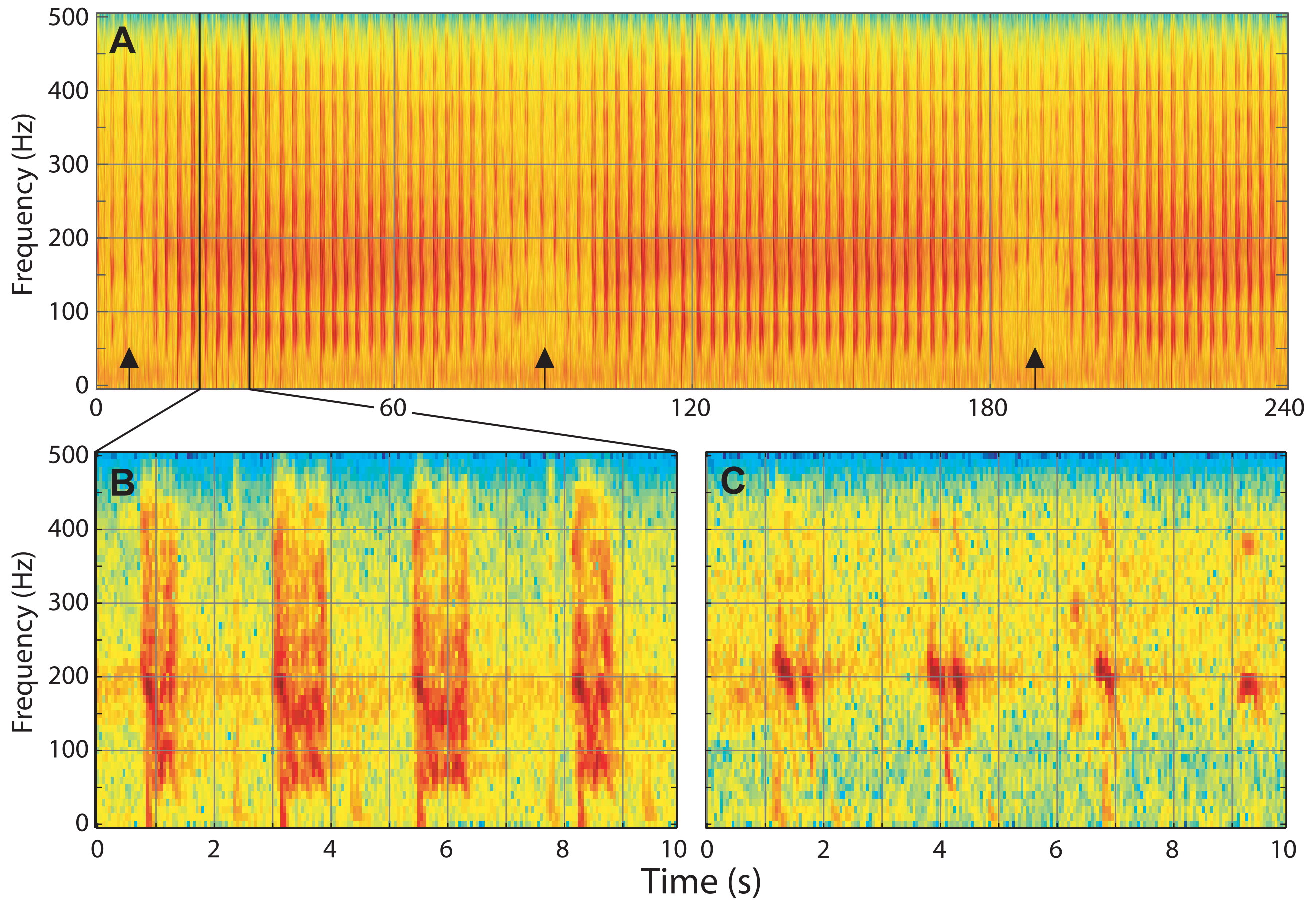

FIG. 8. Spectrograms of call sequences. (A) Four minutes of data recorded by DASAR EB starting at 23:27:00 on 18 September 2004. Black arrows indicate "weak periods" (see text). (B) Expanded 10 s segment of (A), starting at 23:27:21, showing the "double grunt" type call. (C) Ten seconds of data recorded by DASAR EA at 15:33:44 on 15 September 2004, showing the "ou" type call (see text for details).

Prudhoe Bay/Northstar area off northern Alaska. Also, we provide information about diel and seasonal patterns in calling and the acoustic characteristics of calls. Little information about bowhead calling behaviour during autumn migration has been published previously (but see Ljungblad et al., 1982; Moore et al., 1989a); therefore, we often compare our autumn results with related data reported by other authors for the spring migration period.

Call Numbers and Locations

Both the total number of calls detected and the total number of calls estimated inside the analysis area increased through the four years of the study (Table 1). The increase from 2001 to 2002 was in part due to minor improvements in the DASAR design and data processing (see Greene et al., 2004). The increase in detected whale calls between 2002 and later years was likely due to a shoreward shift in the location of the migration corridor in 2003 and 2004. As described below, this interpretation is partly supported by the locations of visual sightings in the Alaskan Beaufort Sea during autumn, as determined via systematic aerial surveys implemented by or for the U.S. Minerals Management Service (MMS) since 1982. These sightings are summarized in Figure 10. MMS splits the aerial survey data into an eastern and a western region; Northstar is in the western region, but it is close to the boundary (at Prudhoe Bay) between the regions. Inter-annual comparisons of the mean distances from whale sightings to shore during these aerial surveys yielded the following results:

- In 2001 the mean distance from shore was within the 25th–75th quartile range for 1982–2001 (Treacy, 2002).
- In 2002 the mean distance from shore in the western region was not different from that in 1982–2001, whereas sightings in the eastern region were significantly closer to shore (Monnett and Treacy, 2005).
- In 2003 the mean distance from shore for sightings in both regions was not significantly different from that of 1982–2001 (Monnett and Treacy, 2005).
- In 2004 the mean distance from shore for sightings in both regions was significantly smaller (i.e., closer to shore) than in 1982–2001 (Monnett and Treacy, 2005).

There is, therefore, general agreement between our data set and the MMS results except for 2003, when aerial surveys provided no evidence that the whales were closer to shore than usual.

Annual sighting rates during the MMS surveys, which take place off the entire north coast of Alaska, mirror our

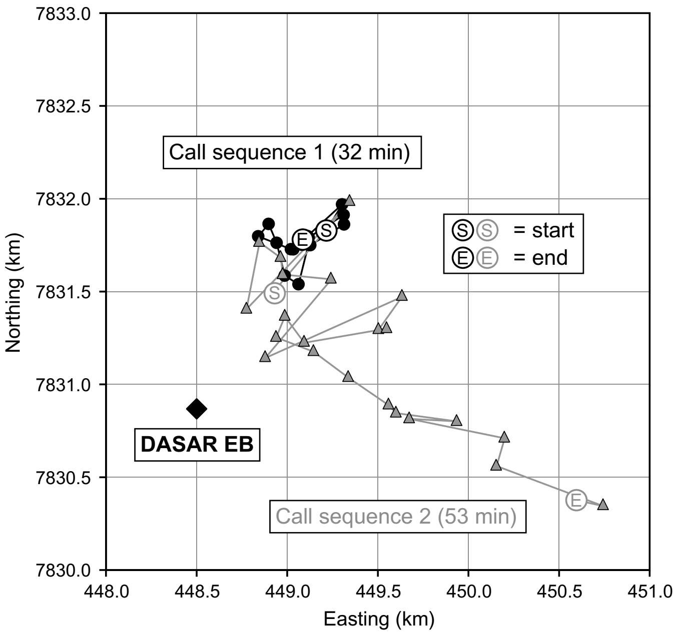

FIG. 9. Tracks of vocalizing whale(s) during two consecutive call sequences on 18–19 September 2004, in relation to the location of DASAR EB in the eastern part of the DASAR array (see Fig. 1). Call sequence 1 (black lines and dots): 23:26:45–23:59:05; call sequence 2 (grey lines and triangles): 23:59:45–00:52:32. The grid squares on the plot are 500 × 500 m.

annual call detection rates, though the number of whales seen by MMS each year was far less than the number of calls detected. MMS sighting rates were 0.91, 1.38, 6.13, and 7.52 individual bowheads per hour of random line-transect survey in 2001–04, respectively (calculated from data in Treacy, 2002; Monnett and Treacy, 2005). The DASAR array detected averages of 307, 441, 1521, and 2070 bowhead calls per day, or 13, 18, 63, and 86 calls per hour, in the same years (Table 1). Thus, in two seasons when few whales were heard on the DASAR array over a period of about a month, few whales were seen in a much larger survey area, roughly from Point Barrow to the Canadian border, over ~seven weeks in September and October. It is not clear why the sighting rate during aerial surveys was much lower in 2001–02 than in 2003–04, given that the aerial surveys extended much farther offshore than did the DASAR array. The small amount of effort expended by the MMS aerial surveys in the Northstar study area, and the low number of sightings there, preclude further meaningful quantitative comparisons.

Call detection rates are implicitly used as an index of the number of migrating bowhead whales, but it is important to remember that the proportion of whales calling at any time is not known. Studies to date have not shown a consistently close link between the number of calls detected (by sonobuoys or fixed passive listening stations) and the number of whales seen, either from ice-based observatories (such as Point Barrow in the spring) or from aircraft during aerial surveys. The relationship between whales heard and seen has alternatively been reported as significant (Moore et al., 1989a; see also Ljungblad et al., 1988), non-significant (Ljungblad et al., 1986b; Ko et al., 1986), and equivocal (George et al., 1995, 2004). In addition, George et al. (1988a) and Philo et al. (1990) have shown that calling rates are not necessarily consistent over time, i.e., a high call detection rate at one hydrophone does not necessarily predict a high call detection rate at a second hydrophone farther along the whales' migration pathway. Environmental factors such as ambient sound levels, visibility, presence of ice, etc., have variable influences on the effectiveness of acoustic and visual detection and likely contribute to the inconsistent relationships between the two.

Moore (2000), Treacy (2002), and Treacy et al. (2006) used aerial survey data to assess the relationship between ice coverage and distances from shore during the fall. These studies considered up to 19 years of survey data and showed that bowheads tended to select shallow inner-shelf waters close to shore during years with moderate and light ice, and deeper slope habitat farther from shore in heavy ice conditions. On the basis of sea ice severity rankings from the U.S. National Ice Center, ice coverage in the Alaskan Beaufort was rated as "moderate" in 2001, "relatively light" in 2002 and 2003, and "very light" in 2004 (Treacy, 2002; Monnett and Treacy, 2005). This progression was confirmed by our own observations on the presence and density of ice floes during DASAR deployments in late August, during which ice coverage out to ~24 km offshore of Northstar was as follows: 2001: less than 20%, 2002: less than 10%, 2003: 0%, 2004: 0%. Our data show that the bowhead migration corridor was particularly close to shore in 2003 and 2004 (Fig. 3), which agrees with the concept that the migration corridor is closer to shore in light-ice years.

The clustering of the calls in time and space (Figs. 4, 5) is consistent with numerous observations by both native whalers and researchers (Braham et al., 1979; Würsig and Clark, 1993). Clustering or "pulses" in whale calls and sightings is an intrinsic part of the spring migration off Point Barrow (e.g., Carroll and Smithhisler, 1980; Clark et al., 1986b; George et al., 1995). Clustering is not necessarily dependent on the presence of ice (i.e., bowheads accumulating behind a closed lead), as it occurs in spring seasons both with and without extensive ice (Carroll and Smithhisler, 1980). Also, in early to mid autumn, it is rare for there to be sufficient ice cover to obstruct the migration, and there certainly was no ice-related impediment to autumn migration in 2001–04. Clustering of calls could be produced by higher calling rates during some activities or periods than in others. However, "pulses" are also evident in visual sightings by scientists and whalers, so clustering in calls is not entirely attributable to variable calling rates. Clustering may also be related to seasonal changes in the age and sex composition of the passing whales, combined with a tendency for larger whales to occur farther from shore (e.g., Koski and Miller, 2002; Koski et al., 2005). However, seasonal changes in age and sex composition are gradual, with considerable variety in the categories of

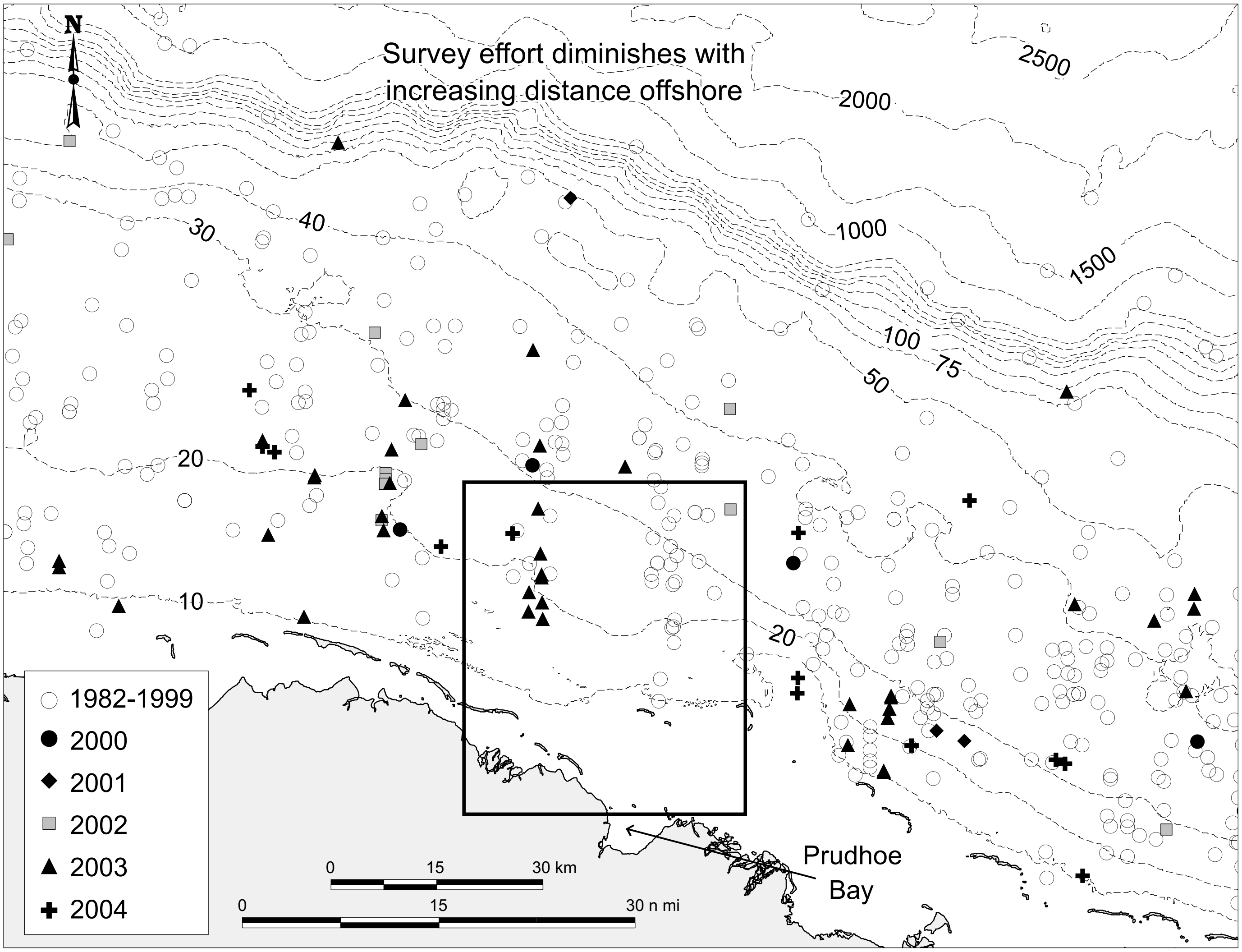

FIG. 10. Locations of bowhead whale sightings along systematic north–south transects during MMS aerial surveys, 1982–2004. Open circles, 1982–99 (before Northstar construction); closed symbols, 2000–04. The black rectangle shows the area plotted in Figure 3. Data courtesy of Dr. C. Monnett and S. Treacy, MMS Alaska OCS Region. Water depths are in meters.

whales present on most dates, and this alone is unlikely to account for complex patterns of change in numbers and locations of calls. Finally, variation in calling behaviour of any individual whale might also have an effect on the clustering of calls.

Both aerial surveys and our acoustic data suggest that autumn-migrating bowheads often concentrate at one distance from shore on a particular occasion and at a different distance from shore on another date. On one day, successive migrating whales may listen to one another's calls and effectively "follow" one another. Native whalers believe that this is common. A second possible explanation for some of the clustering as shown in Figure 5 is that there may be temporal changes in relative calling rates at different distances offshore. These two explanations are not mutually exclusive. Further examination as to why bowhead calls were clustered in time and space would require independent information on the actual number of whales moving through the study area in conjunction with acoustic data.

The distribution of whale call locations in 2003 and 2004 (Fig. 3) contains finger-like projections where the density of whale calls is higher than in adjacent areas. These "fingers" are mainly visible in the western side of the area plotted in Figure 3. We do not know whether this phenomenon is biological in origin or is related, at least in part, to some unknown artefacts of the instrumentation or data analysis (i.e., triangulation).

Diel Patterns

We did not detect a strong diel pattern in call detection rates that was consistent over the years of the study. However, the two-hour bin with the most calls was during nighttime in all four years (Fig. 6), and the call detection rate was significantly higher during the dark hours than during daylight in all four years. Moore et al. (1989a), examining bowhead calls recorded during the fall migration in 1986 and 1987, reported nighttime (18:00–06:00) call detection rates that were higher than daytime rates, but not significantly so. During the 1984 spring migration off Point Barrow, Ko et al. (1986) found that significantly more sounds were detected at "night" (18:00–06:00) than during the "daytime," and calling rates were particularly low from 15:00 to 18:00. (There is 24 hr daylight at Barrow during much of the spring bowhead migration, but the sun is lower in the sky at "night.") Somewhat in contrast to those 1984 results, data from 158 hr during the spring of 1982 at Barrow showed two peak periods of sound production: a primary peak at 06:00 to 08:00 and a weaker peak at 16:00 to 18:00 (Cummings and Holliday, 1987). The lack of significant day-night differences in mean wind speeds or background sound levels during 2001–04 suggests that higher call detection rates at night were likely not due to a diel pattern in ambient sound levels.

In summary, the above studies and our data indicate that bowhead whales tend to call more during "nighttime" both in autumn (when it is dark at night) and in at least some spring seasons (when there is often 24-hour daylight). This pattern has also been found in other mysticetes. For example, in blue whales *Balaenoptera musculus*, Stafford et al. (2005) showed that there were significantly more "B calls" during dark and twilight periods than during light periods. However, in the short term, variations in call detection rates at a fixed monitoring site may be governed principally by the timing of pulses of migrating bowhead whales passing the recording hydrophone, and less influenced by diel calling patterns. This theory could account for the observed variation among studies, among years within the same study (Fig. 6), and among the same time bins on consecutive days (Fig. 4).

Call Types

The few studies that have tried to infer functions associated with the different bowhead call types have had limited success. It seems complex calls are more commonly recorded near socializing whales and less commonly recorded near resting or swimming (migrating) whales (Würsig et al., 1985; Ljungblad et al., 1986b; Richardson et al., 1995). Ljungblad et al. (1986b) found significant relationships in the use of different call types, suggesting that call use changes with concomitant behaviour. However, the apparent flexibility of bowhead calling behaviour, combined with the difficulty of determining whether a whale observed from an aircraft was the individual responsible for calls detected via a sonobuoy, prevented them from identifying any clear associations.

The autumn migration in the central Beaufort Sea tends to begin with younger animals, gradually changing to predominantly larger, older animals (Koski and Miller, 2002; Koski et al., 2005). Therefore the lack of clear trends in call type with date (Table 4) would suggest that the relative use of simple or complex calls is not strongly linked to the age of the animals.

Table 3 shows that "up" calls were most common in all years but 2003. "Down" calls were usually the next most common, followed by "constant" and "inflected" calls. Similarly, of 5655 calls recorded in the Canadian Beaufort Sea during the summers of 1980–84 in the absence of seismic pulses, 34% were up calls, 22% were down calls, 18% were constant calls, and 8% were inflected calls (Richardson et al., 1986). During the spring migration at Barrow in 1984, the corresponding numbers were 37%, 19%, 12%, and 17%, respectively, of 15 876 calls (C.W. Clark, in Würsig et al., 1985).

The percentage of the calls in our data set that were simple ranged from 65% to 82% in various years (Table 3). Ljungblad et al. (1982) recorded bowhead calls in the fall of 1979 and reported that 86% of their sample consisted of calls of the simple type. During the spring migration off Point Barrow in 1984, about 86% of calls were simple (Clark et al., 1986a). These values are somewhat higher than our results, particularly for the years 2002–04 (Table 3).

During the spring migration off Point Barrow, the ratio of simple to complex calls changes over the course of the season, with complex calls becoming proportionately less common later in the season (Würsig and Clark, 1993). Concurrent with the decrease in the proportion of complex calls are decreases in singing and in social activity (Würsig and Clark, 1993). During autumn, in contrast, no seasonal trend in the proportional occurrence of complex calls was evident in our data, whether the four years were analyzed separately or together (Table 4). However, the need to retrieve DASARs before freeze-up required us to end data collection before the end of the migration.

In 2002, in 2004, and in all four years combined, the proportion of calls that were complex was significantly related to the daily total number of calls. This implies that a higher proportion of calls were complex when more whales were calling or when whales were calling more often. Along the same lines, from 2001 to 2004 there was an increase in both the yearly percentage of calls that were complex (from 18% to 36%, Table 3) and the yearly number of whale calls recorded (Table 1). Richardson et al. (1995) recorded 890 calls near socially active groups of bowheads in Baffin Bay. Complex calls made up nearly 89% of their sample. Those authors suspected that this high percentage of complex calls was related to the ongoing social and sometimes sexual behaviour of the whales. Similarly, while monitoring bowhead calls off Barter Island and Barrow in the fall, Ljungblad et al. (1988) noted a higher percentage of complex calls on days of peak calling rate. In addition, "growls" (a type of complex call) were significantly correlated with calling rate. Perhaps our data set indicates that higher densities of whales led to more social behaviour and consequently a higher proportion of complex calls.

Call Sequences

Würsig and Clark (1993, but see also Würsig et al., 1985) report that in the spring and summer, bowhead whales have been heard to produce series of 5–15 similar

FM calls at fairly regular 3–15 second intervals. They considered these sounds to be call sequences and not songs, and state that the calls were typical FM types. Ljungblad et al. (1982) made sonobuoy-based recordings in spring and fall 1979 and describe "sequential sounds" from the spring recordings only. These sequences consisted of an alternating series of three types of moans and contained both FM and AM sounds. However, it is likely that these "sequential sounds" were what Cummings and Holliday (1987) and Würsig and Clark (1993) later called songs. What distinguishes songs from call sequences is chiefly the level of complexity. Songs typically consist of 1–5 notes assembled into phrases, themselves organized into two or three themes (Würsig and Clark, 1993). In contrast, the call sequences we describe included only a single call type that was repeated for the duration of the sequence. Another difference is that song notes are usually long in duration, lasting up to several seconds, whereas the calls in our sequences rarely exceeded 1 s. Finally, songs have been heard only in early spring, but are suspected to occur during winter in the Bering Sea (Würsig and Clark, 1993). In our autumn recordings, call sequences were only found in 2004. This may indicate that they are an optional component of bowhead whale calling behaviour during the fall migration.

Two sequences that we describe lasted longer than 30 min. Even though bowhead songs only last about a minute, song bouts can go on for hours (Würsig and Clark, 1993). Similarly, humpback whales *Megaptera novaeangliae* are known to repeat half hour songs during bouts lasting many hours (Payne and McVay, 1971), and both finback *Balaenoptera physalus* (Watkins et al., 1987) and blue whales (Mellinger and Clark, 2003) produce song bouts lasting from hours to more than a day.

One noteworthy feature of the two long call sequences was the regular presence of "weak periods" in calling, lasting ~20 s and occurring on average every 1.75 min. These weak periods could be seen in the records of all the DASARs that recorded a particular call sequence, so they were not the result of directionality in calling. What is known of singing or intently vocalizing baleen whales seems to indicate that they do not vocalize at the surface, but rather while fully submerged underwater. For example, blue whales vocalize at depths of 10–40 m (Thode et al., 2000), humpback whales sing at depths of 15–25 m (Spitz et al., 2002), and finback whales vocalize at depths of ~50 m (Watkins et al., 1987). If we assume a whale is vocalizing with a constant sound output, pressure-release effects at the surface would predict a decrease in received levels (at a stationary DASAR on the seafloor) if the source of sound moves from a depth at or below ~10 m to the surface. The decrease would be most pronounced for low-frequency components, which is what we observed (Fig. 8). We therefore hypothesize that the weak periods in the call sequences correspond to surfacings, probably to breathe, by the calling whale. This phenomenon has been described in both humpback whales (Tyack, 1981) and finback whales (Watkins et al., 1987). Signals recorded at the DASARs could also decrease in amplitude if the whale decreases the source level of its calls as it comes to the surface to breathe. We have no definitive way to distinguish that effect from the effect of the pressure-release phenomenon. However, the greater reduction at low frequencies is consistent with what would be expected from the pressure-release phenomenon.

We found that weak periods had a median duration of 20 s (range 8–50 s) and were separated by a median of 1.75 min (range 35 s to 3 min 50 s). In bowheads of the eastern Alaskan Beaufort Sea in September-October, mean durations of surfacing sequences were 1.1–1.8 min, depending on whale activity (Thomas et al., 2002). Corresponding figures for durations of sounding dives were 5.5–16 min. Although there was much variation around these means, a 20 s surfacing sequence is unusually short, allowing time for only 1–2 blows rather than the usual 5–9 blows per surfacing. A 1.75 min dive, although shorter than average, is not especially unusual (Thomas et al., 2002). Thus, both the "weak" periods in the call sequences and the intervals between weak periods were short as compared with typical surfacings and dives. Consistent with that pattern, short surfacings by bowheads (with few blows per surfacing) tend to be associated with short dives (Würsig et al., 1984). Thus, the data are consistent with the idea that a weak period in a call sequence represents a surfacing, during which the whale would blow once or twice, followed by a relatively short dive. This type of diving pattern has been seen in socializing whales or during pseudo-sexual activities in late summer and early fall (Richardson et al., 1995; Thomas et al., 2002).

CONCLUSION

This study used an array of directional autonomous seafloor recorders to monitor the autumn migration of bowhead whales. The method has the advantage of being independent of time-of-day constraints and largely independent of weather, and it provides a continuous acoustic record over several weeks. It yielded large amounts of information on diel and seasonal patterns of calling rates and call types. In addition, the DASARs' directional capability allowed us to gather spatial information on the overall location of the migration corridor and its intra- and inter-seasonal fluctuations.

DASARs provided high-resolution, continuous information on the occurrence, distribution, and calling behaviour of bowhead whales in a limited area of their migration corridor. The DASAR method therefore complements aerial surveys carried out over a much larger geographical area, but with low spatial and temporal resolution and small sample size. However, some drawbacks to the method should be mentioned: (1) The whale call analysis was labour-intensive and would benefit from some form of automation. (2) Whales that do not call cannot be detected.

(3) Presumed variations in calling rate complicate interpretation of the data. (4) The lack of independence between calls (pseudoreplication) can be an issue in certain analyses, requiring specialized analysis methods to avoid misinterpretation.

Recordings from DASARs have confirmed that the fall migration of bowhead whales through the Alaskan Beaufort Sea has various similarities to the spring migration, as well as some differences. In both seasons, the migration is pulsed in nature (both in time and space), and the whales' acoustic behaviour is similar in terms of the types of calls used and diel patterns in calling. There are large year-to-year variations in the location of the migration corridor relative to shore in fall. A positive correlation is known to exist between distance from shore and ice cover (Moore, 2000; Treacy, 2002; Treacy et al., 2006), but it is uncertain why that trend occurs. No bowhead songs were recorded in the fall, in contrast to the situation in spring, but call sequences occur in both seasons and were a prominent feature in one autumn out of four. The function of these sequences is not known, but at times when they occur, they provide an opportunity for acoustic tracking of individual whales.

Future work should include additional collection of call recordings, both at the Northstar location and elsewhere. It may be especially informative to compare calling behaviour during different seasonal activities, such as mating, feeding, and migration. It may also be instructive to compare calls during potentially stressful periods; for example, it would be interesting to know if calling behaviour changes when bowheads encounter hunters, or when bowheads encounter anthropogenic sounds such as those generated by pile driving, vessel traffic, and industry seismic operations. (Some data on this last point already exist: Richardson et al., 1986; Greene et al., 1999.) By using the calibrated received sound levels at the DASARs, the calculated distance to each localized calling whale, and an assumed or semi-empirical sound transmission loss model, it would also be possible to estimate the distribution of whale call source levels. Lastly, long-term monitoring of bowhead calls may document changes related to Arctic warming, increasing bowhead population size (and population density), changes in anthropogenic noise related to increased industrial development, and other environmental changes.

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