Factors that influence aerial line transect detection of Bering-Chukchi-Beaufort Seas bowhead whales

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ABSTRACT

This paper presents a rich, complex dataset including 25 years of aerial line transect surveys for bowhead whales in the Bering, Chukchi and Beaufort Seas, for which a distance detection function was estimated. The analysis was limited to the autumn migratory period and to the portions of the Beaufort and Chukchi Seas occupied by bowhead whales during this period. The primary purpose of the work was to improve the understanding of what factors significantly affect detection. Comprehensive model selection efforts based on the AIC identified useful predictors. Results showed that Beaufort Sea state, ocean depth, inter-sighting waiting distance and year were among the factors affecting detections. For example, increased depth and long wait distances between sightings were both associated with narrower effective strip widths. Some of the results can be interpreted as evidence for a relationship between detection probabilities and whale behaviour. The complexity of the overall dataset required substantial data organisation and offered many alternative analysis approaches, but the results were fairly consistent across such choices. Notwithstanding successful estimation of the detection function, the data present substantial challenges to standard abundance estimation using line transect methods.

KEYWORDS: ARCTIC; NORTHERN HEMISPHERE; BOWHEAD WHALE; BERING SEA; CHUKCHI SEA; BEAUFORT SEA; SURVEY-AERIAL; MODELLING

INTRODUCTION

In June 1978, a proposed oil and gas lease sale in the Beaufort Sea prompted the US Bureau of Land Management and subsequently the Minerals Management Service (MMS) to study the possible effects of industrial activity on the marine and coastal environment in this region. In response, from 1979-2007 annual aerial surveys of marine mammals were conducted in the Bering, Chukchi, and Beaufort Seas (B-C-B). These aerial surveys were named the Bowhead Whale Annual Survey Program (BWASP) and were carried out by the MMS, the Naval Ocean Systems Center and affiliated MMS contractors. Particular interest focused on the spatio-temporal distribution of bowhead whales (*Balaena mysticetus*) and the effects - if any - of industrial activity on this distribution. The primary types of industrial activities of concern included the exploration and development of petroleum resources, including seismic exploration. Industry impacts would have important implications for resource conservation and utilisation as well as for industrial regulation. The B-C-B bowhead whale population is utilised by native Inupiat and Yupik communities in northern and western Alaska, who conduct limited aboriginal hunting to satisfy subsistence and cultural needs as permitted by the International Whaling Commission. Bowhead whale avoidance of industrial activity could reduce availability of whales to the hunters and require villagers to venture greater distances at greater personal risk in order to hunt.

During the period of the surveys, the abundance of B-C-B bowhead whales has at least tripled from point estimates of 2,264 (with a 'range of uncertainty' of 1,082) in 1978 (Braham *et al*., 1979) to 10,470 (95% confidence interval 8,100 to 13,500) in 2001 (George *et al*., 2004). Even if bowhead whales avoided sites of industrial activity, counts of whales at such sites might increase over time merely due to increased total abundance. Therefore, indices of relative abundance would better detect spatio-temporal changes in migratory patterns in response to the growth of industrial activity in various locations over time. Although modelling the bowhead migration over time will be a key element of upcoming efforts to gauge potential industry impacts or other migratory changes, the goal here is more modest: to estimate an appropriate detection function for these surveys to better understand the impact of possible covariates on detection.

There are several reasons for this limited focus. The BWASP data have been statistically analysed only rarely and merit greater study. Organising the BWASP data for this analysis was in itself an enormous task and documenting this effort will aid future work while providing a common corrected database for analysis. Second, there are presently opportunities to improve the BWASP protocol. The results presented here can inform this process by identifying changes to survey design and more focused choice of covariates, thereby enabling a more efficient and effective survey. For example, there is discussion of how block randomisation is critical and how longitude and whale behaviour are vastly more important than sky and ice conditions in fall surveys. Finally, the detection function estimation presented here could serve as a component of a more sophisticated ongoing effort to build a spatio-temporal characterisation of the bowhead migration using methods similar to those of Hedley and Buckland (2004) and Hedley *et al*. (2004). Such modelling is beyond the scope of this study but it requires the careful estimation of a detection function and its dependence on covariates described here.

The multiple covariate distance sampling analysis used in this paper has proved useful in other situations where important covariates (Marques and Buckland, 2003; Marques *et al*., 2006) must be accounted for. In such cases, resorting to the pooling robustness notion of Buckland *et al*. (2001) - which would generally argue against fitting covariate effects in detection functions - can be a less useful approach. Reliance on pooling robustness is more relevant when estimating (relative) abundance, in which case integration over extra variation due to possible covariates is sensible.

Several authors have previously analysed subsets of the BWASP data. For example, Manly *et al*. (2007) analysed the 1996-98 BWASP data to explore how human activities

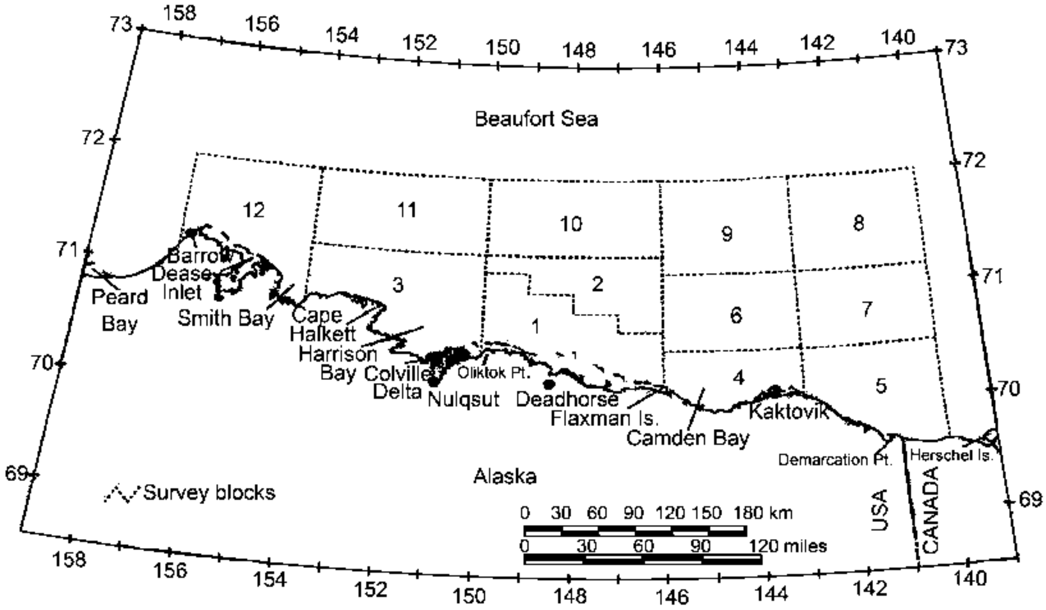

Fig. 1. Map of BWASP survey blocks [Monnett and Treacy, (2005), used with permission].

affected bowhead distribution. In their preliminary study based on these three years of data, the authors binned the transects into 5km long sampling units and used Poisson regression models to infer that there is evidence that seismic activity is associated with reduced numbers of observed bowhead whales. They also investigated whether whale swimming direction was impacted by marine seismic activity and found some evidence that it was. Schick and Urban (2000) found that bowhead whale distribution patterns were correlated with distance to oil drilling rigs. Treacy *et al.* (2006) investigated the effect of annual variation in ice distribution on bowhead migration patterns in the BWASP data, finding significant evidence that bowhead whales tend to migrate further offshore during heavy ice years compared to years with moderate or light ice.

Detailed description of BWASP survey methods is given by Treacy (2002) and Monnett and Treacy (2005). The analysis presented here was limited to 1982-2006, as equipment and protocol differences before then clearly render the earlier data incomparable. Survey methods were comparable from year to year thereafter. The 2000 survey described below illustrates key details of the protocol.

Survey methods

The surveys were conducted mainly in autumn between 140°W and 157°W and south of 72°N. Fig. 1 shows that the survey area was subdivided into 12 blocks. All survey flights began from Deadhorse, Alaska. There is no specification of a maximum sea state beyond which flights were cancelled; flights were conducted 'weather permitting'. For a given survey block, a random transect grid was determined by dividing the block into 30-minute of longitude sections. Minute marks along both the northern and southern edges of each partition were randomly chosen and connected with straight lines to create transect legs. This procedure was repeated for all 30-minute sections within the survey block. Northern and southern transect ends were connected alternately to form a flight path, and the start and end points were connected to Deadhorse. Fig. 2 shows a typical flight pattern.

During the 1982-2006 period, each year included between 23 and 93 flights. During each survey season, the pattern of block coverage was chosen opportunistically based on

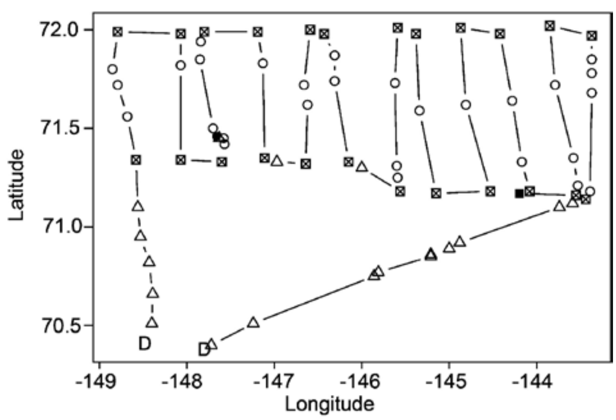

Fig. 2. Example flight path. Deadheads are 'D'. Points on search, connect, and transect are triangles, squares and circles, respectively. In these cases, hollow shapes are records with no sightings and solid shapes had sightings. Squares with 'X' in them are transition points to/from on-connect segments.

prevailing weather, a desire to investigate regions of potential industrial impact and sometimes on suspected regions of greater whale abundance. East of 154°W, two-week spatio-temporal coverage was disproportionately targeted towards areas of suspected higher relative abundance as inferred from past surveys (1979-86). Consequently, survey coverage yielded proportionally greater effort in near-shore regions and therefore increased total sightings by focusing on the primary migration corridor.

The partially opportunistic survey scheme violates one of the key assumptions of distance sampling analysis: that the transect lines should be randomly placed with respect to the distribution of animals (Buckland *et al*., 2001). It is important to emphasise, however, that concern about non-random block selection is mitigated here because no estimate of relative abundance will be produced; the interpretation of covariates that are associated with whale sightings here is in the context of the sampling design.

Surveys used a *de Havilland Twin Otter Series* 300 aircraft equipped with two medium-size bubble windows behind the cabin bulkhead and one on the aft starboard side.

These enabled complete trackline viewing and the pilot and co-pilot seats provided good viewing forward and to the sides. Sighting distances were measured orthogonal from the transect line abeam of the plane, and computed from altitude and hand-held clinometer readings. The nominal flight altitude was 458m (1,500ft). Observers and pilots communicated using a common communication system. Data were recorded on a laptop computer connected to a *Garmin III* Global Positioning System with external antenna, using a customised data-entry system.

Observers on the port side included the primary observer, positioned at a bubble window affording a view from the trackline below the aircraft to the horizon, the pilot, and an occasional secondary observer or visitor at an aft flat window. On the starboard side at a bubble window sat a data recorder-observer who partially focused on guarding the trackline, and a team leader at an aft bubble window. The co-pilot was also starboard.

Focus was limited to the area shown in Fig. 1 and to the period from August 28 to October 23, which encompasses the vast majority of the autumn bowhead migration in the survey area while excluding most summer residents (to the extent they may exist). Occasionally, a portion of a flight extended beyond the boundaries of the survey region. Therefore, a flight was deemed to be within the study area if no more than 10% of the positions recorded during that flight were outside the area. Only a few flights were eliminated on this basis.

For analysis, each single flight was broken into discrete portions, or segments, defined as a period of flight between two recorded events such as a sighting or incidental record of plane location taken during a lull. Each data record corresponds to the start or end of one segment. There are many more data records than sightings because additional data were recorded between sightings, as described below.

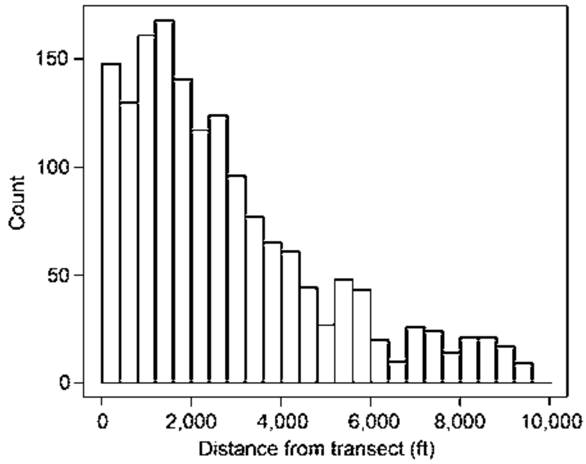

Fig. 3. Histogram of on-transect sighting distances (ft).

Flight segments to and from Deadhorse were denoted 'on-search', except that all flight portions over land were denoted as 'deadhead'. Segments on transect legs were denoted 'on-transect', with segments on connective legs between transects denoted 'on-connect'. Sightings during such legs were labelled as 'sighting-on-transect' and 'sighting-on-connect' (referred to below as 'sot' and 'soc'). Transect legs began and ended with 'start-transect' and 'end-transect' (referred to below as 'st' and 'et'). Occasionally, a possible cue or tentative sighting of some animal was detected. To investigate, a 'divert-transect' event was recorded, and the flight continued 'on-search' until the plane began 'resume-transect'. During on-search effort, the goal was to confirm or refute that the possible sighting was a bowhead whale. These on-search periods were generally characterised by a

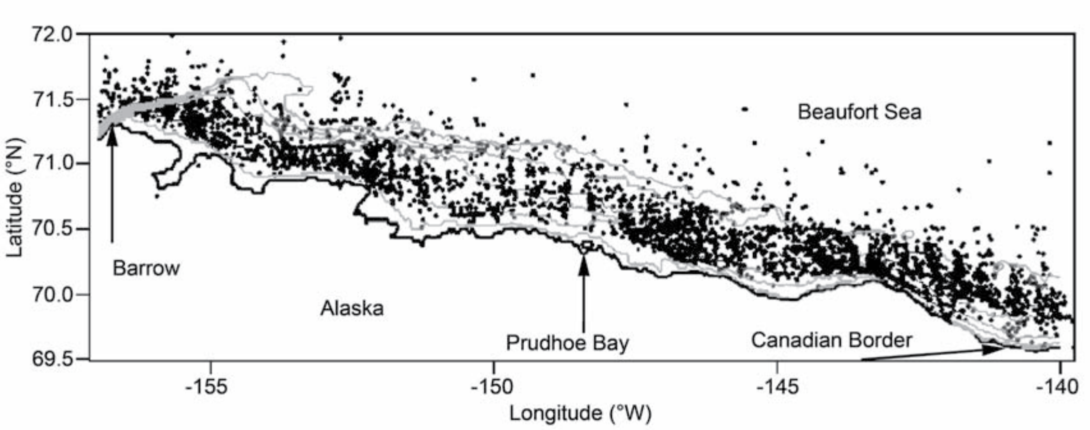

Fig. 4. All bowhead sightings. Contours of depth from 5m to 65m in increments of 10m are shown with light grey lines.

Table 1

Key covariates in the BWASP dataset. Counts of missing values are among only bowhead whale sightings not excluded for other reasons described in the text.

Observed variable	Levels	Number missing for bowhead whale sightings
Beaufort Sea State	B0,...,B8	15
Visibility on side of plane corresponding to sighting (km)	0, <1, 1-2, 2-3, 3-5, 5-10, unlimited	1
Sky condition	clear, overcast, partly cloudy	500
Percent ice (ICE)	0-100	0
Year since 1982 (YEAR)	0-24	0
Day (DAY)	Aug. 28-Oct. 23	0

limited period of circling. If at any time during the on-search period additional whales were sighted, they were recorded as 'sightings-on-search'. Perpendicular distances to on-search sightings were measured in the same manner as on-transect sightings, to the extent possible. Aside from sightings, records of location were recorded at 'point-on-transect', 'point-on-connect', and 'point-on-search' at convenient times between sightings (referred to below as 'pot', 'poc' and 'pos', respectively). Sightings of species were treated aside from bowhead whales as points on segments rather than sightings on segments. Rare circumstances required 'abort-flight' events. A histogram of on-transect sighting distances is shown in Fig. 3. Fig. 4 shows all bowhead whale sightings in the dataset.

MATERIALS AND METHODS

The raw dataset contained 1,187 flights consisting of 84,543 records including 4,469 bowhead sightings and over 750,000km of total flight distance. The number of bowhead whales per sighting (cluster size) was initially ignored in the analysis because the distribution of cluster sizes was extremely skewed. Although whale behaviour likely has important implications for detection, it was not explicitly included in estimation of detection probabilities because the key behaviour, feeding, was only observed in 2.8% of cases. For each sighting (and frequently for other types of records during the flight), a variety of covariates were recorded. Key covariates are listed in Table 1. It is important to note that the 'visibility' variable describes the atmosphere, not some informal combination of atmosphere, sea conditions and other factors. Ice coverage and visibility were judged subjectively. English units are used on occasion for covariates for consistency with the original data records.

A variety of data coding errors and omissions were detected during the analysis. Out of the 84,543 records, there were 4,816 corrections to sea states, 37,757 corrections to visibilities, 3 corrections to ice coverage, and 1 event type correction, mostly due to inconsistent data coding. Twelve missing visibility entries were imputed when visibilities were discernable from long sequences of identical entries in temporal windows surrounding the missing entry. Finally, 78 event types were altered to the most sensible alternative because the original entry was not sensible. For example, a sighting-on-transect (sot) entry would be changed to sighting-on-connect (soc) if it occurred in the sequence st-pot-pot-pot-et-poc-poc-**sot**-poc-poc-poc-st-pot-pot-et.

Of the available flights in this corrected dataset, 786 flights were retained for being within the time and space limitations described above. The data for these flights comprised 50,463 records after deleting 1,712 records with failed or missing clinometer readings and 91 repeat sightings. Among these data, there were 2,786 bowhead whale sightings comprising 1,695 observations on-transect, 1,000 on-search and 91 on-connect.

From these raw data, a variety of additional covariates were constructed (Table 2). Sea-state and visibility were categorised. The categorisation of Beaufort Sea state was intended to bin sea-states into glassy, intermediate, and choppy conditions and is hereafter labelled BSS. Visibility categories (VIS) were constructed to provide sufficient bin counts and to maximise between-bin differences in detection probabilities. Later, for the purposes of averaging, the 'unlimited' category was treated as 20km. Available GIS data (NOAA, 2008) were used to determine the water depth (DEPTH) at each sighting. Preliminary comparisons of the effects of water depth and offshore distance indicated that depth was a more effective covariate. These two variables are very highly correlated due to the bathymetry of the region, where depth contours closely match the shoreline except along the west edge of the survey region in the Barrow Canyon. In addition to providing slightly better predictive power, depth may also be the more ecologically sensible covariate (see Discussion).

To investigate spatial patterns, an idealised shoreline was created, which is a straight line from Point Barrow to the point on the coast at the Canadian border. Given this definition, the distance along this idealised shoreline (DAS) was calculated for each sighting. Due to the shape of the northern Alaska coastline (Fig. 1), DAS correlates strongly with longitude. This variable was standardised so that the distance from Barrow to Canada was approximately three standard deviations, with smaller values indicating greater proximity to Barrow.

Many of the additional covariates pertain to sums or averages accumulated along the flight path, not only at sightings but also for most other segments along the flight path. The 'waiting distance' (WAIT) was defined to be the total distance along the flight path from the previous sighting (or from the start of the survey) until the present sighting. Covariates were averaged over this wait, reflecting the possibility that conditions associated with a sighting may be better summarised by typical conditions while awaiting the detection rather than specifically at the moment of detection. One justification for this approach is that it reduces variability when measurement of conditions includes a notable white noise component. The approach is also useful when covariate observations at the moment of detection are missing.

Covariate averages were computed as follows (e.g. Fig. 5). Each waiting distance comprises a collection of one or more shorter segments determined by records of point-on-transect, etc., as described above. A covariate average over a waiting distance was defined to be the segment length-weighted average of the covariate values over all non-

Table 2

Additional covariates created for analysis, including those averaged or summed over waiting distances.

Computed variables	Method of calculation
Categorical sea state (BSS)	Low (B0-B1), Medium (B2-B3), and High (B4 and above)
Categorical visibility (VIS)	Low (≤5), High (>5)
Raw Beaufort Sea state average	Average of values from 0 to 8
Categorical BSS average	Average of values of 1, 2 or 3
Raw visibility average	Average of midpoints of original visibility intervals
Categorical visibility average	Average of VIS
Raw ice coverage average	Average of values from 0% to 100%
Waiting distance until sighting, std. units (WAIT)	Accumulated as described in text
Location of sighting along idealized shoreline, std. units (DAS)	See text

missing data along the segment. Specifically, for a given flight, let n denote the number of segments within a flight, determined by records at points $p_0,...,p_n$. Denote the between-point segment lengths $l_1,...,l_n$. Let the covariate x_i be measured at some or all of the points. Then let the indicator z_i equal 1 if x_i is observed and 0 if it is missing, so that x_i contributes to the average only when z_i=1. Finally, let integers $s_j \in \{1,...,n\}$ index sightings and locations so that $s_j=k$ if the jth sighting occurs at p_k. The weighted average covariate value corresponding to the jth sighting is given by

$$\overline{x}_{s_j} = \frac{z_{s_{j-1}} x_{s_{j-1}} l_{s_{j-1}+1} + \left\{\sum_{i=s_{j-1}+1}^{s_j} z_i x_i \left(l_i + l_{i+1}\right)\right\}}{z_{s_{j-1}} l_{s_{j-1}+1} + \sum_{i=s_{j-1}+1}^{s_j} z_i \left(l_i + l_{i+1}\right)}$$

for j=1,...,b, where s_0=0, the number of bowhead sightings on the flight is $b \geq 1$, and l_{s_j+1} must exist since no flight ends with a sighting. Furthermore, the above discussion over-simplifies the definition of the z_i: there are reasons aside from missing data when x_i should not contribute to the waiting period. For example, any single segment from deadhead to abort-flight should not count in the average.

When the covariate x is categorical with levels 1,...,M, analogous expressions can be defined for the weighted average level (averaging level values) and for the weighted average proportion of the waiting period spent in level m (averaging binary indicators of state). The former approach is not sensible unless the levels are at least ordered.

The analysis was based on only the on-transect sightings. The *DISTANCE* program (Thomas *et al*., 2006) was used to fit parametric models for detection functions with covariates. For example, a detection function based on an underlying hazard function model (see below) can take the form

$$g(y) = 1 - \exp\{-(y/s)^{-\alpha}\}$$

where

$$s = \beta_0 \exp\left\{\sum_{i=1}^{c} \beta_i X_i\right\}$$

and the X_i denote covariates 1,...,c. The parameters of this model are α and β_i for i=0,...c.

Initial model selection was conducted by incorporating each covariate listed in Tables 1 and 2 in a separate model for estimation of the detection function, using *DISTANCE 5.0* (Thomas *et al*., 2006). Half-normal (with possible Hermite expansions) and hazard function (with possible polynomial expansions) models were investigated. On the basis of Akaike's information criterion (AIC) and log likelihood comparisons between models using the alternative versions of the same covariate, a preferred version or binning of each covariate was selected. These covariates have been assigned capitalised labels in Tables 1 and 2, namely BSS, VIS, ICE, WAIT, DAS, DEPTH, DAY, and YEAR. Sky condition was never found to provide any useful information and is hereafter ignored. The distribution of depths at sighting locations was extremely skewed, with a heavy tail to the right. Concern about the influence of this skew led to consideration of using log(depth). After experimentation, it was determined that a more reliable approach was to eliminate the 2.6% of sightings at depths exceeding 200 feet (61m).

With these data and covariates, model choice was made using a forward selection strategy with AIC (Burnham and Anderson, 1998) as the comparison metric, stopping when no additional variable reduced AIC by at least 2.0 units. This model selection exercise was conducted independently for two choices of data truncation. For the first choice, observations with distances exceeding 5,280 feet (1,609m) were excluded, roughly corresponding to the distance at which a preliminary estimated detection function equalled 0.15. For the second choice, observations with distances exceeding 9,500 feet (2,896m) were excluded, closely corresponding to 95th percentile of distances. Both strategies are among those offered by Buckland *et al*. (2001).

Table 3

Results from stepwise AIC model selection. For truncation at 9,500 feet, there was an inconsequential tie.

Model	ΔAIC
Truncation at 5,280 feet	
BSS +WAIT+YEAR+DEPTH	0.0
BSS+WAIT+YEAR	2.2
BSS+WAIT	5.6
BSS	9.5
NULL	15.2
Truncation at 9,500 feet	
WAIT+DEPTH+DAS+YEAR	0.0
WAIT+DEPTH+DAS	2.5
WAIT+DEPTH	7.6
WAIT+DAS	7.6
WAIT	11.6
NULL	20.8

RESULTS AND DISCUSSION

Model choice

Initial model fitting showed that the normal model was always worse than the hazard model. Therefore model selection was limited to the hazard model for the detection function. Although polynomial covariate terms were not considered in the model, polynomial expansions to the hazard model were investigated. These usually did not improve AIC, therefore model selection was also limited to models with no series expansion terms.

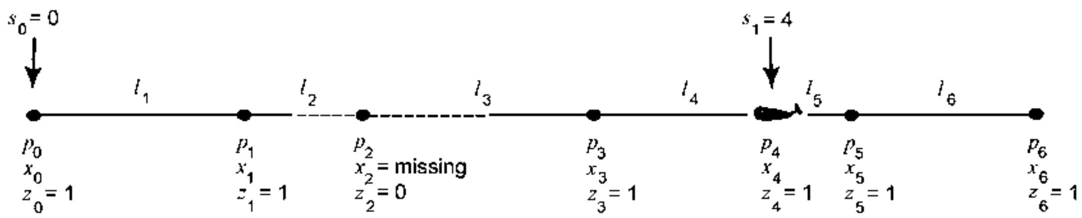

Fig. 5. Illustration of segment-weighted averaging for the first sighting on a transect. At point p_4 a bowhead was sighted. The covariate values x_1, x_3 and x_4 contribute (in proportion to their respective surrounding segment lengths) to the average covariate value during the wait until the sighting (at the fourth point here). The value at x_2 cannot contribute because it is missing.

Table 3 shows the model selection results for the datasets with distance truncations at 5,280 and 9,500 feet, respectively, using the simple hazard model. Aside from the null model, models constituting steps in a logical progression of nested models leading to the best model and having improvements of at least 2.0 AIC units are shown.

Having identified good models, the question of cluster size effects was revisited. To compensate for the extremely skewed distribution of this covariate, cluster size was separated into three categories: 1 whale; 2 whales; and at least 3 whales. The addition of this variable raised AIC, indicating an inferior model fit adjusted for the increased number of parameters. Thus, contrary to expectations, cluster size did not affect the detection function. This may reflect the fact that most sightings occurred in good sea states and good visibility conditions with little sea ice. However, since the distribution of cluster sizes is highly positively skewed, there may be too few data to obtain a reliable estimate of cluster size effects, particularly since the comparative impact of large cluster sizes is likely most severe at extreme distances but sighting distances were truncated at 5,280 feet for analysis.

The on-connect and on-search data were not used in the main on-transect analyses. The protocol employed during on-connect survey effort was similar to that for on-transect except that some observers may rest. There are 66 additional on-connect sightings with no relevant missing covariates. Fitting a model identical to the best one shown in Table 3 but including the on-connect data yielded a similar estimate of the detection function found in our chosen model, and the average effective strip width was decreased by less than one percent. Notwithstanding this result, future survey protocol could be improved by clearly articulating the goal for on-connect effort. Ideally, on-connect effort should be identical to on-transect effort and the protocol should reflect this goal.

The protocol for on-search survey effort was qualitatively different than for either other survey mode. However, a histogram of on-search distances is virtually indistinguishable from on-transect distances. The same model identification and fitting strategy as above was experimented with, applying it only to the on-search data truncated at 5,280 feet. In this case, only DAS influenced detection. Recall that on-search effort is triggered by the sighting or suspected sighting of a whale. Therefore, variables that assess sighting conditions (such as BSS, ICE, VIS) and variables that reflect relative density (such as WAIT and YEAR) should no longer matter. The importance of DAS for on-search data probably relates again to whale behaviour: feeding and clustering in the eastern Beaufort as opposed to swimming further westward. Of course, the on-search analysis cannot be considered reliable due to its survey protocol.

Model results and diagnostics

Table 4 provides the parameter estimates for the two models discussed above. Hereafter the model using distance truncation at 5,280 feet is focused on. This model should be less sensitive to the right tail of the distance distribution, thereby likely providing a better fit to the bulk of the data.

The average effective strip half-widths (ESW) were 3,635 feet (1,108m) and 4,246 feet (1,300m) for the small and large truncation distances, respectively, with CVs of less than two percent.

Buckland *et al.* (2004) describe several goodness-of-fit model diagnostics. A quantile-quantile plot showed good correspondence between observed and fitted cdfs, except that the observed data include some zero distances, as would be due to heaping or rounding. The model need not be adjusted in this case (Buckland *et al*., 2004). The cosine-weighted Cramer-von Mises test provided no evidence of a poor fit (p>0.15). Informal examination of graphs of the model fit also identified no severe problems.

Interpretation and discussion

For BSS, we found that glassy sea state (B0-B1) reduced the effective strip width compared to when sea state is merely good (B2-B3). This is counterintuitive because one would expect greater ease of detecting distant whales when conditions are excellent. However, for white whales (*Delphinapterus leucas*) DeMaster *et al.* (2000) found no convincing relationship between BSS and ESW. It is suspected that the finding presented here may partially reflect observer behaviour. Despite the intended survey protocol, observers may have favoured nearby effort during excellent conditions because sightings were comparatively easy. Nevertheless, other past studies of bowhead whales (Cosens *et al*., 1997) and other cetaceans (e.g. Kingsley and Reeves, 1998) have found that sightings per unit effort were reduced in poorer sea states.

An alternative explanation for the BSS finding is that the binning of sea state categories may not have been the best choice. To investigate this, a different binning of BSS was considered, namely low (B0,B1,B2) and high (BSS≥3). Such a binning separates unbroken surfaces from surfaces with some breaking crests. The model was re-fitted using this binary BSS pooling and found virtually no effect for BSS. Although this represents a weakening of the primary BSS finding, it still fails to indicate a reduction in ESW as sea states deteriorate. Perhaps one could infer that when sea states are poor, sightings are so difficult that it doesn't much matter how nearby you look.

It is also difficult to disentangle a BSS effect from potential effects of location and behaviour. There is a strong relationship between BSS and sighting location. The median sighting location during excellent sea states (B0-B1) is 69% further eastward than during good (B2-B3) states. In addition, whales sighted in the eastern Beaufort tend to be feeding (particularly before the peak migration), whereas whales in the western Beaufort and eastern Chukchi are migrating (see Fig. 6). The median cluster sizes for diving, swimming, and feeding whales are 1, 1, and 5, respectively.

DEPTH is another influential term in the models. The ESW narrows with increasing depth. Whales sighted at locations having large sea depths generally are swimming quickly as they migrate westward at high latitudes with little clustering. Feeding whales tend to be in shallow water (see

Table 4

Parameter estimates (standard errors) for selected models.

Truncation	DEPTH	WAIT	YEAR	BSS (low)	BSS (high)	DAS	β_0	α
5,280	-0.0023	-0.090	-0.015	-0.22	0.47	NA	4,358	2.52
	(0.0012)	(0.043)	(0.006)	(0.09)	(0.92)		(63)	(0.91)
9,500	-0.0030	-0.118	-0.011	NA	NA	0.073	3,999	2.13
	(0.0012)	(0.043)	(0.006)			(0.067)	(53)	(0.75)

Fig. 6). If distant whales are more difficult to detect unless they spend relatively more time near the surface and/or if lone whales are more difficult to detect at large distances than are clusters, then the observed inverse correlation between ESW and depth would be expected.

Next the effect of WAIT was considered. Fitting an adjustment term for WAIT is the continuous analogue to stratifying the analysis by encounter rate as described by Buckland *et al.* (2001). It was found that long waits between sightings are associated with reduced ESW. One explanation for this may be that long waits are associated with poor sighting conditions, during which periods of effort might tend to be focused closer to the plane. More importantly, long waits clearly serve as a proxy for all sorts of unmeasured variables that effect sighting probability. Although the BWASP dataset contains data on several such variables, many other factors (known and unknown) probably impact detection probabilities as well. WAIT is effectively an indirect measure of such effects. It should be emphasised that WAIT is not a factor that can be controlled by the surveyors. However, one implication of the finding is that it may be useful to stratify data by encounter rate when analysing bowhead whale aerial survey data.

The results in Table 2 for the model with truncation at 9,500 feet show that the only covariate substitution in the alternative models is the exchange of BSS for DAS. As discussed above, there is a strong positive correlation between increasing DAS and improved sea states. These two variables act as partial surrogates for each other. Furthermore, the presence of DAS in the model explains why calendar day is not selected in the modelling. Recall the spatio-temporal nature of the migration. Early in the autumn season, when weather tends to be better, the whales are mostly in the eastern portion of the survey region and sightings predominate there. Later in the autumn as the weather degrades, the whales (and sightings) are mostly in the west. Although these correlations involve DAY too, we believe that the position along shore is a superior indicator of the location of whales during the migration because the day-to-day timing of the migration exhibits substantial inter-annual variability.

Increasing YEAR decreases the ESW. George *et al.* (2004) have estimated that the bowhead whale population abundance has increased dramatically over the BWASP survey period. Thus the results presented here confirm again that encounter rate affects the detection function.

Due to serious concerns about the survey design and features of the data, a reliable estimate of total abundance cannot be obtained from the BWASP data. Nevertheless, a crude reality check based on these results is not alarming. For the year 2000 on-transect data only, there were 46 sightings over a survey region of 1.185e+12 ft^2. Effort was strongly imbalanced in 2000, so the analysis was stratified into two regions: one with sparse effort and one with heavy effort. Across both regions the total transect length was about 3.485e+7ft and the average effective strip width was taken to be the estimate for the model with distance truncation at 5,280 feet. These results yielded uncorrected abundance estimates of 63 and 141 whales for the sparse and dense regions, respectively. Krutzikowsky and Mate (2000) provide estimates of correction factors for availability due to bowhead whale diving behaviour. They estimate that bowhead whales are sufficiently near the surface to be available for visual detection from the airplane 11.1% of the time. Heide-Jørgensen *et al.* (2007) offer a perception bias correction factor of 0.48. The mean cluster size in the data presented here is 2.04. Adjusting for all these correction

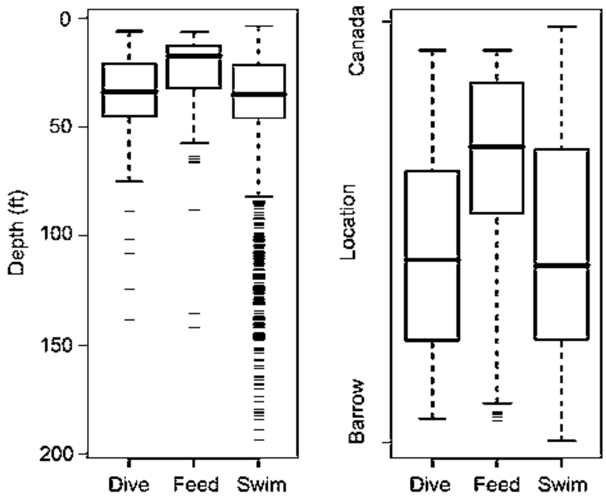

Fig. 6. Boxplots of depth and location of sightings split by whale behaviour.

factors yields a crude estimate of total abundance of 7,836 whales. One notable source of downward bias in this estimate is that it ignores 38 additional whales seen on-connect and on-search with comparatively little extra survey effort. For 2001, a reliable abundance estimate is 10,470 with 95% confidence interval (8,100-13,500); see George *et al.* (2004).

Although the BWASP data constitute one of the longest and richest time series of data regarding bowhead whales, they also present serious challenges for analysis and interpretation. Most notably, the block coverage was not wholly random with respect to the distribution of animals, although transects within blocks were random. Non-random block selection can bias estimates of relative density. However bias in estimation of the detection function should be reduced if detection probabilities are independent of location and adequate covariate sampling is maintained. The transect locations also changed every season. Although this might be important for a monitoring programme, it is not necessary for estimation of absolute or relative abundance, nor for the detection function estimation we present here.

The spatio-temporal variation in whale presence, survey coverage, and whale behaviour (and hence availability) presents another challenge for analysis. Adjustment for short-term and long-term changes in encounter rates merits consideration. Stratification by encounter rate can be implemented in the survey design, or in *post hoc* analysis. In general, stratification can be carried out on the basis of encounter rates and/or covariates shown to influence the detection function. For the model fit to data truncated at 5,280 feet, the only covariate available for stratification during the survey would be depth. Such stratification could be particularly effective because whale presence is extremely strongly (negatively) correlated with depth.

Over the 25 year period of surveys, many aspects of the survey effort and region must have changed: migration patterns may have systematically evolved over time; weather conditions may have changed, and ice coverage has clearly decreased over the period despite substantial interannual variation; observers have changed, along with equipment. Such variations raise the question of whether a single detection function can reasonably be fitted to data collected over such a long period.

Despite the above difficulties, several other important distance sampling assumptions listed by Buckland *et al.* (2001) appear quite reasonable for this dataset. Compared to the scale of transect strip widths, animals are detected at their initial locations for all practical purposes. There is probably little response to the aircraft: for example Patenaude *et al*. (2002) estimated that only 2.2% of bowhead whales reacted to overflights of a *Twin Otter* aircraft and that the vast majority of these occurred at flight altitudes not exceeding 182m. In the BWASP data, the target flight altitude was 458m and only 2% of on-transect sightings occurred at less than 182m. Clinometer readings should be reliable, except that there was heaping on 5° increments (variation in altitudes meant that no heaping was seen for distances). There are some distance outliers when clinometer readings were very small, but these were eliminated during the data truncation phase. Finally, a shoulder in the histogram of sighting distances is clearly seen near zero (Fig. 2), providing a better basis for estimation of the detection function.

Considering the results overall, it appears that the detection function depends notably on whale behaviour. When information on behaviour is sparse or lacking, it appears that variables related to space and time can be used as surrogates, as long as information about spatio-temporal patterns of behaviour is available. Annual surveys like BWASP are likely to continue in the near future, providing even greater opportunity to improve understanding of bowhead whale detection, distribution, behaviour and migration in the region.

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