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Spatial modelling of narwhal density in fiords during the 2013 High Arctic Cetacean Survey (HACS)

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Narwhal stocks in Baffin Bay, Jones Sound and Smith Sound were surveyed in the 2013 High Arctic Cetacean Survey (HACS). Previous studies have shown that narwhals spend time inside narrow inlets and fiords on their summer distribution range. Thus, any surveying effort must include these areas to provide a credible abundance estimate. Estimating abundance in fiords, however, creates logistical and statistical difficulties because of their narrow complex shapes and high cliffs, preventing the use of conventional distance sampling based on systematic transects. To address these issues, we used a two-stage cluster sampling design in which fiords designated as primary sampling units were selected in a way that maintained equal probability and systematic coverage. Within each fiord, we estimated density and abundance of narwhals using spatial density modeling. Density surface models do not require track lines to be designed according to a formal survey sampling scheme, and accommodates both non-random and unequal coverage. Moreover, the resulting variance of the abundance estimate incorporates both the variance from the detection function and that of the spatial model. Because no observations were made in West Ellesmere fiords, no abundance estimate was produced. Sightings of narwhals in the other fiords during HACS were highly variable. After expanding the abundance estimates to unsurveyed fiords, total (surface) abundance estimates were 45 for Jones Sound fiords (CV 94%), 1,916 (CV 45%) for Smith Sound fiords, 143 (CV 85%) for Admiralty Inlet fiords, 1,135 (CV 19%) for Eclipse Sound fiords, and 3,799 (CV 35%) for east Baffin Island fiords. Abundance estimates for the fiord strata will be added to other strata estimated via conventional distance sampling.

Modélisation spatiale de la densité des narvals dans les fjords pendant l'inventaire des cétacés dans l'Extrême-Arctique (ICE-A) de 2013

RÉSUMÉ

L'inventaire des cétacés de l'Extrême-Arctique (ICE-A) de 2013 portait sur les stocks de narvals de la baie de Baffin, du détroit de Jones et du détroit de Smith. Des études antérieures ont montré que l'aire de répartition estivale des narvals comprend d'étroits bras de mer et des fjords. Ainsi, tout effort déployé pour des relevés doit comprendre ces zones afin de fournir une estimation crédible de l'abondance. Toutefois, l'estimation de l'abondance dans les fjords présente des difficultés logistiques et statistiques en raison de leur forme étroite et complexe et de leurs hautes falaises, ce qui empêche l'utilisation de la méthode d'échantillonnage classique fondée sur des relevés systématiques le long des transects. Pour surmonter ces difficultés, nous avons utilisé un plan d'échantillonnage en deux étapes dans lequel les fjords, désignés comme principales unités d'échantillonnage, ont été choisis afin d'obtenir des probabilités égales et une couverture systématique de chaque point. Dans chaque fjord, nous avons estimé la densité et l'abondance des narvals grâce à la modélisation spatiale de la densité. Les modèles de surface de densité n'ont pas besoin que le tracé des avions soit conçu selon un plan d'échantillonnage formel et conviennent à une couverture spatiale non aléatoire et inégale. De plus, le calcul de la variance de l'estimation d'abondance tient compte à la fois de la variance de la fonction de détection et de celle du modèle spatial. Étant donné qu'aucune observation n'a eu lieu dans les fjords de l'ouest de l'île d'Ellesmere, aucune estimation de l'abondance n'a été produite pour cette strate. Les observations de narvals dans d'autres fjords pendant l'ICE-A étaient très variables. Après avoir extrapolé les estimations de l'abondance aux fjords n'ayant pas fait l'objet d'un relevé, les estimations de l'abondance totale (en surface) étaient de 45 (coefficient de variation [CV] 94 %) pour les fjords du détroit de Jones, de 1 916 (CV 45 %) pour les fjords du détroit de Smith, de 143 (CV 85 %) pour les fjords de l'inlet de l'Amirauté, de 1 135 (CV 19 %) pour les fjords du détroit d'Eclipse et de 3 799 (CV 35 %) pour les fjords de l'est de l'île de Baffin. Les estimations de l'abondance pour les strates des fjords seront ajoutées à celles estimées dans les autres strates au moyen de l'échantillonnage avec mesure des distances classique.

INTRODUCTION

Narwhal stocks in Baffin Bay, Jones Sound and Smith Sound were surveyed in the 2013 High Arctic Cetacean Survey (HACS) to estimate their abundance. Previous surveys (Asselin and Richard 2011; Richard et al. 2010), land-based observations (Marcoux et al. 2009) and telemetry studies (Dietz et al. 2001), as well as a DFO reconnaissance survey flown along the coast of Ellesmere Island in 2012, showed that narwhals spend a lot of time inside narrow inlets and fiords on their summer distribution range. Thus, any surveying effort must include these areas to provide a credible abundance estimate. Moreover, fiords are often where Inuit hunters observe and harvest narwhals, and therefore a better understanding of the occurrence and space use of narwhals within these areas is particularly relevant to management efforts.

There are, however, several challenges to estimating abundance of narwhals in fiords. First, fiords along the coasts of Ellesmere and Baffin islands are numerous and spread out over a vast area, making it logistically difficult to survey them all. A proper sampling scheme is therefore needed to select among fiords and yield estimates that are representative of the whole stratum.

Secondly, while some of these bodies of water are large enough to be surveyed using conventional systematic line-transect designs (e.g., Admiralty Inlet, Navy Board Inlet, which we do not consider “fiords” in the context of this document), most have narrow, complex shapes, with high-elevation relief on their sides, preventing the use of systematic parallel lines or zig-zags. This usually forces aircrafts to follow the shore line or to fly down the middle of the narrowest fiords, thus violating several assumptions of traditional distance sampling methods: non-random starting point of transects, unequal coverage probability, and the detection function is truncated by the shore line in places.

Estimating uncertainty around the abundance estimate is also problematic. Variance in line transect density estimates results from three components: variance in the detection function, variance in group size, and variance in encounter rates among transects. Flights in fiords essentially consist of one long continuous transect, which makes it impossible to calculate among-transect variance in traditional ways.

For these reasons, fiords and narrow inlets were treated separately in HACS, both in terms of design and analyses. At the design stage, allocation of survey effort among fiords was based on a cluster sampling scheme, in which each fiord represented a primary sampling unit, and a custom algorithm was used to select the units to survey where each fiord unit had a probability of being selected proportional to its area in an attempt to maintain equal coverage probability within fiord strata (Thomas et al. 2007). Abundance of narwhals in fiords was estimated using density surface modelling (DSM, Hedley and Buckland 2004).

Unlike design-based methods (e.g., Conventional Distance Sampling, CDS) that provide estimates of abundance for predetermined survey blocks with equal coverage probability, DSM is a model-based approach in which animal density is modelled as a function of geographical, physical and environmental covariates. Such spatial line transect models do not require track lines to be designed according to a formal survey sampling scheme and accommodate both non-random and unequal coverage (Hedley and Buckland 2004). Moreover, the resulting variance of the abundance estimate incorporates both the variance from the detection function and that of the spatial model (Miller et al. 2013a). Finally, they may provide additional insights into species-environment relationships (Williams et al. 2006).

METHODS

SURVEY DESIGN

Allocation of effort among fiords

Fiords were sampled separately from the main water bodies in six areas, each considered a distinct stratum: West Ellesmere (WEF), Jones Sound (JSF), Smith Sound (SSF), Admiralty Inlet (AIF), Eclipse Sound (ESF) and East Baffin Island (EBF). Ideally, every fiord in a given stratum would be surveyed. This was possible in AIF and ESF. However, in the other strata, the number of fiords and distances between them made it impossible to survey all of them. Therefore, following Thomas et al. (2007), we used a two-stage sampling design. At stage 1, each fiord was considered a primary sampling unit (PSU) and a custom algorithm was used to select a subset of PSUs where each fiord had a probability of being selected proportional to its area in an attempt to maintain equal coverage probability within fiord strata. At stage 2, distance sampling was conducted within each selected fiord.

A GIS was used to select and clip sections of the shore line that were considered separate fiords. This process relied on published nautical charts and local knowledge, and was somewhat arbitrary when fiords had complex shapes with multiple openings into a larger body of water, or when it was difficult to distinguish a fiord/inlet from a bay. Any fiord smaller than a cut-off value of 20 km^2 was excluded from the design. This process yielded a total of 111 fiords, ranging in area from 21 to 1,236 km^2 (Table 1). Ideally, 10–20 fiords (PSUs) per stratum should be sampled to obtain a reliable abundance estimate (Buckland et al. 2001). When logistics preclude this, it is advisable to have at least five (Thomas et al. 2007).

All 14 fiords in Admiralty Inlet and Eclipse Sound (seven in each) could be surveyed (Fig. 1 and 2). For the other strata, we decided to sample five out of 15 fiords in Smith Sound (Fig. 3), five out of 17 in Jones Sound (Fig. 4), and ten out of 54 in East Baffin Island (Fig. 5). Due to exceedingly large transit times, only three out of 11 fiords could be selected in West Ellesmere (Fig. 4). The algorithm to select the fiords (PSUs) had to have the following properties:

(1) the probability of selecting a fiord should be proportional to its area, so that each part of the stratum will have the same chance of being in a sampled fiord;

(2) there should be a good geographic spread of fiords (e.g., from north to south or east to west) – this implied the use of a systematic scheme;

(3) no fiord should be selected twice.

This last property could be achieved by sampling without replacement (i.e., removing each fiord from the pool of potential samples once it is selected), but a disadvantage of this type of algorithm is that variance estimation is greatly complicated. Instead a systematic algorithm developed by Thomas et al. (2007) was used that samples with replacement, but fulfils the first two of the above criteria and has zero probability of sampling the same fiord twice at low sampling intensities. Each fiord had a probability of being selected that was proportional to its area, so that any point in a fiord stratum had the same chance of being sampled.

Allocation of effort within fiords

Contrary to Thomas et al. (2007), equal coverage design could not be maintained within fiords. Many of the fiords were non-convex with long, thin sections, and cliffs on the sides that rose higher than the target survey altitude (300 meters). Therefore, it was impractical to use systematic or random transects within the selected fiords (PSUs) and density surface modeling was used instead. To reduce possible bias in the spatial model, flights were planned as continuous tracks and adjusted on site by the navigator to follow the main axis of each fiord, while aiming to spread coverage uniformly according to distance from the shore when the fiords were wide enough, and to minimize duplicate coverage of any area.

Data collection

Data were collected using the same protocol as non-fiord areas, i.e., using a double-platform visual survey, with observers collecting information on time sighted, time abeam, species, count and declination angle of each sighting, as well as environmental conditions and ancillary data (e.g., direction of travelling).

DENSITY SURFACE MODELLING

Statistical framework

We used a density surface modelling framework to model spatially-referenced count data with the additional information provided by collecting distances to account for imperfect detection. Modelling proceeds in two steps: a detection function is fitted to the perpendicular distance data to obtain detection probabilities for clusters of individuals. Counts are then summarised per segment (contiguous transect sections). A generalised additive model (GAM, Wood 2006) is then constructed with the per-segment counts as the response with segment areas corrected for detectability. GAMs provide a flexible class of models that include generalized linear models but extend them with the possible addition of splines to create smooth functions of covariates.

Transect lines need to be split into contiguous segments (indexed by j), which are of length l_j. Segments should be small enough such that neither density of objects nor covariate values vary appreciably within a segment. The area of each segment j is $A_j = 2 \cdot w \cdot l_j$ (where w is the truncation distance). Count per segment is then modelled as a sum of smooth functions of covariates (e.g., location, depth, measured at the segment level) using a GAM. Smooth functions are modelled as splines, providing flexible curves and surfaces to describe the relationship between the covariates and the response.

The general model for the count per segment is:

$$E(n_j) = \hat{p}_j \cdot A_j \cdot exp\left[\beta_0 + \sum_k f_k(z_{jk})\right]$$

where z_{jk} represents the value of the k_{th} explanatory spatial variable in the j_{th} segment, and function f_k is a smooth function of the covariate z_{jk} and β_0 is an intercept term (Hedley and Buckland 2004). Multiplying the segment area (A_j) by the probability of detection ($\hat{p}_j$) gives the effective area for segment j. If there are no covariates other than distance in the detection function then the probability of detection is constant for all segments.

It would be unrealistic to expect narwhal sightings to be spread randomly throughout the region (Forney 2000). Therefore, after examination of the data, we decided against using a Poisson distribution (where the variance of each observation is assumed to be equal to its mean) and instead we modelled counts as a negative binomial distribution.

Data management

As per standard line distance sampling methods, declination angles of abeam sightings were transformed into perpendicular distances by dividing the recorded altitude by the tangent of the angle. Missing or uncertain measurements were recovered from photographic data when possible (as described in Pike and Doniol-Valcroze 2015). Duplicate sightings between primary and secondary observers were identified as described in Pike and Doniol-Valcroze (2015). Double-platform distance sampling is not yet implemented in the DSM framework. Therefore, we used CDS with all unique sightings (i.e., sightings made by either the primary or the secondary observer).

The response variable for the spatial modelling approach is the number of groups in each segment of effort. Each transect of survey effort was divided into segments of comparable lengths (approximately 10 seconds of flying time or 514 meters), characterized by uniform environmental covariates (sea state, ice cover, glare, etc.). The location of the midpoint of each segment was calculated. Latitude and longitude coordinates were projected in meters so that distances were uniform in all directions (map projections differed depending on geographical location of each stratum). For each segment and observation, we extracted two spatial covariates: distance from the nearest shore and distance from the nearest mouth of the fiord (into the adjacent open-water stratum). Distance from the fiord mouth was calculated as the shortest path not intersecting land, therefore taking into account the complex shapes and multiple branching of some fiords (see example in Fig. 6).

Spatial modelling requires the abundance of groups to be predicted throughout the survey area, which needs to be divided into a grid. A grid of cells of resolution 250 m x 250 m was constructed to cover the whole area of each fiord. Cell size was arbitrary, but constrained by two requirements: resolution had to be coarser than segment lengths, but small enough for values of the explanatory variables to not vary much within each cell. Values for the explanatory variables (latitude, longitude, depth, and distance offshore) were calculated using the value at the midpoint of each grid square. Extensive simulations revealed that model descriptions and predictions were robust to variation in choice of grid size (Hedley and Buckland 2004).

Detection function

As mentioned, the methodology involves two separate statistical models. The first model fitted a detection function to the perpendicular sighting distances, as in a conventional distance-sampling analysis, to estimate the effective strip width. Exploratory analyses showed that the histogram of detection distances in fiords differed in shape and extent from that of other water bodies. Therefore, instead of pooling all HACS narwhal sightings together, we restricted this analysis to perpendicular distances within fiord strata (the analysis was still “global” in the sense that all narwhal fiord sightings were pooled together to produce one detection function for all fiords). In addition to perpendicular distance, environmental variables that may affect detectability (Beaufort sea state, cloud cover, glare intensity, and ice cover) were incorporated as covariates (Marques et al. 2007). Detection function models were selected based on AIC.

Spatial model fitting

The second model is the spatial density component. The number of narwhals seen in each segment was described by a GAM with a spatial smoother and by the effective area of each segment (i.e., the product of its effective strip width and its length). DSMs are typically fitted with thin-plate regression splines (Wood 2003). However, previous work has highlighted that in some cases, the fitted surface tends to increase unrealistically as predictions are made further away from the locations of survey effort (Miller et al. 2013a). This problem can be alleviated using a generalization of thin plate regression splines called Duchon splines (Miller and Wood 2014). Problems can also occur when smoothing over areas with complicated boundaries (Wood 2008). If two parts of the study area are linked by the model without taking into account obstacles, then some boundaries (e.g., peninsula, island) can be “smoothed across”. Therefore, we also fitted a “soap film” smoother (Wood 2008), which usually performs better for complex study regions by reducing smoothing of density contours across land boundaries and minimizes edge effects. The soap film is a bivariate smooth of spatial coordinates only and cannot include covariates such as distance to mouth and to shore.

We fitted models with and without covariates, for each of the three types of spatial smoothers, in the package *dsm* (Miller et al. 2013b), available within the R software (R Core Team 2014). There were two levels of model selection. Within each model, flexibility (estimated degrees of freedom) and removal of model terms were based on functions from the *mgcv* package (Wood 2001), which uses restricted maximum likelihood to choose a statistically defensible degree of smoothing, with penalties for unnecessary flexibility. Then, the best model (choice of smoother and covariates) was selected based on AIC. Goodness of fit was examined with random-quartiles Q-Q plots on the residuals (Dunn and Smyth 1996).

If no model could be fitted for a given fiord (i.e., no significant coefficients) or if there was only one sighting made, then a DSM was not used for that PSU and we used instead a “naïve” abundance estimate, equal to the number of individuals seen divided by the effort (length multiplied by effective strip width) and multiplied by fiord area. The CV of such estimates was calculated using an empirical estimate of variance (assuming a Poisson distribution for fiords with only one sighting, i.e., variance is equal to the mean, the CV was 1.00).

Prediction of density surface and uncertainty estimation

Following selection of the best spatial model in each fiord, predicted values were mapped across the prediction grid. The output of the model was an estimate of the predicted number of narwhal groups in each grid cell, based on each cell’s latitude, longitude, area, and potentially distances to shore and to fiord mouth (in case fiords act as potential refuges from predation). This predicted count was converted to density for mapping purposes by dividing the count by the area of each cell. The density surface was integrated over the whole area of each fiord to obtain the estimate of the total number of narwhal groups and then multiplied by mean group size in each fiord to yield total narwhal abundance. To allow for comparison between approaches, we calculated the naïve estimate described above for each fiord.

Variance in spatial models of abundance is often estimated by resampling, in particular through the use of moving-block bootstraps (e.g., as in the Distance software, version 6.0, Thomas et al. 2010). In practice these bootstrapping techniques frequently yield unstable and biased results when models are smoothed, especially in cases such as ours in which survey design precludes easy identification of an independent resampling unit (Williams et al. 2006). Therefore, we used the alternative Bayesian approach as proposed by Wood (2006) that does not suffer from the bias associated with the bootstrapping approaches. This method simulates replicate parameter sets from the posterior distribution of the estimated parameters of the spatial model to obtain a measure of the variance in the spatial model.

Spatial models also include variability that comes from estimating the parameters of the detection function because the effective area of each cell is based the estimated strip half-width. The variance of abundance of each fiord (PSU), s_i^2, was estimated using the delta method (Seber 1982) to combine the variance of the effective area (detection model) with the variance from estimation of the spatial component to as suggested by Hedley and Buckland (2004). This method allows us to obtain a confidence interval and coefficient of variation around each estimate of abundance. If needed, it allows us to map the CV on the prediction grid.

STRATUM-WIDE ESTIMATES OF DENSITY AND ABUNDANCE

Within each fiord stratum, we used a two-stage sampling design in which the first stage consisted of sampling with replacement among potential fiord candidates (PSUs). Appropriate estimators for the density $\widehat{D}$ and total surface abundance $\hat{\tau}$ in a stratum are given by a ratio estimator (Cochran 1977):

$$\hat{D} = \frac{\sum_{i=1}^{n} \hat{y}_i}{\sum_{i=1}^{n} A_i}$$

$$\hat{\tau} = A_t \cdot \frac{\sum_{i=1}^{n} \hat{y}_i}{\sum_{i=1}^{n} A_i}$$

where A_i and $\hat{y}_i$ are the area and the estimated abundance in each of the *n* surveyed fiords (PSU) in the stratum, respectively, and A_t is the total stratum area. Note that this is equivalent to averaging the estimated narwhal densities of all fiords, weighted by their respective areas. Note also that when all fiords in a given stratum are surveyed (as in Admiralty Inlet and Eclipse Sound), $\sum_i^n A_i = \sum_i^N A_i = A_t$, and thus the equation simplifies to the sum of the abundance estimates, as per a standard stratified design (Buckland et al. 2001).

The sample variance of the estimated density among fiords, with fiords of unequal areas, was adapted from the formula proposed by Innes et al. (2002):

$$\widehat{Var}(\hat{D}) = s_a^2 = \frac{n}{A^2(n-1)} \cdot \frac{\sum_{i=1}^{n} A_i^2 \left(\frac{\hat{y}_i}{A_i} - \frac{\sum_{i=1}^{n} \hat{y}_i}{A}\right)^2}{n-1}$$

where $A = \sum_i^n A_i$ is the sum of the areas of the surveyed fiords.

Because we used a two-stage sampling scheme, the variance of the total abundance has two components: among-fiord variance and within-fiord variance. The among-fiord variance is equal to $A_t^2 s_a^2$ with the addition of a finite population correction $(1 - f)$ and the within-fiord component is the sum of the variances of each surveyed fiord, multiplied by the inverse of the sampling fraction. Thus, the estimator of the variance is:

$$\widehat{Var}(\hat{\tau}) = A_t^2(1-f) \cdot s_a^2 + \frac{1}{f} \cdot \sum_{i=1}^{n} s_i^2$$

where $f = \frac{n}{N}$ is the sampling fraction, s_i^2 is the variance of the i^{th} fiord (obtained from the DSM) and s_a^2 is the among-fiord variance of the estimated density. Note that when all the fiords within a stratum are sampled (i.e., $f = 1$), the first term disappears and the multiplier of the second term becomes unity, i.e., the total variance is the sum of the within-fiord variances, as per a standard stratified design (Buckland et al. 2001).

RESULTS

SAMPLING COVERAGE AND SIGHTINGS

Table 1 summarizes which fiords were selected in each stratum and which were successfully surveyed. As scheduled, all fiords in Admiralty Inlet and Eclipse Sound were surveyed in good conditions. Narwhals were observed in one fiord in each of these two strata. In West Ellesmere, one fiord was completely covered in ice and could not be surveyed, leaving only two surveyed fiords, with no narwhal sightings. Five fiords in Jones Sound were surveyed twice, once on August 10 and once on August 26, and one fiord was surveyed only on August 26; no sightings were made on the first survey but narwhals were observed in two fiords on the second survey. One of the five selected fiords in Smith Sound could not be surveyed because of dense fog; narwhals were observed in three of the other fiords. In the East Baffin Island fiord stratum, we selected ten fiords out of 54, and were able to survey nine, with narwhal sightings in six of them.

Overall, sightings were both highly aggregated among fiords (i.e., a small proportion of fiords with sightings) and highly clustered within fiords.

DETECTION FUNCTION MODEL

A total of 521 unique narwhal sightings were made in fiords by front and rear observers of the three aircraft. Of these, 76 were missing a declination angle, even after verification using photographic data. Examination of the perpendicular distance suggested right-truncation at 750 m, which removed 22 distant sightings. Left truncation did not improve the fit and therefore was not used. This left 423 sightings for detection function fitting. We fitted MCDS models to the data with different key functions, with and without covariates. The model that best fitted the data was a hazard-rate key function with no covariates, and therefore a single global detection function was used for all fiord strata with p(x) estimated at 0.457 and the effective strip half-width estimated at 343 m (CV 4.6%, Fig. 7).

SPATIAL MODELS

Spatial models were fitted to the ten fiords in which more than one narwhal observations were made. We use fiord SSF03 (Mackinson Inlet) as a detailed example of model fitting, checking and selection. Models featuring multiple combinations of the three types of spatial smoothers and the inclusion of covariates were fitted to the observation data. Four examples are shown in Fig. 8. A model using only a spatial smoother (Duchon splines) was able to identify the main gradients in density but had difficulty capturing the multi-modal distribution around the complex topography (Fig. 8a). A model using only distance to shore and to mouth covariates was better able to fit density gradients around the tortuous shoreline, but predicted narwhals in areas where few were observed, including in a narrow branch of the fiord that was located at the same distance from the mouth as the area where most narwhals were seen in the main branch (Fig. 8b). A model combining the covariates with the spatial smoother was better able to fit the main distribution cores of narwhal sightings (Fig. 8c), as was a model using the soap film smoother (Fig. 8d).

According to AIC, the spatial smoother with covariates provided the best fit and was therefore selected to estimate abundance in the entire fiord. The DSM estimate of 812 narwhals was similar to the naïve estimate of 871, but the use of spatial modelling allowed us to quantify uncertainty based on the variance in GAM parameters, resulting in a CV of 0.36 (1.6% of the total variance come from the CV of 0.046 of the detection function and 98.4% of the total variance are due to the CV of 0.36 of the DSM). Examination of residuals showed that modelling assumptions were met (Fig. 9). The relationship of observed counts with “distance to mouth” is shown on the lower right panel of Fig. 9, indicating that narwhals were predominantly seen at the entrance of the fiord, with few observations beyond 45 km from its mouth.

Model selection for all PSU is summarized in Table 2. Duchon splines or soap films were always selected over the thin-plate regression splines. Spatial covariates were retained in three final models. A high degree of smoothing (i.e., effective degrees of freedom) was often needed to fit to the high degree of clustering in narwhal sightings. Modelling attempts failed in EBF12, with no significant coefficients (spatial or covariates), and thus a naïve estimate was computed. The naïve approach was also used for SSF11, EBF14 and EBF36, which all had only one narwhal sighting.

Density surfaces for each stratum are shown in Figures 10–14. Sightings in AIF01 were located so close to the shoreline that a finer scale (i.e., a 100 m x 100 m cell size) was needed to capture the relationship between sighting location and distance to shore. This was the fiord in which the two spatial covariates had the largest influence on the spatial model (Fig. 12).

ABUNDANCE ESTIMATES

Surface densities were integrated to produce surface abundance estimates for each fiord (PSU) (Table 2). Overall, DSM estimates were similar or slightly lower than naïve estimates, except in ESF01 and EBF03 where there was a large difference between the two estimates. In both cases, large aggregations of narwhals in narrow passages where the effective strip width overlapped significantly with the shoreline caused the naïve approach to overestimate the local density of narwhals. Moreover, in ESF01, the track overlapped itself when the aircraft turned around at the end of the fiord, resulting in double-coverage that was taken into account by the DSM but not by the naïve approach.

The CVs around within-fiord abundance estimates ranged from 6.5–84% (not counting the fiords for which the naïve CV of 100% was used), with higher CVs prevalent in fiords with few observations or where observations were tightly clustered. Jones Sound fiords that were surveyed twice were modelled once using the total effort and data of the two surveys, i.e., the resulting estimates reflect the average density weighted by effort.

After expanding the abundance estimates to unsurveyed fiords (Table 3), total (surface) abundance estimates were 45 for JSF (CV 94%), 1,916 (CV 45%) for SSF, 143 (CV 85%) for AIF, 1,135 (CV 19%) for ESF, and 3,799 (CV 35%) for EBF. Because no observations were made in WEF, no abundance estimate was produced.

Sightings in all the fiords of the East Baffin Island stratum were reported by observers as having occurred in murky or opaque waters, which was confirmed by examination of the photographs taken underneath the plane. This suggests that observers would not have been able to detect and identify narwhals as deep as 2 m, as is usually assumed.

DISCUSSION

The coast lines that characterize the summer ranges of narwhals in the Canadian High Arctic are complex and contain numerous fiords. Narwhals are frequently observed in those fiords and it is apparent from previous studies, as well as from the distribution of sightings during the present survey (HACS), that narwhals enter these fiords in large numbers. Therefore, any credible abundance estimate must include these areas, which, in the case of the East Baffin Island stock, make up almost the entirety of their summering range.

Simply including these fiords as parts of the wider open strata in a systematic line transect design would not ensure that they are surveyed properly. The complex shapes of fiords make it unlikely that randomly placed transect lines would provide a representative coverage, and extrapolating stratum-wide density estimates to the fiords' small areas would likely underrepresent their importance to narwhals. This is why fiords were treated in separate strata in this analysis.

An ideal sampling design for fiord strata would be to survey all of them in each stratum, and to use a systematic sampling design within each fiord (e.g., as in Thomas et al. 2007). During HACS, surveying all fiords in a given stratum was only achieved in Admiralty Inlet and Eclipse Sound, which are relatively small strata with fiords located close to one another and to a refueling point. In other strata, it was impossible to survey all fiords for logistical reasons. Using a systematic design within each fiord could not be achieved because of the limitations on aerial surveys imposed by the high-elevation of cliffs on the sides of most of the fiords.

The impossibility of surveying all the fiords within each stratum was addressed by using a cluster sampling design, in which fiords designated as primary sampling units (PSU) were selected in a way that maintained equal probability and systematic coverage, and allowed us to integrate in our final estimate the uncertainty from the within-fiord and between-fiord variances.

The impossibility of using conventional transect lines or zig-zags within each fiord was addressed by using a spatial density model. Density surface modelling allows abundance to be estimated for any subset of a survey region, by numerically integrating under the relevant section of the fitted density surface. In contrast, conventional line transect methods restrict estimation of abundance to a set of predefined survey blocks, defined at the design stage of a survey using random or systematic sampling. A spatial model is thus less susceptible to the problem of small sample sizes in sub-regions than are stratified schemes, does not require track lines to be designed according to a formal survey sampling scheme, and accommodates both non-random and unequal coverage (Williams et al. 2006). Moreover, the resulting variance of the abundance estimate incorporates both the variance from the detection function and that of the spatial model (Hedley and Buckland 2004). This approach allowed us to take into account the uneven, non-random transect design of our fiord surveys, and also to estimate a CV for each abundance estimate.

Spatial models, however, have their own sources of uncertainty. In fiords (PSUs) with few observations, it was often difficult to select the right set of smoothers and their level of flexibility, and the resulting abundance estimates were therefore imprecise and sensitive to modelling decisions. Even in some fiords with larger narwhal numbers, the goodness-of-fit of spatial models was not always satisfactory, suggesting there was unmodelled spatial heterogeneity due to covariates that were not included (e.g., AIF01 where 143 sightings still yielded a CV of 0.85).

We assumed that larger fiords were more likely to contain narwhals based on their area. An alternative approach would be to consider each fiord as a unit of equal value (i.e., probability of containing narwhals), regardless of its size. Ultimately, we do not know what characteristics of fiords are attractive to narwhals (area, length, coastline complexity, etc.). There could also be latitudinal or longitudinal gradients in narwhal density among fiords but we did not have enough data to model narwhal distribution at a larger (among-fiord) scale. These assumptions could introduce biases in the estimates. It is possible that detailed analyses of narwhal movement among fiords, using satellite tracking, could yield insights on this issue, but such data are missing at present for most fiord strata (Smith Sound, Jones Sound, East Baffin Island).

As in design-based approaches, the main source of uncertainty (and the reason for the relatively large CVs that characterize the total stratum estimates) are the high aggregation rates at two scales: within, and more importantly, among fiords, as well as the relatively small effort in terms of the number of fiords surveyed, even though the total area covered was in most cases comparable to that of regular strata (e.g., in EBF, nine out of 54 fiords were surveyed, but their total area was equal to 48% of the stratum area). These relatively large CVs reflect the imprecision in our estimates and their sensitivity to the random selection of PSUs: for instance, if the first PSU of AIF (or ESF) had not been surveyed, the abundance estimate for the entire stratum would be zero instead of 143 (or 1,135 for ESF).

Another source of potential bias was that identifying duplicates between primary and secondary observers in fiords proved difficult due to the highly aggregated nature of narwhal sightings and the fact that observers were often overwhelmed by large groups. This made it difficult to reliably estimate the proportion of sightings missed by both observers. We chose a conservative approach of modelling the unique sightings (i.e., sightings made by any or both observers), thus making use of the increased detection probability of the double-platform, but without correcting for the proportion of narwhals missed by both platforms (i.e., we assumed that, combined together, the observers detected all narwhals). We know this likely creates a downward bias. Conversely, the use of an erroneous correction factor for perception bias could result in non-conservative abundance estimates. Analyses using photographic data from the survey would not face the same issues and would likely result in more accurate estimates.

The DSM abundance estimate for the East Baffin Island fiord stratum (EBF) was 3,799, which is similar to the previous surface estimate of 3,487 from the 2003 survey (Richard et al. 2010). The 2013 CV is slightly larger (35% vs 27%). Note that our approach to estimate abundance and uncertainty differed from that of Richard et al. (2010). Richard et al. (2010) considered the aircraft track on each fiord as a sampling line, and calculated the among-line variance as if each fiord survey was a regular line transect, whereas our variance estimate includes an additional within-fiord variance component. The HACS survey also had lesser coverage: nine fiords out of 54 were surveyed in 2013 whereas half of the fiords (27 out of 54) were surveyed in 2003.

The stratum-wide estimates are for surface abundance. They can be added directly to other non-fiord strata of the same narwhal stock, before applying any correction for the availability bias. However, observers reported murky conditions in East Baffin Island fiords that may have prevented the observation of narwhals under water. In such cases case, we suggest it would appropriate to use a different correction factor based on the assumption that narwhals could only be detected down to 1 m below the surface (Watt et al. 2015).

Our objective was to obtain the most precise abundance estimates while taking into account the specific characteristics of surveying in narrow and complex fiords. Constructing a model in which variability in animal density is explained by covariates describing the environment can also provide information on distribution and use of habitat by narwhals on their summering range, and the resulting models can improve our understanding of which features of the environment influence density. In our case, spatial covariates (distance to shore and to the fiord mouth) were seldom retained in the final models. This is partly due to the high degree of aggregation of narwhals within each fiord (i.e., there was little variability within each fiord in terms of covariates). A more meaningful analysis of species-environment relationship should investigate the effect of covariates at a wider scale (e.g., how often are narwhals located at a certain distance from the fiord mouth) and include additional covariates such as depth, bottom slope, bottom sediment, ice cover and prey concentrations, with physical variables being more likely to be useful in the short term than biological variables, given the increasing availability of remote sensing methods.

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TABLES

Table 1. List and characteristics of fiord that are the primary sampling unit (PSU) in each fiord stratum. Selected: whether the fiord was drawn by the cluster sampling algorithm (note that AIF and ESF fiords were all selected by design). Surveyed: whether the selected fiord was successfully surveyed (with reason for non-coverage). Narwhal sightings: whether narwhals were observed by any of the visual observers while on effort.

Stratum	PSU	Area (km^2)	Selected	Surveyed	Narwhal sightings
West Ellesmere (WEF)	1	43			
	2	22			
	3	47			
	4	181			
	5	580	yes	no (ice)	-
	6	104			
	7	50			
	8	464	yes	yes	no
	9	65			
	10	74	yes	yes	no
	11	18			
Jones Sound (JSF)	1	14			
	2	187	yes	yes	no
	3	144			
	4	120			
	5	199	yes	yes	no
	6	140			
	7	146			
	8	182	yes	yes	no
	9	75			
	10	140			
	11	214	yes	yes	yes
	12	218	no	yes	yes
	13	31			
	14	391	yes	yes	no
	15	19			
	16	39			
	17	155			
Smith Sound (SSF)	1	110			
	2	430			
	3	930	yes	yes	yes
	4	35			
	5	296	yes	no (fog)	-
	6	269			

Stratum	PSU	Area (km^2)	Selected	Surveyed	Narwhal sightings
	7	271			
	8	88	yes	yes	yes
	9	469			
	10	259			
	11	416	yes	yes	yes
	12	187			
	13	46			
	14	34			
	15	397	yes	yes	no
Admiralty Inlet (AIF)	1	97	yes	yes	yes
	2	71	yes	yes	no
	3	255	yes	yes	no
	4	42	yes	yes	no
	5	246	yes	yes	no
	6	29	yes	yes	no
	7	172	yes	yes	no
Eclipse Sound (ESF)	1	162	yes	yes	yes
	2	68	yes	yes	no
	3	123	yes	yes	no
	4	37	yes	yes	no
	5	599	yes	yes	no
	6	253	yes	yes	no
	7	44	yes	yes	no
East Baffin Island (EBF)	1	132			
	2	121			
	3	151	yes	yes	yes
	4	217			
	5	44			
	6	187			
	7	442			
	8	26			
	9	899	yes	yes	yes
	10	732	yes	yes	yes
	11	331			
	12	573	yes	yes	yes
	13	574	yes	yes	
	14	1,237	yes	yes	yes
	15	702			
	16	67	yes	yes	no
	17	61			

Stratum	PSU	Area (km^2)	Selected	Surveyed	Narwhal sightings
	18	131			
	19	298			
	20	175			
	21	26			
	22	42			
	23	43			
	24	170	yes	No (wind)	-
	25	64			
	26	185			
	27	24			
	28	121			
	29	80			
	30	146			
	31	51			
	32	29			
	33	24			
	34	24			
	35	205			
	36	180	yes	yes	yes
	37	77			
	38	196			
	39	114			
	40	84			
	41	32			
	42	44			
	43	34			
	44	143			
	45	48			
	46	134	yes	yes	no
	47	188			
	48	102			
	49	58			
	50	45			
	51	115			
	52	50			
	53	66			
	54	45			

Table 2. Spatial density models. For each surveyed fiord in which narwhals were sighted, the best spatial density model is shown. n_{groups}: number of unique narwhal groups sighted; $n_{individuals}$: total number of individuals; $\widehat{N}_{naïve}$: naïve abundance estimate (no spatial model); xy smoother: best selected smoother among thin plate regression splines, Duchon splines and soap film (with effective degrees of freedom); covariates: distance to mouth and distance to shore (with effective degrees of freedom); $\widehat{N}_{dsm}$: abundance estimate from spatial density model. CV have two components: distance detection function (ddf) and density spatial model (dsm). Note that when there was only one sighting in a fiord (SSF11, EBF14, EBF36) or when a spatial model with significant coefficients could not be fitted (EBF12), the naïve estimate was used.

Stratum	PSU	Effort (km)	Area (km^2)	n_{groups}	$n_{individuals}$	$\widehat{N}_{naïve}$	Spatial model		Deviance explained	$\widehat{N}_{dsm}$	CV		
							xy smoother (edf)	covariates (edf)			ddf	dsm	total
JSF	11	194	214	2	6	9	soap (1.6)	-	86.3%	**9**	4.6%	4.7%	6.5%
	12	122	219	5	13	34	duchon (4.7)	-	78.9%	**21**	4.6%	11.6%	12.5%
SSF	3	221	931	62	142	871	duchon (4.3)	dmouth (1.3) + dshore (1.0)	46.9%	**812**	4.6%	36.0%	36.3%
	8	31	88	3	6	21	duchon (0.96)	-	23.1%	**20**	4.6%	83.7%	83.8%
	11	98	416	1	1	**6**	-	-	-	-	4.6%	100.0%	100.1%
AIF	1	61	97	32	124	286	duchon (0.32)	dmouth (1.58) + dshore (2.05)	96.2%	**143**	4.6%	84.5%	84.6%
ESF	1	96	161	111	1,411	3,438	soap (2.21)	-	68.8%	**1,135**	4.6%	18.8%	19.3%
EBF	3	63	151	237	544	1,929	duchon (15.9)	-	78.6%	**969**	4.6%	17.9%	18.5%
	9	202	907	50	76	498	duchon (12.8)	dmouth (1.75) + dshore (1.26)	74.6%	**271**	4.6%	22.9%	23.4%
	10	205	738	51	105	550	duchon (8.75)	-	89.9%	**448**	4.6%	32.9%	33.2%
	12	162	577	2	2	**10**	-	-	-	-	4.6%	100.0%	100.1%
	14	288	1,247	1	2	**13**	-	-	-	-	4.6%	100.0%	100.1%
	36	166	182	1	1	**2**	-	-	-	-	4.6%	100.0%	100.1%

Table 3. Abundance estimates by stratum. N PSU: total number of fiords in each stratum; n sampled: number of fiords surveyed in each stratum.

Stratum	N PSU	Total area (km^2)	n sampled	Sampled area (km^2)	Surface abundance	CV
JSF	17	2,413	6	1,391	**45**	**0.94**
SSF	15	4,237	4	1,831	**1,916**	**0.45**
AIF	7	912	7	912	**143**	**0.85**
ESF	7	1,286	7	1,286	**1,135**	**0.19**
EBF	54	10,091	9	4,547	**3,799**	**0.35**

FIGURES

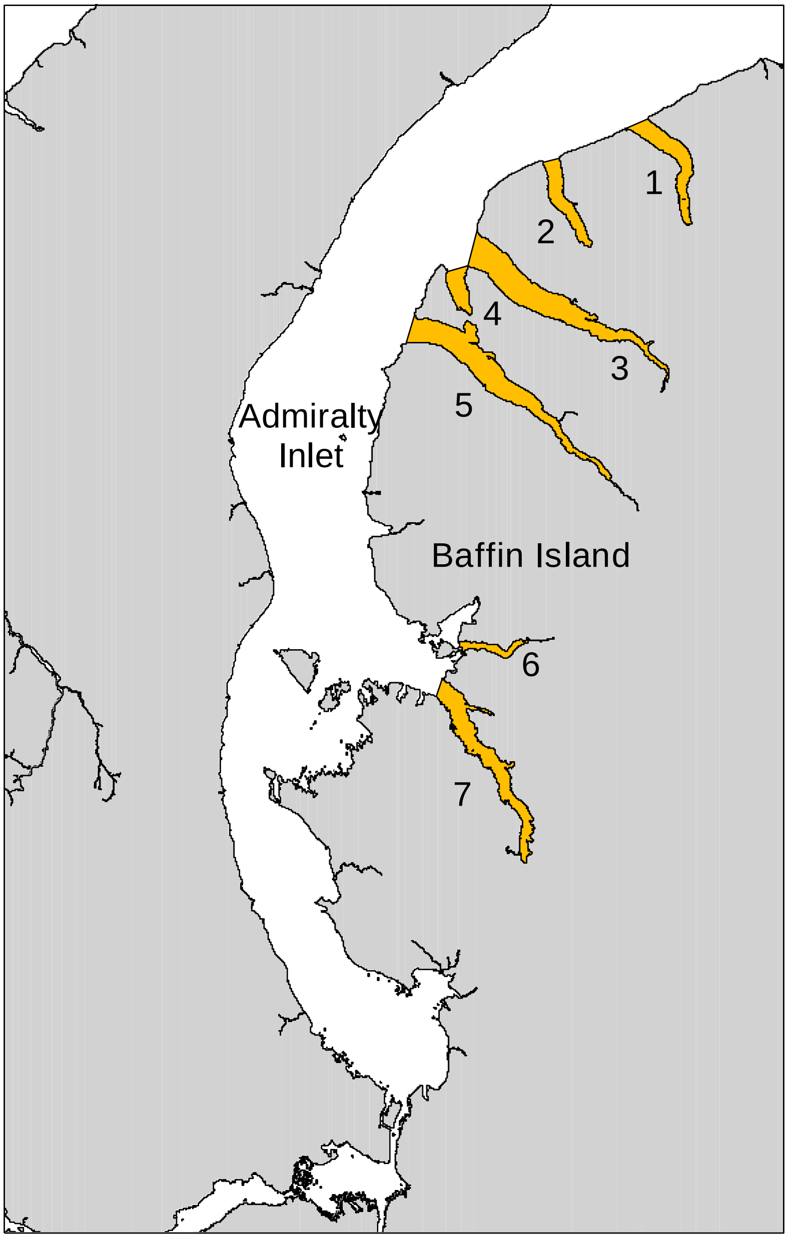

Figure 1. Map of fiords in the Admiralty Inlet fiord stratum. All fiords were surveyed.

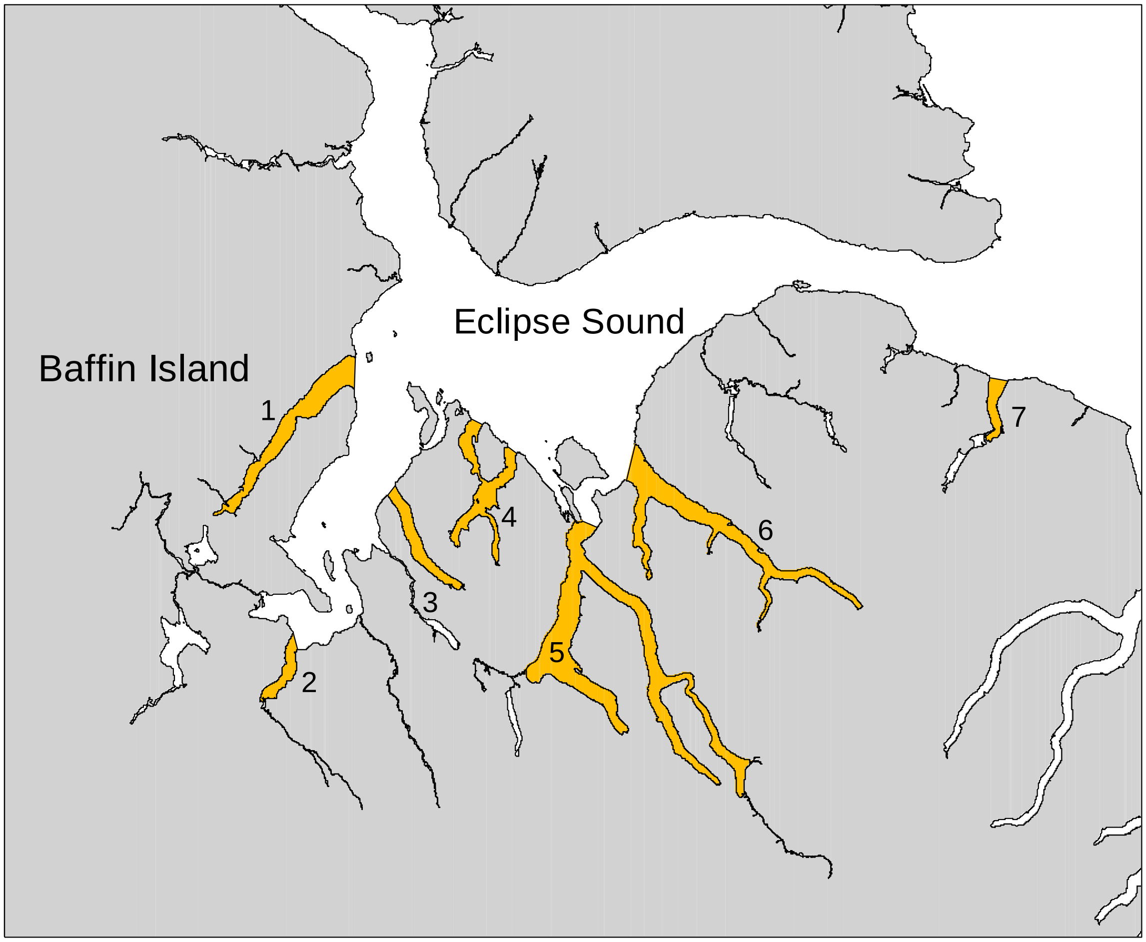

Figure 2. Map of fiords in the Eclipse Sound fiord stratum. All fiords were surveyed.

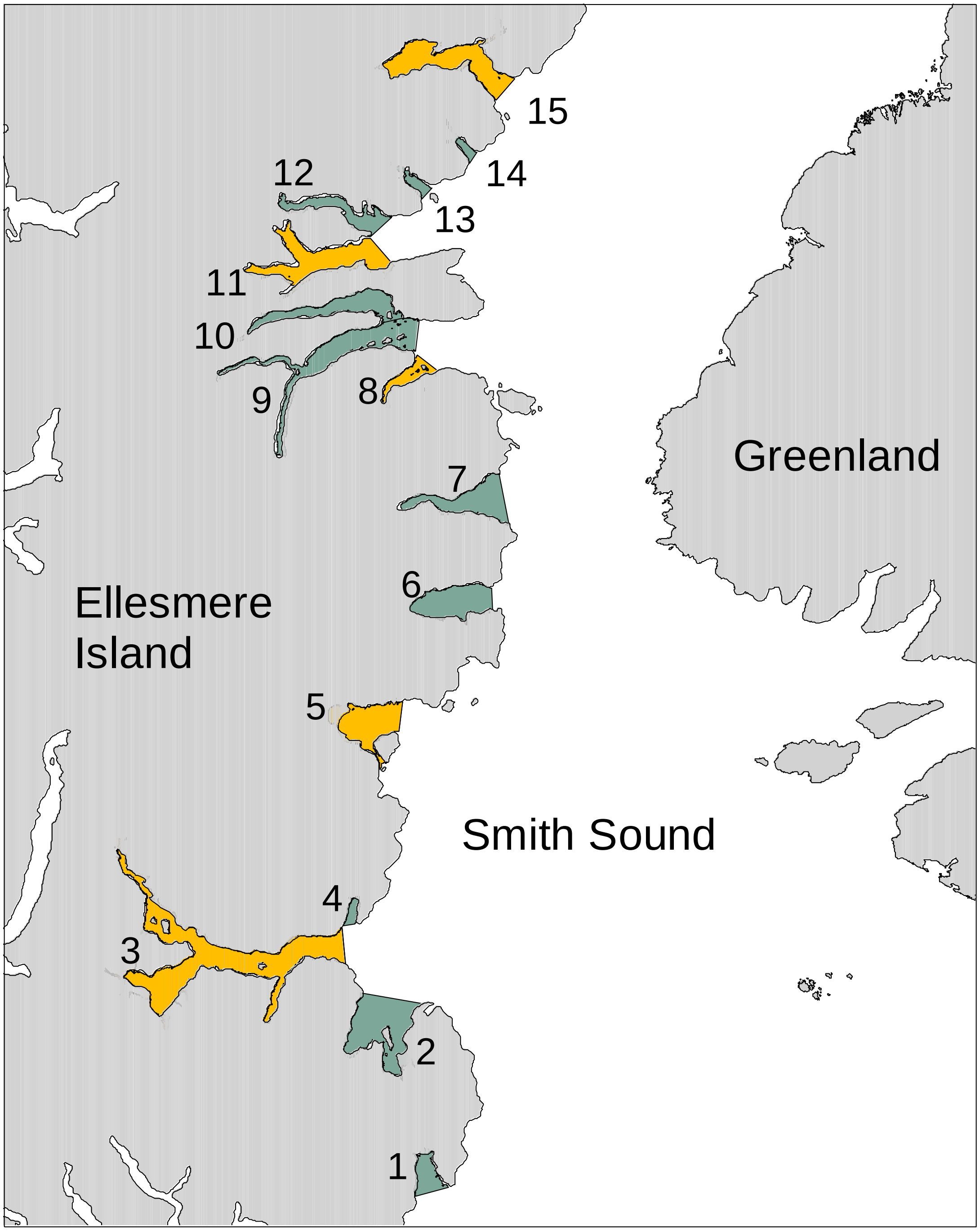

Figure 3. Map of fiords in the Smith Sound Fiord stratum. Fiords highlighted in orange are those selected by the cluster sampling algorithm

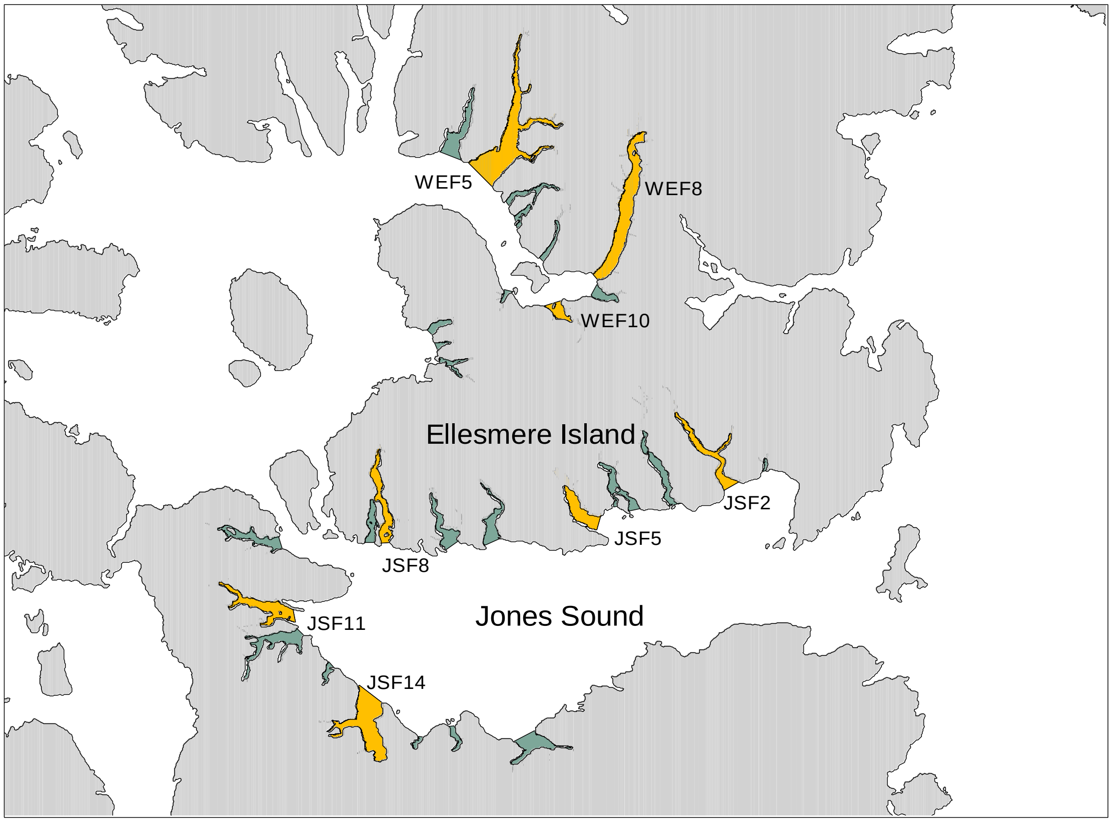

Figure 4. Map of fiords in the Jones Sound (JSF) and West Ellesmere (WEF) strata. Fiords highlighted in orange are those selected by the cluster sampling algorithm.

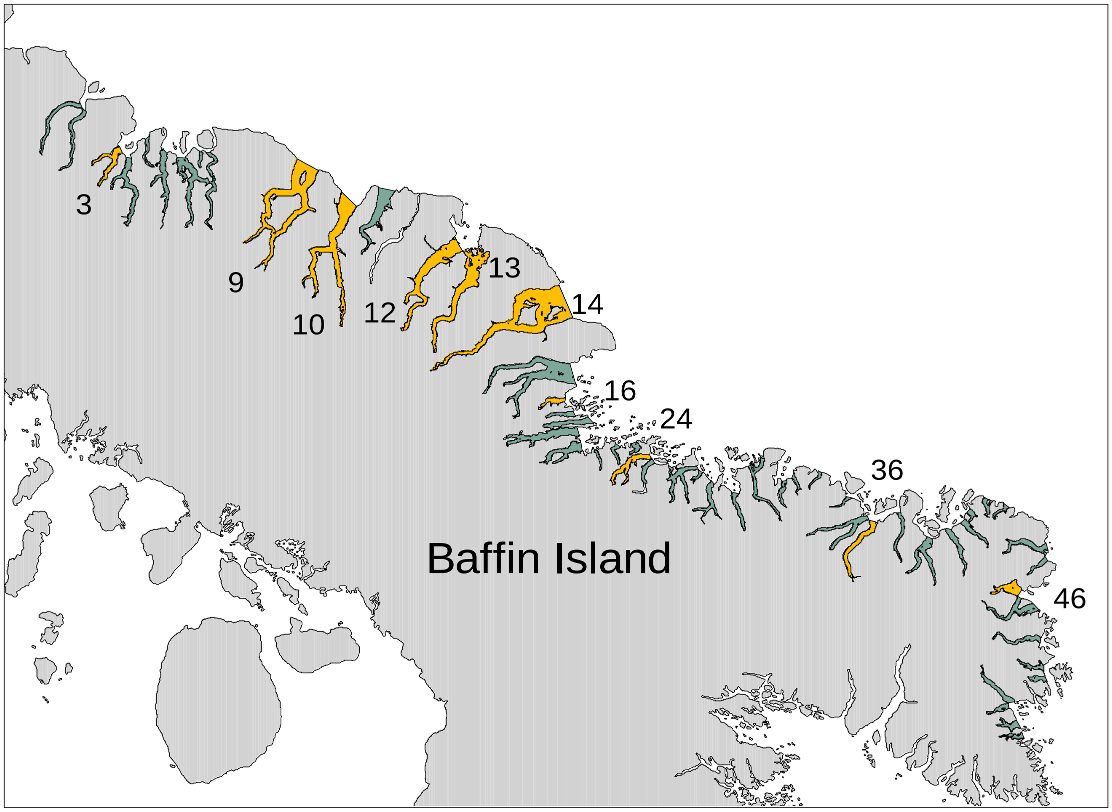

Figure 5. Map of fiords in the East Baffin Island fiord stratum. Fiords highlighted in orange are those selected by the cluster sampling algorithm.

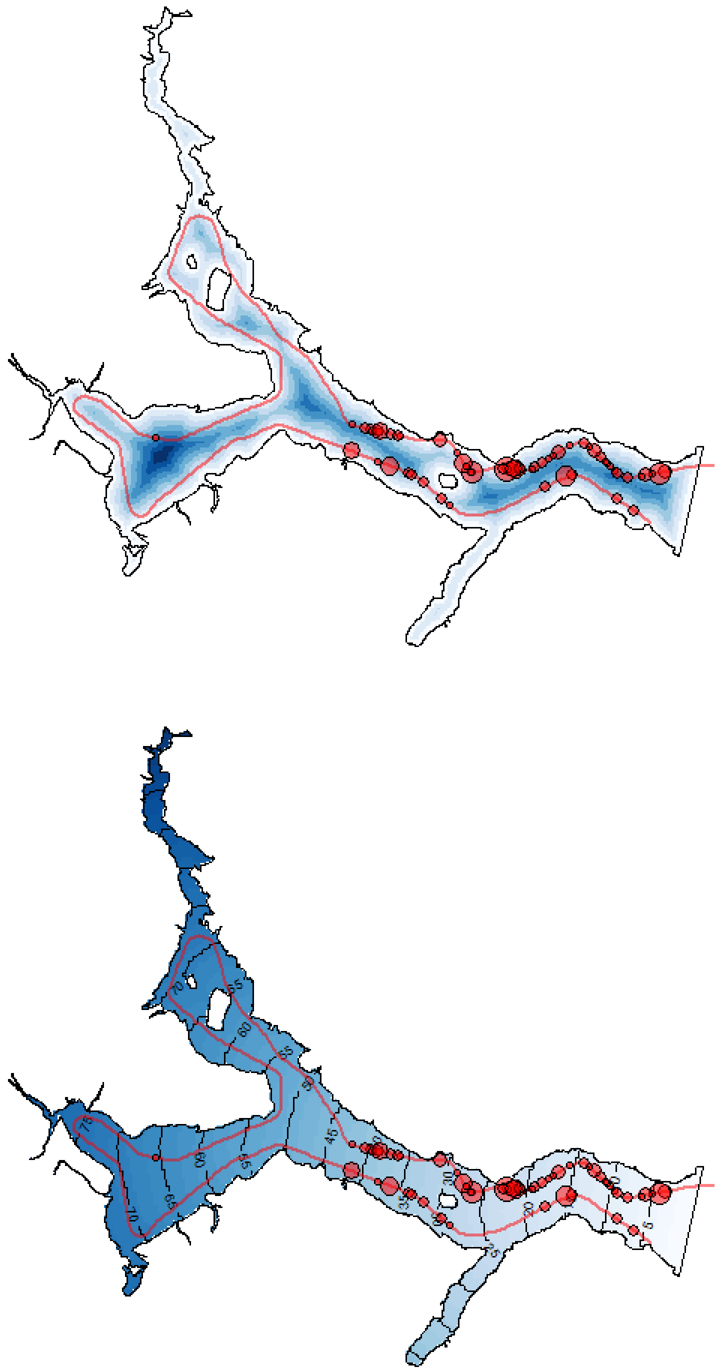

Figure 6. Example of covariates "distance to shore" (top) and "distance to fiord mouth" (bottom), computed for Mackinson Inlet (PSU 3 of Smith Sound Fiord stratum). Contour lines on bottom map in kilometres. Red line: track of aircraft. Red circles: sightings of narwhal groups (larger circles indicated larger group size).

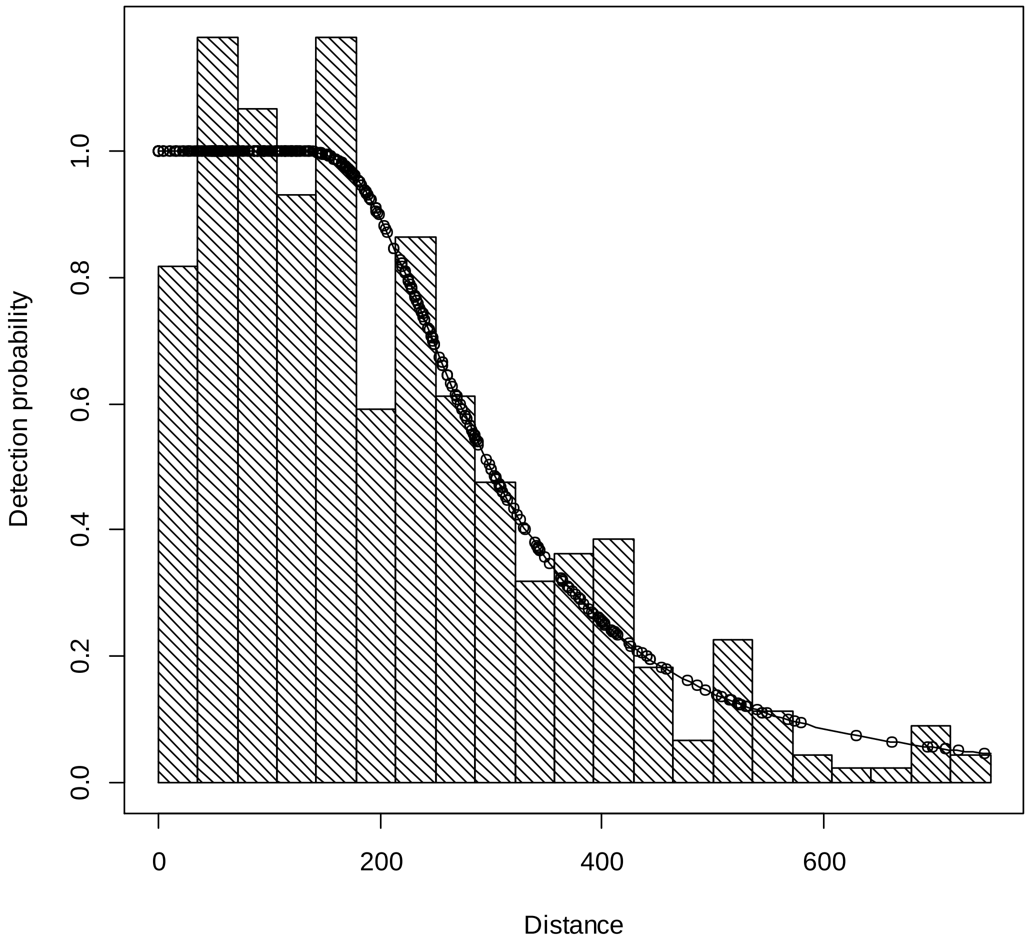

Figure 7. Histogram of perpendicular distances of narwhal sightings in all fiord strata, with fitted hazard-rate detection function. Data were right-truncated at 750 m. No left truncation was applied.

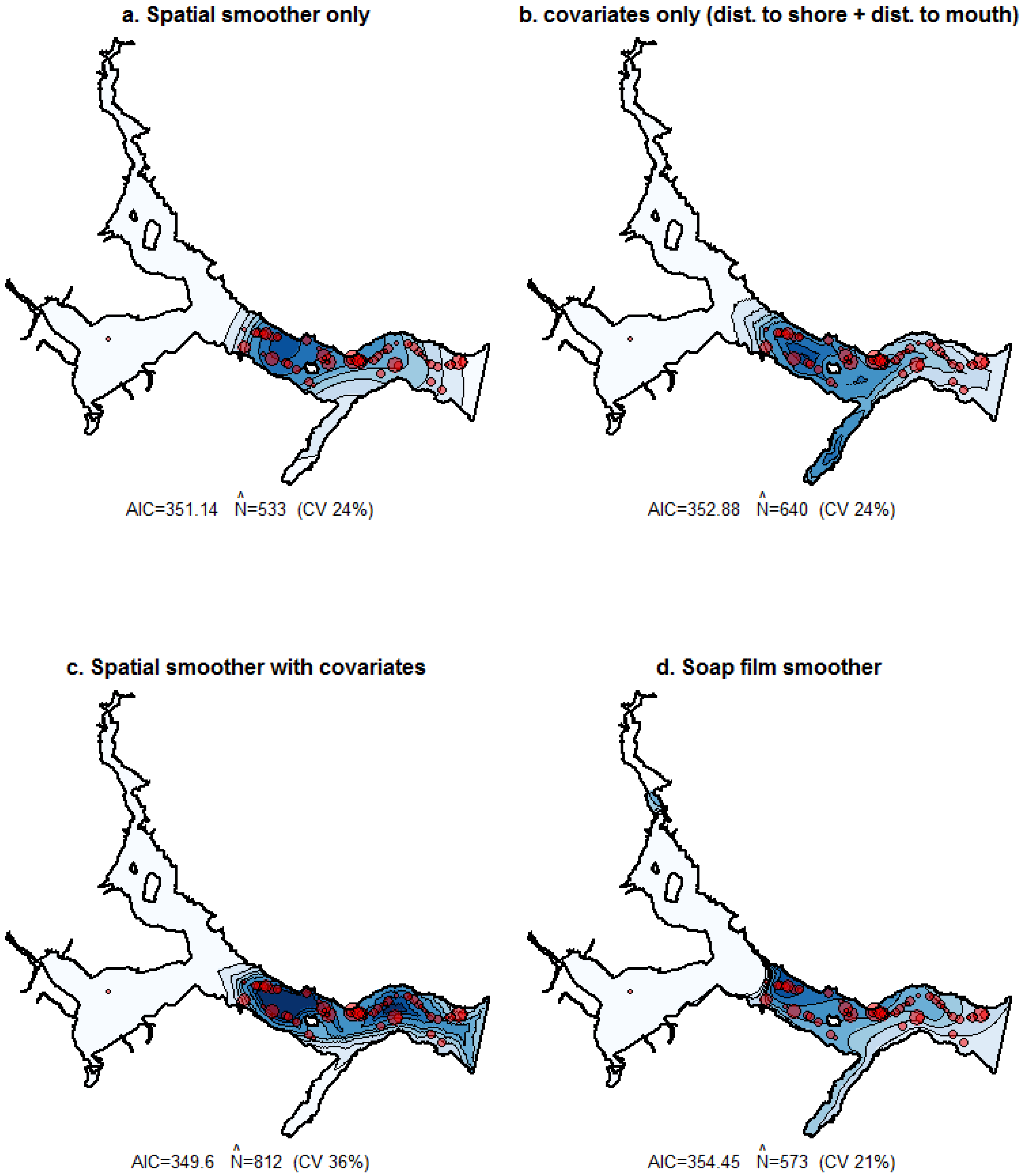

Figure 8.Examples of density spatial models applied to sighting data in fiord SSF03 (Mackinson Inlet). Red circles: sightings of narwhal groups. Darker shading indicates higher predicted density.
$\widehat{N}$ = estimated surface abundance.

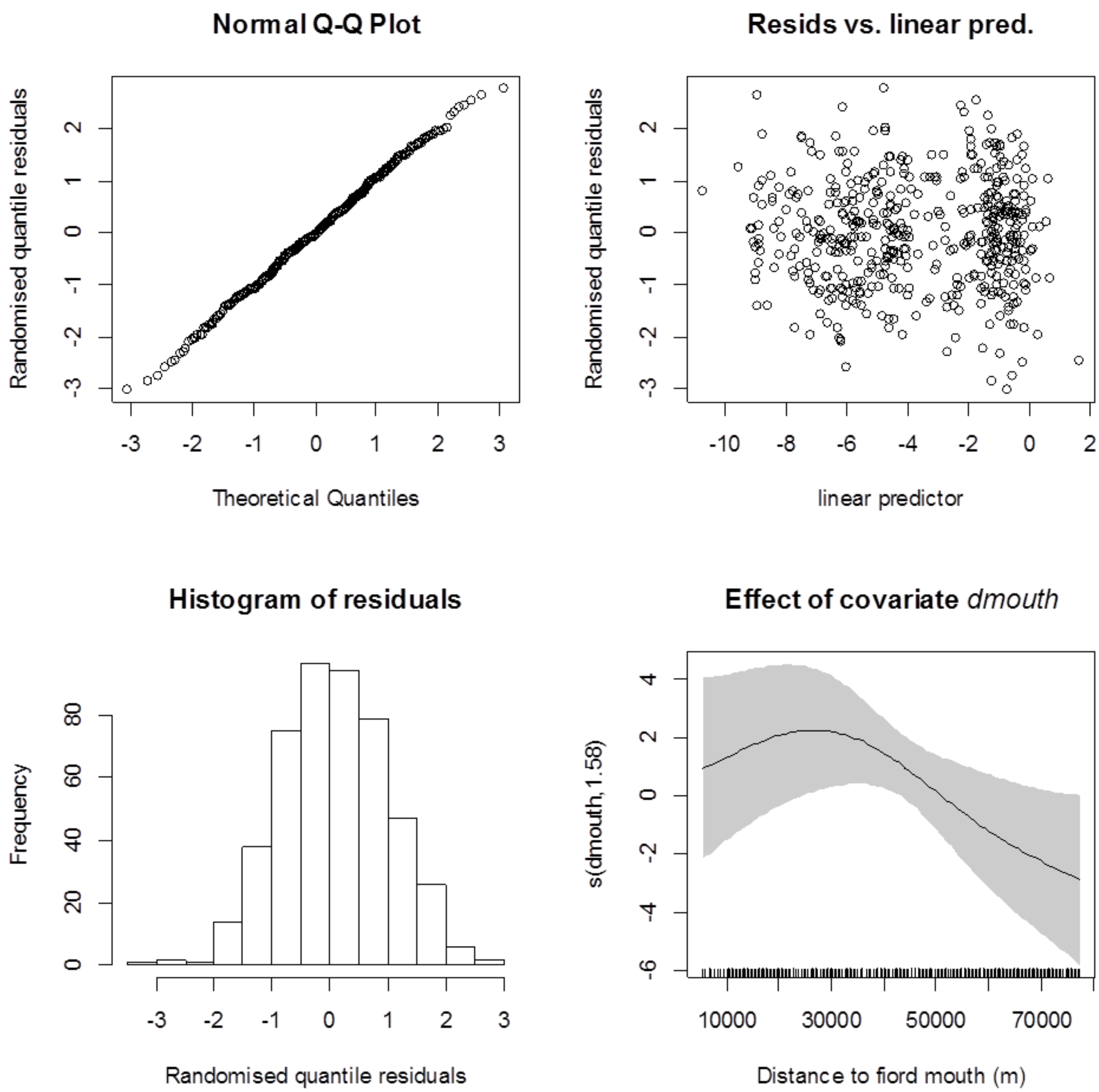

Figure 9.Top row and bottom left: Diagnostic plots of randomised quantile residuals for the density spatial model fitted to the sighting data in fiord SSF03, using a Duchon splines spatial smoother and covariate "distance to fiord mouth". Bottom right: smooth function of the covariate in the GAM.

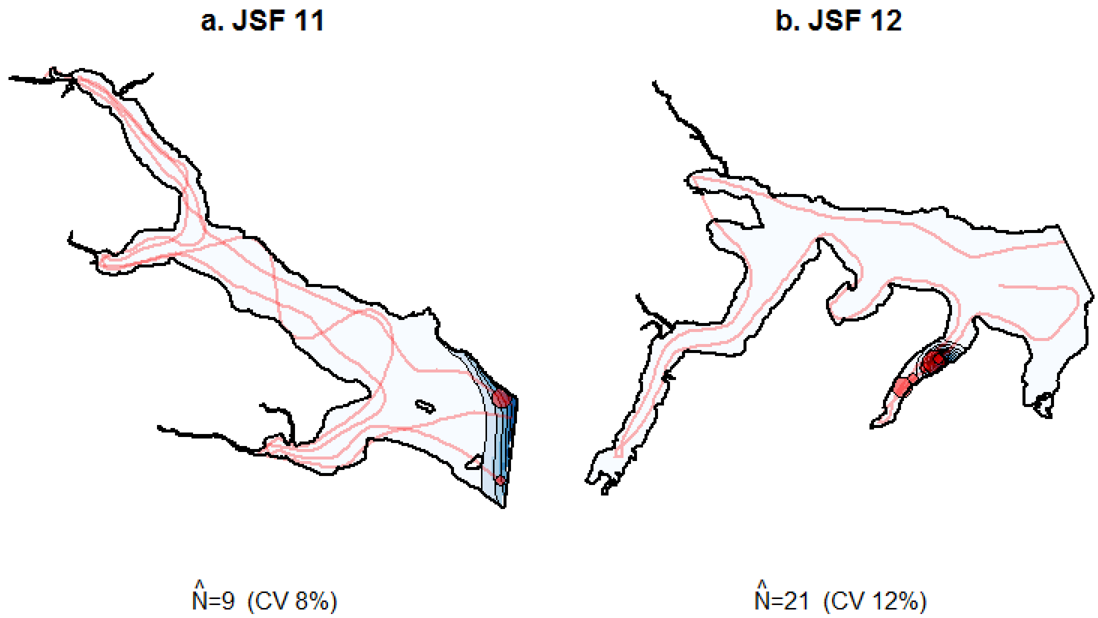

Figure 10. Spatial density surfaces of narwhal abundance in Jones Sound fiords. Red line: track of aircraft. Red circles: sightings of narwhal groups. Darker shading indicates higher predicted density. $\widehat{N}$ = estimated surface abundance.

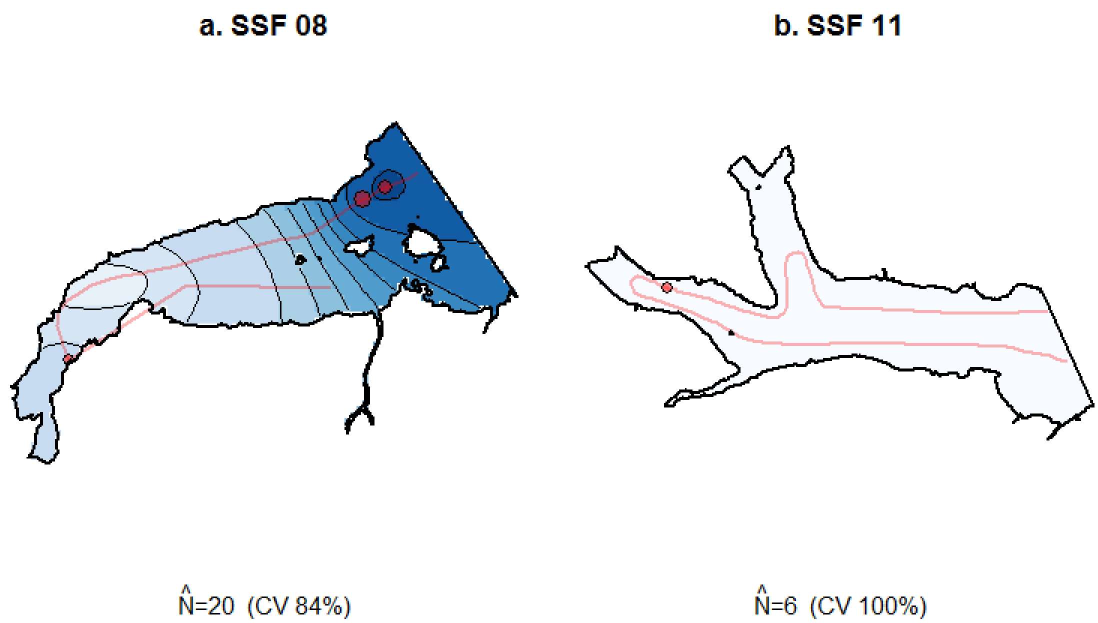

Figure 11. Spatial density surfaces of narwhal abundance in Smith Sound fiords. Red line: track of aircraft. Red circles: sightings of narwhal groups. Darker shading indicates higher predicted density. $\widehat{N}$ = estimated surface abundance. SSF 11 was not fitted with a DSM because there was only one sighting.

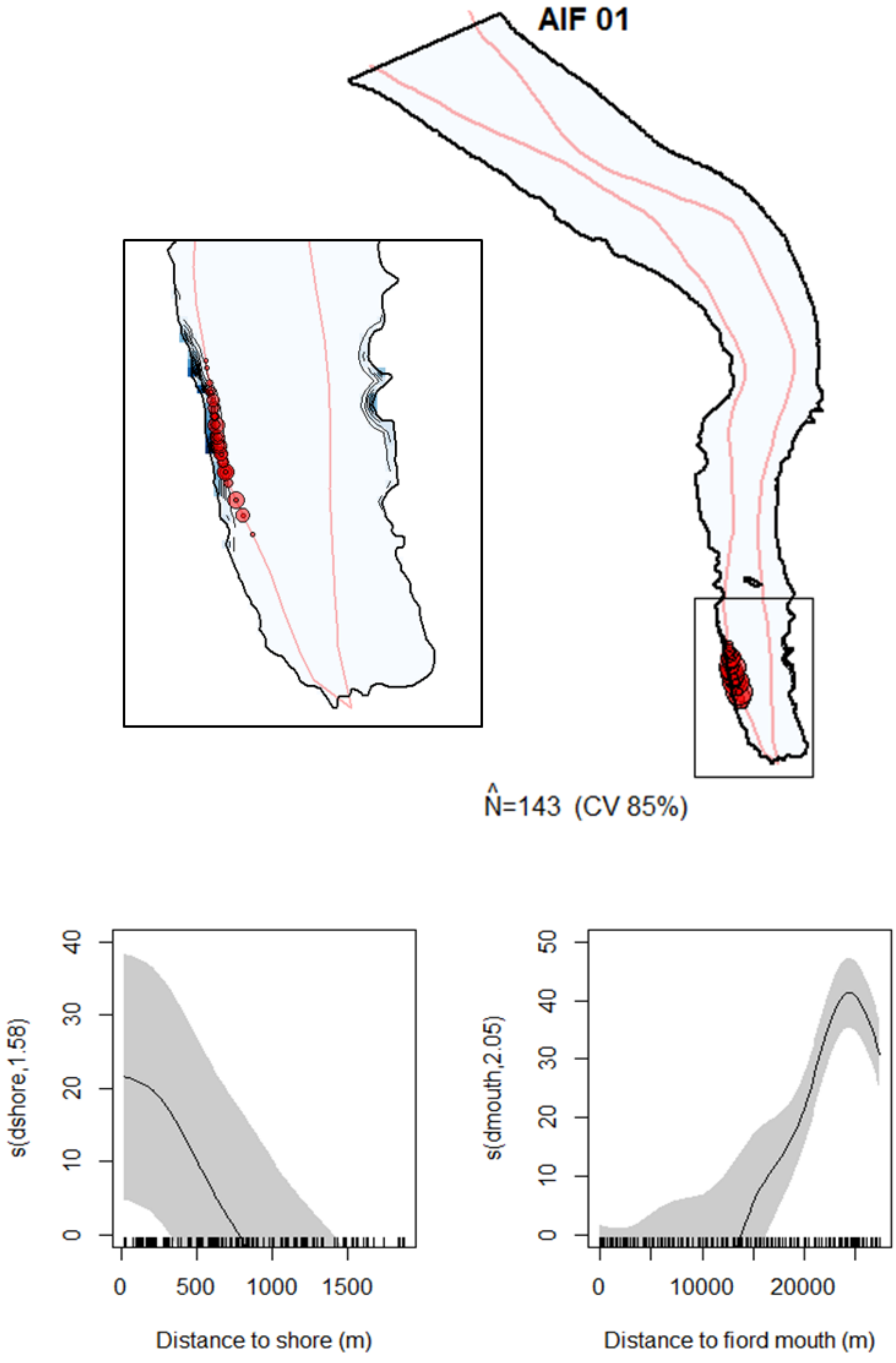

Figure 12.Top: spatial density surfaces of narwhal abundance in Admiralty Inlet fiord AIF01. Red line: track of aircraft. Red circles: sightings of narwhal groups. Darker shading indicates higher predicted density. $\widehat{N}$ = estimated surface abundance. Inset: enlarged map of the area where narwhals were observed. Bottom: smooth functions of the covariates in the GAM.

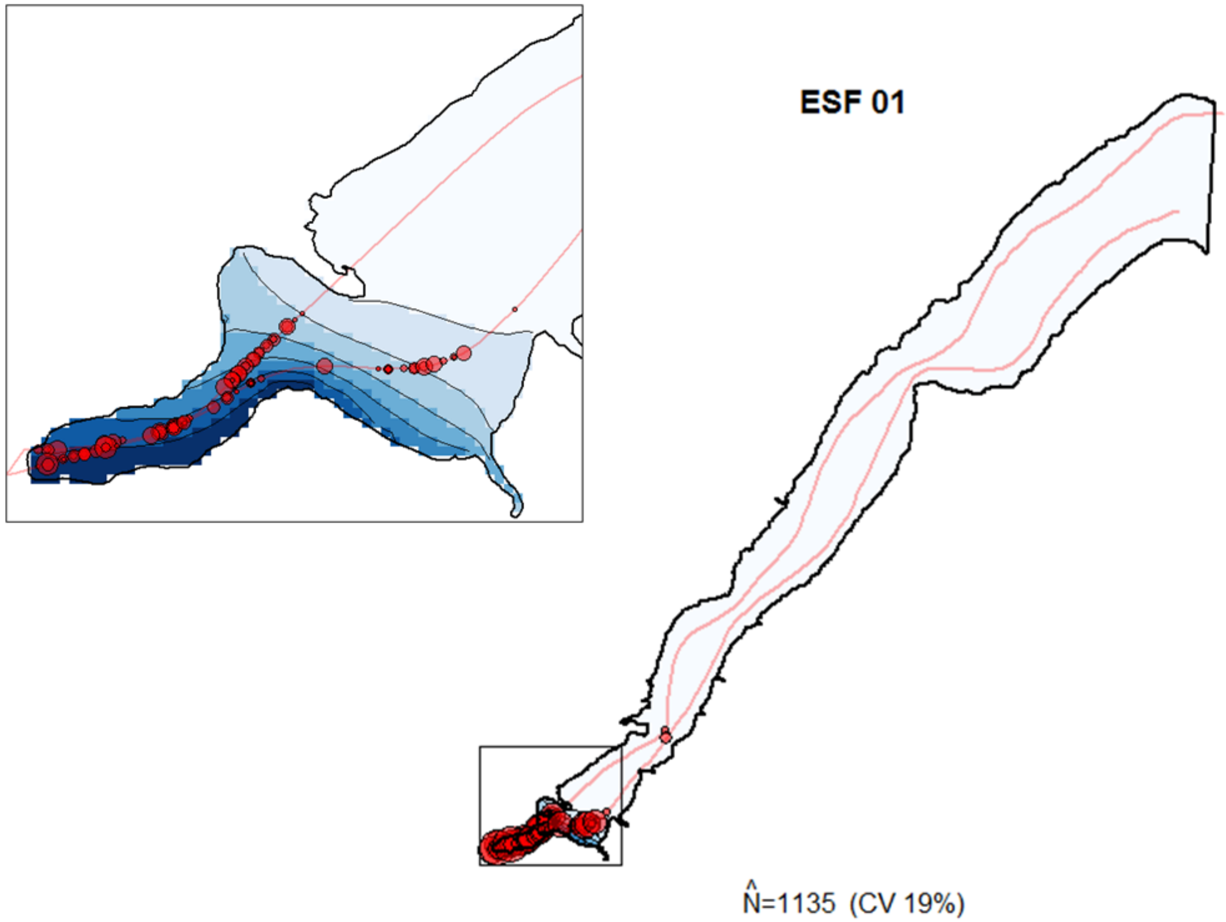

Figure 13.Spatial density surfaces of narwhal abundance in Eclipse Sound fiord ESF01. Red line: track of aircraft. Red circles: sightings of narwhal groups. Darker shading indicates higher predicted density. $\widehat{N}$ = estimated surface abundance. Inset: enlarged map of the end of the fiord, where a large concentration of narwhals was observed.

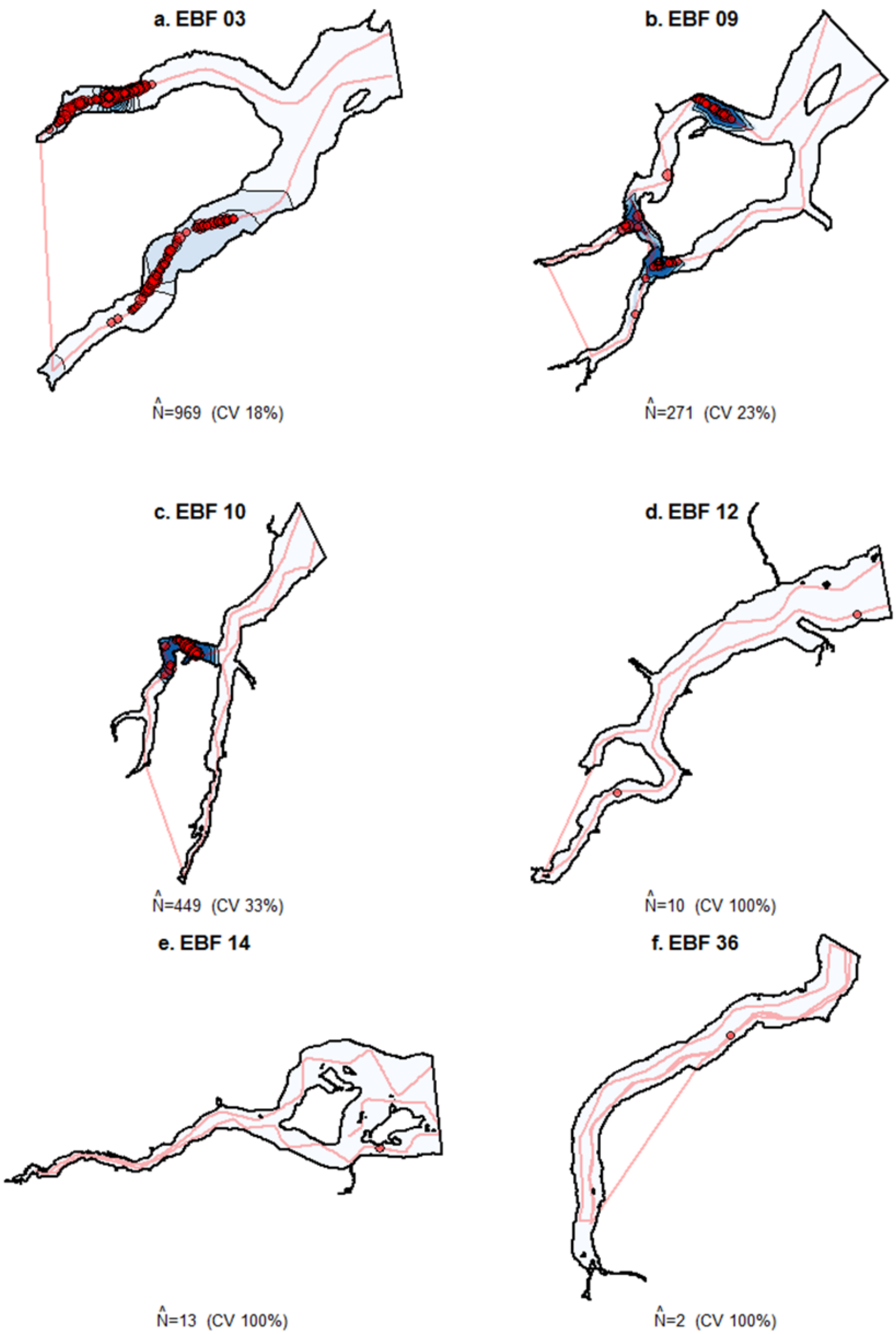

Figure 14.Spatial density surfaces of narwhal abundance in East Baffin Island fiords. Red line: track of aircraft. Red circles: sightings of narwhal groups. Darker shading indicates higher predicted density. $\widehat{N}$ = estimated surface abundance.