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Harvest allocation modelling for narwhal (*Monodon monoceros*) stocks shared between eastern Canada and West Greenland

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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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TABLE OF CONTENTS

ABSTRACT

Narwhals (*Monodon monoceros*) from the Baffin Bay population overwinter in the Davis Strait and Baffin Bay and migrate in the summer to fiords and inlets in northern Canada and West Greenland. Based on these summer aggregations, the population is subdivided into stocks for assignment of hunting quotas to individual communities to ensure sustainability of the local aggregations. Previously, stocks have been managed independently of one another, but many animals from the summer stocks are available to hunters in other regions during the migration and winter periods. As a result, a model which considers mixing of stocks is required to ensure quotas are sustainable. We present a model for the exploitation of narwhals in Canada and western Greenland. The model consists of two parts, one that develops the connection between stocks and hunting areas and allocates catches to the different summer aggregations (referred to as the stock exchange model), and one that analyzes the impacts of these catches on the population dynamics of the eight narwhal stocks (referred to as the population dynamics model). We present an example of the model output using abundance estimates and catch statistics from Canada and West Greenland. The stock exchange model could be used in the future to assess the sustainability of catch levels for all stocks. Regarding the population dynamics model, for some stocks there is little information on abundance or distribution and in these cases, rather than using the population dynamics model, a Potential Biological Removal (PBR) can be calculated to determine sustainable catch levels, with the stock exchange model used to determine how catches will distribute across the various stocks. For stocks with sufficient information, modelling using both the stock exchange and a population dynamics model could be useful for determining sustainable catch levels. The population dynamic stock exchange model can advise on catches from the main hunting areas and assess how these are influencing the different stocks; how these catches can be allocated to individual communities in Canada and Greenland will have to be determined with the support of co-management groups. Furthermore, there is a need to develop reference points and corresponding stock status zones using a Precautionary Approach framework that can then be applied to narwhal population management in Canada.

INTRODUCTION

Narwhals (*Monodon monoceros*) are part of an annual subsistence narwhal hunt in the Arctic in both Canada and Greenland. There are two populations of narwhals that frequent Canadian waters. The largest population, referred to as the Baffin Bay population, has approximately 140,000 individuals (Doniol-Valcroze et al. 2015) and spends summers in the inlets and fiords of northeastern Canada and western Greenland. The other population, which is spatially and genetically distinct from the Baffin Bay population, is located in northern Hudson Bay in summer and southern Davis Strait in winter (Richard 1991, Petersen et al. 2011) and is not considered in this modelling exercise. Typically narwhals show fidelity to the same summering regions year after year (Dietz et al. 2001, Heide-Jørgensen et al. 2002, Heide-Jørgensen et al. 2003, Dietz et al. 2008, Watt et al. 2012) and because of this, individual summer aggregations of the Baffin Bay population have been identified (referred to as stocks) and are managed independently of one another. There are four defined narwhal stocks in the Baffin Bay population in northern Canada: Admiralty Inlet, Somerset Island, Eclipse Sound, and East Baffin Island stocks, and two putative stocks, the Smith and Jones sound stocks (Doniol-Valcroze et al. 2015) (Figure 1). In West Greenland there are two defined stocks from the Baffin Bay population known as the Melville Bay and Inglefield Bredning stocks (Heide-Jørgensen et al. 2013) (Figure 1).

Narwhals are hunted in a number of communities across the Canadian Arctic and West Greenland (Figure 2). In Canada, the hunt occurs primarily in the summer months, but individuals hunted from the Baffin Bay population spend the winter in the Davis Strait and Baffin Bay, and pass through a number of communities on the migration to and from their wintering areas where they are available for hunting (Heide-Jørgensen et al. 2013). In addition, whales from some of the Canadian stocks are also available to hunters in West Greenland on the fall and winter hunting grounds (Heide-Jørgensen et al. 2013). Historically, the stocks have all been managed independently of one another, but because of the mixing of stocks during the migration and on the fall and winter grounds, a framework that considers stocks to be shared across multiple communities of the two countries is needed to ensure the conservation and sustainable management of narwhals. In this way, the risk of overexploitation of local stocks can be decreased.

Here we present a two-step modeling approach for the exploitation of narwhals in Canada and West Greenland based upon Witting (2017). The model consists of two components; the first relates the number of narwhal in each summering aggregation (or stock) to the availability of narwhals to hunters in hunting areas and seasons and allocates catches to the different stocks (referred to as the stock exchange model). The second model component (referred to as the population dynamics model) analyzes the impacts of these catches on the population dynamics of the eight narwhal stocks. The two models interact and thus run together, iteratively, until the stock specific catch histories estimated by the stock exchange model and the abundance trajectories that are estimated by the population dynamics models converge.

DEVELOPMENT OF MODELS

STOCK EXCHANGE MODEL

The joint working group of the North Atlantic Marine Mammal Commission (NAMMCO) and the Joint Canada Greenland Commission on Narwhal and Beluga (JCNB) developed a stock exchange model to allocate catches taken in different hunting regions and seasons to eight summer aggregations (stocks) of narwhals in eastern Canada and West Greenland (NAMMCO 2016). The model provides a mechanism for assigning all hunted animals to stocks based on existing data and expert knowledge, where it is assumed that each individual belongs to a specific stock (defined by their summer distribution). The matrix produced, referred to as the stock exchange matrix, estimates the proportion of whales in each stock that is available to hunters in different regions and seasons.

Satellite telemetry data and phenology of occurrence and catches are used to determine the proportional availability of each stock in the different hunting sites, for each season. These proportions are calculated as the number of tagged whales from a stock that visits a hunting site during the hunting season (x) divided by the total number of tagged whales from that stock that were transmitting during that season (n). Decisions to ascertain whether a tracked whale entered the area "available" to the hunters of a given community are based on observation of its trajectory and expert opinion.

Some hunting grounds only have summer hunts and the stock summering at these hunting grounds is identified as supplying the hunt. This implies a defined fixed proportional availability of 1 for the summer hunt occurring within their own summer range, with no uncertainty ("known hunts"); however, in cases with movements to other hunting areas, there is generally uncertainty around the proportional availability. This uncertainty is quantified by assuming that the number of whales observed in a certain area follows a binomial distribution with a sample size equal to the number of transmitting tags (n) and a probability equal to the true proportion of the whales in that stock that visit the area. This true proportion is unknown but is estimated using a beta distribution (Beta(x+1, n-x+1)).

When no movements are documented between a particular stock and a hunting ground, we distinguish between movements that are deemed extremely unlikely based on expert knowledge and movements that are considered unlikely, but not impossible. The former ("defined zeros") are assigned a proportional availability of 0, with no uncertainty. The latter ("probable zeros") are also assigned a proportional availability of 0, but are given a Beta(1, Z) probability distribution, where Z is an uncertainty parameter that can vary from 1 to infinity (larger values represent higher certainty). Finally, there is the case of "probable availability", which is parameterized by a Beta(Z, 1) distribution, and represents cases where there are no documented movements, but a strong connection is expected based on expert opinion.

The eight columns of the stock exchange matrix are the individual summer stocks of Smith Sound, Jones Sound, Inglefield Bredning, Melville Bay, Somerset Island, Admiralty Inlet, Eclipse Sound, and East Baffin Island. The rows represent 24 hunting grounds divided up by region and in some cases also by season; thus, for each stock and hunt there is a cell in the matrix and the matrix is devised so that when transposed and multiplied by a vector of reported takes by each hunt in a year, the number of removals from each stock can be determined (Table 1).

Each cell of the stock exchange matrix, **A**, has the value:

$$\mathbf{A}_{ij} = \frac{\mathbf{P}_{ij}\, N_i}{\sum_i \mathbf{P}_{ij}\, N_i}$$

Where, $\mathbf{A}_{ij}$ is the proportion of the *j*th hunt that is assigned to the *i*th stock; $\mathbf{P}_{ij}$ is the proportional availability of the *i*th stock to the *j*th hunt; and N_i is the abundance of the *i*th stock.

This model assumes that for each stock there is a portion between zero and one, $\mathbf{P}_{ij}$, that is available to hunters during the hunting period on the hunting grounds. Each individual that is available is then at equal risk of being taken in the hunt. The sum of the $\mathbf{P}_{ij}$, however, do not have to add up to 1 because the same stocks can be hunted in several regions across their migration.

To set up the proportional stock exchange matrix, **P**, we review each cell so that each cell in the matrix is given one of five designations:

1. Defined zero: This designates cells that represent impossible situations such as a summer hunt that was not at a summering ground (e.g., a narwhal hunted in summer in Resolute could not come from the Smith Sound stock by definition since they are summering in Smith Sound) and to hunts in areas that could not have originated in a particular summering ground based on known movements.
2. Probable zero: This designates cells in which a stock was unlikely to be hunted but proximity during the hunting season did not rule out takes.
3. Partial hunt: This designates cells with tag data showing a portion of the stock is available to hunters or no tag data indicates availability, but hunting is possible due to proximity.
4. Probable hunt: This designates cases where proximity between the summering and hunting grounds makes migration to the hunting ground almost certain, but where no exchange of whales from satellite telemetry has yet been identified.
5. Defined hunt: This designates cells representing hunts on summering grounds or known wintering areas of stocks.

Two versions of the proportional stock exchange matrix are considered with different treatments of the probable values. In the fixed version both “defined” and “probable” zeros and ones are given the value zero or one, and the “partial hunts” are given a set of random proportions that are drawn from the beta distribution of the tags that travel into the hunting areas. The second version includes a set of random proportions also for the “probable” values, with the variance (uncertainty) of the beta distribution increasing with smaller values of the Z parameter. The first matrix is used for the base case, and the second for sensitivity analysis in relation to our uncertainty about the connectivity between the hunting and summering grounds.

POPULATION DYNAMICS MODEL

Population dynamic models are fitted to relative and absolute abundance estimates of narwhals in the identified stocks in Canada and West Greenland, with separate and independent models for each stock. All models use a Bayesian modeling framework that is age- and sex-structured with an even sex ratio and a Pella-Tomlinson form of density regulation on the birth rate described below (Pella and Tomlinson 1969, Witting and Born 2005).

The number of animals in age classes larger than zero is

$$N^{m/f}_{t+1,a+1} = \left(N^{m/f}_{t,a} - C^{m/f}_{t,a}\right) p \; 0 \le a \le x-2$$

$$N^{m/f}_{t+1,x} = \left(N^{m/f}_{t,x} - C^{m/f}_{t,x}\right) p_x + \left(N^{m/f}_{t,x-1} - C^{m/f}_{t,x-1}\right) p_{x-1}$$

where x = 15 is the lumped age class of animals 15 years and older, $N^{m/f}_{t,a}$ is the number of males/females of age *a* at the start of year t, $C^{m/f}_{t,a}$ is the catch of males/females (*m/f*) of age *a* during year *t*, with the age distribution of the catches being sex-specific and proportional to the product between the age- and sex-specific abundance $N^{m/f}_{a}$ and an age- and sex-specific catch selectivity factor $C^{m/f}_{a}$. The proportionality of the age-structured catch to the product $N^{m/f}_{a} C^{m/f}_{a}$ can be obtained for all age classes only when the total catch is so low that the catch from any sex- specific age class does not exceed the abundance in that class. If instead the estimated catch exceeds the abundance in an age class, the catch in that age class is set to the abundance of that class, while the remaining catches are reallocated to the remaining classes in proportion to the age- and sex-specific selectivity factors and abundances. If necessary, this redistribution of the catches continues until it is possible to redistribute the remaining catches in an age and sex structure where the catch from any class does not exceed the number of individuals in that class.

The annual survival rate (p) applies to all animals older than two years, and the survival during the first year is p_0. The number of births at the start of year t is

$$B_t = \sum_{a=a_m}^{x} B_{t,a}^{f} + B_{t,a}^{m}$$

where a_m is the age of reproductive maturity given by the first year with reproduction, and $B_{t,a}^{f}$ and $B_{t,a}^{m}$ are the number of female and male births in age class a. These births are

$$B_{t,a}^{f} = \vartheta b_t \widetilde{N}_{t,a}^{f}$$

$$B_{t,a}^{m} = (1-\vartheta) b_t \widetilde{N}_{t,a}^{f}$$

where ϑ is the fraction of females at birth, b_t is the birth rate for mature females at time t, and $\widetilde{N}_{t,a}^{f}$ is the number of mature females in age class a at the start of year t, defined as

$$\widetilde{N}_{t,a}^{f} = \begin{cases} 0 \; if \; a_m > a \\ \widetilde{N}_{t,a}^{f} \; if \; a_m \leq a \end{cases}$$

The component of the population that imposes density regulation is the one plus component

$$\widehat{N} = \sum_{a=1}^{x} N_a^f + N_a^m$$

and the density regulation on the birth rate b_t takes the Pella Tomlinson form

$$b_t = b^* + [b_{max} - b^*]\,[1 - (N_t/N^*)^z]$$

where b^* is the birth rate at population dynamic equilibrium N^*, b_{max} is the maximal birth rate, and z is the compensation parameter.

Although not explicit parameters of the model, the maximum sustainable yield level (msyl) and the maximum sustainable yield rate (msyr) are treated as parameters in the analysis. The msyl depends mainly on the compensation parameter z, and to speed computation the three parameters are defined relative to the mature component of the population, denoted by the symbol ~. Hence, the birth rate is

$$b = b^* + (b_{max} - b^*)\big(1 - \tilde{d}^z\big)$$

where $\tilde{d} = \widetilde{N}/\widetilde{N}^*$ is the depletion ratio. Given no changes in the sex ratio with age, from the steady state $\widetilde{N}_{t-1} = \widetilde{N}_t$ with $\widetilde{N}_{t-1} = \widetilde{N}_t p \vartheta b - s\tilde{y}$, the sustainable yield is

$$s\tilde{y} = \widetilde{N}[p_m \vartheta b - (1-p)]$$

where $s_m = \prod_{i=0}^{a_m-1} s_i$ is survival from birth to age of reproductive maturity. The $s\tilde{y}r$ relative to the depletion ratio $\tilde{d}$ is then

$$s\tilde{y}r = \tilde{d}\big[p_m \vartheta b_{max} - p_m \vartheta (b_{max} - b^*)\tilde{d}^z - (1-p)\big]$$

Solving $\frac{ds\tilde{y}r}{dd} = 0$ for $\tilde{d}$, the $ms\tilde{y}l$ is:

$$m\tilde{s}yl = \left[\frac{p_m \vartheta b_{max} - \ (1-p)}{p_m \vartheta (b_{max} - b^*)\ (1-z)}\right]^{\frac{1}{z}}$$

With the $m\tilde{s}yr$ being the $s\tilde{y}r$ at the $m\tilde{s}yl$.

PRIOR DISTRIBUTIONS

Prior probability distributions were assigned to initial abundance (N_0), the population dynamic equilibrium abundance (N^*), the yearly survival (p), the first year survival (p_0), the birth rate (b), the age of the first reproductive event (a_m), the female fraction at birth (ϑ), the density regulation (γ), the catch history (c_h), and the abundance estimate bias (β_a) (Table 2). Most of the priors in the model are uninformative and uniform (Table 2). The fraction of females at birth (ϑ) was a fixed parameter across all model iterations and was set to 50%. The yearly survival rate was a uniform parameter with minimum and maximum values of 0.97 to 1, while the first year survival rate was assumed to vary from 0.5 to 1. The birth rate for narwhals followed a beta distribution and of 62 narwhals from east and west Greenland, 26 were found to be pregnant (Garde et al. 2015). The age of the first reproductive event was a uniform distribution varying from 8-12 years and was subjectively assessed based on ages of immature females, corpora counts, and ovarian growth in female reproductive tracts from east and west Greenland (Garde et al. 2015).The shape parameter (γ) of the density regulation function is set to values between two and four to obtain a maximum sustainable yield (*msy*) around a maximum sustainable yield level (*msyl)* of about 60% of the carrying capacity (N^*) which is considered reasonable for a cetacean, and the growth potential of the population was estimated by the maximum sustainable yield rate (*msyr).* A discussion of how the catch histories were input into the model is described below.

ABUNDANCE ESTIMATES

Abundance estimates for the different stocks are required as inputs for the models. Abundance estimates from survey data for each stock are corrected for availability bias (Table 3). Perception and availability bias were not applied in the early survey years, and therefore surveys from Admiralty Inlet (1975 and 1985), Somerset Island (1981), and Inglefield Bredning (1985 and 1986) are multiplied by 2.92 (CV = 0.05; Richard et al. 2010) to make them comparable with later surveys that include corrections for perception and availability bias (Table 2).

For stocks with only one or two abundance estimates available (Smith Sound, Jones Sound, Eclipse Sound, Baffin Island) and Admiralty Inlet, which had a very low exploitation rate in the beginning of the period, we assume their abundance was close to the carrying capacity in 1970. For the remaining stocks (Inglefield Bredning, Melville Bay and Somerset Island), with a somewhat larger early exploitation, the abundance in 1970 was set to be lower than the carrying capacity.

HUNTING REMOVALS

Catch histories for narwhals hunted in communities across the central Canadian Arctic and West Greenland are included to describe the total annual removals (landed catch plus loss rate) for the different hunting communities (Table 4). The loss rate used for Canadian catches is assumed to be 1.28 (Richard 2008), while that used for Greenland was 1.3 for all regions except Qaanaaq and Melville Bay-Upernavik areas where 1.15 is used since roughly half of the whales taken there are under requirements to be hand-harpooned before they can be shot which reduces the loss rate (Heide-Jørgensen and Hanse 2012). Catches were assumed to be taken evenly from females and males as most catches were reported with no sex, and they were taken in proportion to the age-structure in the population, except that no calves were taken.

EXAMPLE MODEL OUTPUT

Each annual stock exchange matrix depends on the abundance in the previous summer and then provides the removals for the stock abundance projection in the following summer. In order to allocate the catches from the different hunts to the different stocks, the model requires an abundance estimate for each stock in each year. These abundance estimates are needed to estimate the relative availability of narwhals from each stock to the different hunts, so that catches can be allocated to the stocks. Changes in the abundance of each stock in each year depend on both the allocated catches and density dependence within the population. Thus, a direct approach would begin each population in 1970, calculate the stock exchange matrix and removals from each stock, then project each stock forward a year.

However, in place of the direct iteration described above, we have adopted a computationally more expedient approach in which the catch histories in a run of the population dynamics models for the stocks were estimated by a run of the stock exchange model over the complete catch history starting in 1970 (Figure 3). The annual abundance matrix in the initial run of the stock exchange model is constructed as linear transitions between the abundance estimates (listed in Table 3). In subsequent runs, the abundance matrix is given by the abundance trajectories that the previous run of the population dynamics model estimated for the different narwhal stocks, given the catch histories estimated by the previous run of the stock exchange model (Figure 3). This iteration of the two models was conducted three to five times until the catch histories and abundance trajectories converged (Figure 4).

The catch histories of the hunting grounds are given as a single time series of best estimates, the estimated catch histories for each stock is a distribution that reflects the uncertainty in the allocation of the different hunts between the eight stocks. This uncertainty results from uncertainty in the availability of each stock to each hunt and uncertainty of the abundance of each stock (Figure 5). A distribution of the removals from each stock is developed and the catch histories in the population modelling are drawn from these distributions in order to capture the uncertainty in the allocation of catches.

The complete catch distributions over time, as estimated by the stock exchange model (Figure 6), were simplified to make them easier to handle as priors in the population dynamics model. These prior distributions were described by a minimum catch history (c_{min}, represented by the 1st percentile of this distribution over time) and a maximum catch history (c_{max}, represented by the 99th percentile), and the distribution of possible total removals as estimated by the stock exchange model for 2011 (Figure 5). The latter distribution was then rescaled to run from zero to one, with a value (x) drawn at random from the distribution for each parameterisation, with the resulting catch history calculated as:

$$c_t = c_{min,t} + x(c_{max,t} - c_{min,t})$$

EXAMPLE MODEL RESULTS

The run of the model results in estimated trajectories for the eight summer stocks (Figure 7), and posterior parameter estimates (Table 5; plots of the posterior and realized prior distributions are provided in Appendix A). We assume a management objective aiming to increase populations if they are below the maximum sustainable yield level and allowing for catches up to 90% of the maximum sustainable yield if the population is above the maximum sustainable yield level. The total allowable landed catches (TALC) for the different stocks that will meet this criterion with probabilities from 0.50 to 0.95 are calculated (Table 6). Two examples of possible total allowable takes for the different hunts are provided (Table 7) and the associated estimates of the probabilities that these takes from 2015 to 2020 will allow the management objective to be fulfilled for the different stocks is presented (Table 8). The 90% confidence limits around the probabilities of meeting management objectives reflect the uncertainty about which animals/stocks are supplying a given hunt.

DISCUSSION

The stock exchange and population dynamics models are important tools for allocating catches to specific stocks and to evaluate how various quotas will affect management objectives, whether those aim to increase populations (for those below the maximum sustainable yield level), or to continue to manage populations (for those above the maximum sustainable yield). The population dynamics model allows an evaluation of how different total allowable takes for the different hunts impact the management objectives and can provide guidance on quotas that meet management goals. The population dynamics model was run with example probabilities of population increase from 50% to 95% over a 5 year period to illustrate how quotas could meet different management objectives; however, the models themselves do not inherently set management objectives, these should be clearly defined beforehand. The decision on objectives can change the quotas of narwhal; thus, determination of the probability of increase that meets the management objectives is vital.

The model will estimate the probabilities of increase for the different summer stocks, but it does so based on catches that are taken in the various communities that hunt whales. Setting hunting levels in the different communities will need to be determined at the management level, but the model can guide these decisions through calculation of the associated risks to the different stocks of narwhals.

Narwhals are considered to be data poor, therefore, advice on Canadian catch levels are based on the Potential Biological Removal (PBR) method divided by a struck and lost rate (Richard 2008). PBR is a conservative approach that sets a threshold for human-induced mortality; when removals are below the threshold, the population is likely to increase above, or maintain itself at, the optimum sustainable population (Wade 1998). The method is considered robust to biases in parameter inputs and is the preferred method when stocks are considered data-poor (Hammill and Stenson 2007). A limitation of PBR calculations is that they only provide a single threshold value and do not give fisheries managers an opportunity to choose their risk tolerance to stock decline. Prior to 2011, PBR estimates for the Canadian narwhal stocks considered stocks completely independent of one another, using survey abundance estimates from summer aggregations to calculate future TALCs which were then allocated to communities that hunt the summer aggregation. However, as discussed previously, mixing of stocks occurs on the migration route and on the winter grounds, and animals from summer stocks are then available to hunters in communities outside the summering region. Prior to 2011, allocation of the catches from the calculated PBR did not take into account mixing of stocks; and this was a problem since satellite telemetry data had shown that several stocks, often in fall and winter, contribute to the hunt in communities that are located far away from the summering grounds.

To address this, in 2011 a stock allocation tool solely developed for Canadian catches was developed and considered stocks overlapping in range based on a spatial model of the source and degree of stock mixtures that are hunted (Richard 2011). The allocation model produced possible solutions that maximize the catch, particularly for communities with large historic narwhal catches, while minimizing the risk of over-exploitation of any one stock (Richard 2011).

Since the proportion of animals belonging to any particular stock in the non-summer community hunt is unknown, the model assumed that non-summer catches are taken in proportion to the size of each stock relative to the total number of animals in the mixture of stocks. Richard (2011) analyzed different proposed TALCs to evaluate optimal landed catches assuming different proportions of narwhal were hunted from the different Canadian stocks. The risk analysis of the proposed TALCs showed that in general, reducing the community allocations to 80-90% of the optimized catches significantly lowered the risk of exceeding a stock's TALC (DFO 2013). The downside of this allocation model is that it does not account for whales that may be hunted by communities in West Greenland as well, and does not directly incorporate information from telemetry data that suggests overlap.

The model presented here is an improvement over previous methods since it takes into account the combination of information that each country (Canada and Greenland) has collected about the narwhal stocks. The model integrates assessments of stocks that are shared by Canada and Greenland, and it accounts for the movement of narwhals from different stocks among potential hunting areas and does not assume that the availability of narwhals to communities outside their summering range depends solely on the relative abundance of each stock. The model also uses a Bayesian approach that provides probability distributions useful for providing different catch estimates depending on the probability level of the management objectives. These levels may differ between stocks allowing for joint management between Canada and Greenland even in situations where the two countries have different management objectives. For instance, in this example we have set the maximum sustainable yield level at about 60% of the carrying capacity for both countries, but the management goals could be defined differently for each country. Finally, the population model considers biological parameters such as survival rates and birth rates explicitly, which can improve the model output when there is a good understanding of these rates.

For some of the narwhal stocks there are only one or two abundance estimates available. In these cases it may be useful to calculate a PBR for the stock and then use this information with the stock exchange model to assign catches in relation to the availability of narwhals to the different hunting regions and seasons. Alternatively, for stocks with sufficient input data and where the population dynamics are captured by the model, both the stock exchange and population dynamics models could be used to identify sustainable catch levels. In either case, it would be useful to evaluate the outputs of the model using a precautionary approach framework (Hammill and Stenson 2007).

FUTURE RESEARCH

In addition to basic observations of presence and phenology of occurrence, the stock exchange model depends on movement information obtained from satellite tracking animals from the different stocks. Four of the eight stocks (Smith Sound, Jones Sound, Inglefield Bredning, and East Baffin Island) have never had whales tagged and thus no information is available on where these whales travel beyond the hunting grounds. We know that these four stocks supply the summer hunts located in their respective regions, but it is unknown whether they are hunted in other communities in other seasons. In these cases, expert knowledge assisted with assigning the probability of whales encountering other hunting localities, but additional information from satellite tagged whales would greatly improve the model results and certainty. This, however, can be a daunting task in areas that are difficult to travel to, and where narwhal presence and behaviour is unpredictable.

For stocks where telemetry data are available, increasing the number of tagged whales would increase reliability and improve the model. In particular, more tags on whales from Somerset

Island, which has a large population that likely contributes to hunts during the migration and on the summer grounds in Canada, and fall and winter grounds in West Greenland, is needed to answer questions about hunting availability. Overall, analysis of the stock exchange model can be used to identify where tagging efforts could improve the management value of the model.

The population dynamics model could be improved with increased data and more precise inputs. There is uncertainty surrounding the abundance estimates, but as more surveys are done and methods to reduce confidence intervals are improved, the model results will become more reliable. In addition, accurate reporting of catch statistics, information on the sex of animals hunted, and a better estimate of the struck and loss rate specific to different communities and hunting types would assist with improving the model.

The priors that go into the population dynamics model can have large impacts on the model output. For instance, a better estimate of the variance around the birth rates and age at first reproduction for narwhals from different stocks would also improve the model inputs. Additionally, the model is currently set to assume a take of 50% females. This is not the case in all communities and better information on the average take of males and females in all hunting regions, from all years (back to 1970), has the potential to improve the model outputs.

CONCLUSIONS

- A stock exchange model which allocates catches taken in different hunting regions and seasons to eight summer aggregations of narwhals in eastern Canada and West Greenland was developed. The model uses satellite telemetry data and general knowledge on phenology to determine the proportional availability of each narwhal stock to the different hunting sites, for each season, with a level of uncertainty quantified using a beta distribution.
- A population dynamics model that combines hunt and abundance information since 1970 from both Greenland and Canada, and available data on life history parameters was developed. This model explicitly incorporates uncertainty in a Bayesian framework and provides a more complete portrait of population dynamics than is currently available in determining TALC advice for internationally shared stocks in the Baffin Bay narwhal population.
- The stock exchange model can advise on the sustainability of takes from individual stocks given allowable takes across hunting localities in Canada and Greenland.
- The stock exchange model requires specification of management objectives for each stock and hunting ground. These need to be defined to use the model efficiently.
- For stocks with sufficient input data, and where the population dynamics are captured by the model, both the stock exchange and population dynamics models could be used to identify stock catch levels based upon management objectives.
- If the level of stock knowledge is not considered sufficient we recommend calculating a Potential Biological Removal (PBR) for the stock, and then using this information with the stock exchange model to assign catches in relation to the availability of narwhals to the different hunting regions and seasons.
- We recommend the outputs of the population dynamics model for each stock be evaluated using the precautionary approach framework developed for marine mammals in Canada.

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TABLES AND FIGURES

Table 1. Stock exchange matrix for narwhals from different summering stocks to different hunting regions (x/Z; available (x) / total (Z)) (CCA: Central Canadian Arctic, BIC: Baffin Island Central, BIS: Baffin Island South; see Figure 2 for hunt locations). 0 and 1 are fixed values, but ratios are beta distributions (α = x+1; β = n+1), all ratios over Z are sensitive to changes in Z.

Hunt	Season	Smith Sound	Jones Sound	Inglefield Bredning	Melville Bay	Somerset Island	Admiralty Inlet	Eclipse Sound	East Baffin Island
Etah	Spring	1	0/Z	0	0	0	0	0	0
Qaanaaq	Summer	0	0	1	0	0	0	0	0
Grise Fiord	Spring	0/Z	1	0/Z	0	0/Z	0	0	0
Grise Fiord	Summer	0	1	0	0	0	0	0	0
Grise Fiord	Fall	0/Z	1	0/Z	0	0/Z	0	0	0
Upernavik	Summer	0/Z	0	0	1	0	0	0	0
Ummannaaq	Fall	0	0/Z	0/Z	1/9	1	0/42	0/26	0/Z
Disko Bay	Winter	0	0/Z	0/Z	1/7	0/Z	1/42	1/6	0/Z
CCA	Spring	0	0	0	0	1	0/4	0/5	0
CCA	Summer	0	0	0	0	1	0	0	0
CCA	Fall	0	0	0	0	1	7/42	1/26	0
Arctic Bay	Spring	0	0	0	0	1	1	1/5	0
Arctic Bay	Summer	0	0	0	0	0	1	0	0
Arctic Bay	Fall	0	0	0	0	0/Z	1	6/26	0
Pond Inlet	Spring	0	0/Z	0/Z	0	2/2	4/4	1	0/Z
Pond Inlet	Summer	0	0	0	0	0	0	1	0
Pond Inlet	Fall	0	0/Z	0/Z	0	0/14	4/42	1	0/Z
BIC	Spring	0	0/Z	0/Z	0	0/2	0/4	0/6	1
BIC	Summer	0	0	0	0	0	0	0	1
BIC	Fall	0	0/Z	0/Z	0	0/5	10/42	16/26	1
BIS	Spring	0	0	0	0	0/2	0/4	0/6	Z/Z
BIS	Summer	0	0	0	0	0	0	0	1
BIS	Fall	0	0	0	0	0/5	0/42	2/26	Z/Z
BIS	Winter	0	0	0	0	0/2	0/42	1/6	Z/Z

Table 2. Prior distributions for the models run for each of the eight narwhal stocks. The list of parameters: N_0 is the initial abundance (thousands), N^* the population dynamic equilibrium abundance (thousands), p the yearly survival, p_0 the first year survival, b the birth rate, a_m the age of the first reproductive event, ϑ the female fraction at birth, γ the density regulation, c_h the catch history, and β_a the abundance estimate bias. Abundance is given in thousands. The prior probability distribution is given by superscripts; u: uniform (min, max), U: log uniform (min, max), and b: beta (a, b).

Stock	N_0	N^*	p	p_0	b	a_m	ϑ	γ	c_h	β_a
Smith Sound		2, 80^U	0.97, 1^u	0.5, 1^u	26,62^b	8, 12^u	0.5	2, 4^u	Distribution$^\pm$	
Jones Sound		2, 60^U	0.97, 1^u	0.5, 1^u	26, 62^b	8, 12^u	0.5	2, 4^u	Distribution$^\pm$	
Inglefield Bredning	1, 25^U	3, 30^U	0.97, 1^u	0.5, 1^u	26, 62^b	8, 12^u	0.5	2, 4^u	Distribution$^\pm$	0.01, 1^U
Melville Bay	0.8, 20^U	3, 30^U	0.97, 1^u	0.5, 1^u	26, 62^b	8, 12^u	0.5	2, 4^u	Distribution$^\pm$	
Somerset Island	5, 60^U	25, 90^U	0.97, 1^u	0.5, 1^u	26, 62^b	8, 12^u	0.5	2, 4^u	Distribution$^\pm$	
Admiralty Inlet		10, 40^U	0.97, 1^u	0.5, 1^u	26, 62^b	8, 12^u	0.5	2, 4^u	Distribution$^\pm$	
Eclipse Sound		5, 50^U	0.97, 1^u	0.5, 1^u	26, 62^b	8, 12^u	0.5	2, 4^u	Distribution$^\pm$	
East Baffin Island		3, 60^U	0.97, 1^u	0.5, 1^u	26, 62^b	8, 12^u	0.5	2, 4^u	Distribution$^\pm$	

$^\pm$Distribution produced by the model based on catch data and narwhal movement between stocks

Table 3. Abundance estimates for narwhal from different stocks (CV).

Year	Smith Sound	Jones Sound	Inglefield Bredning	Melville Bay	Somerset Island	Admiralty Inlet	Eclipse Sound	East Baffin Island
1975						28,260 (0.22)		
1981					32,520 (0.1)			
1985						16,400 (0.43)		
1986			8,710 (0.25)					
1996					45,360 (0.35)			
2002					35,810 (0.43)			
2003						5,360 (0.5)		10,070 (0.31)
2004							20,230 (0.36)	
2007			8,370 (0.25)	6,020 (0.86)				
2010						18,050 (0.22)		
2012				2,980 (0.39)				
2013	16,360 (0.65)	12,690 (0.33)			49,770 (0.20)	35,040 (0.42)	10,490 (0.24)	17,560 (0.35)
2014				3,090 (0.5)				

Table 4. Estimated total removal per hunting region in Canada and Greenland per year from 1970 to 2014. G_{sp}: Grise Fjord (Spring). G_s: Grise Fjord (Summer). G_f: Grise Fjord (Fall). C_{sp}: Central Canada Arctic (Spring). C_s: Central Canada Arctic (Summer). C_f: Central Canada Arctic (Fall). A_{sp}: Arctic Bay (Spring). A_s: Arctic Bay (Summer). A_f: Arctic Bay (Fall). O_{sp}: Pond Inlet (Spring). O_s: Pond Inlet (Summer). O_f: Pond Inlet (Fall). B_{sp}: Baffin Island Central (Spring). B_s: Baffin Island Central (Summer). B_f: Baffin Island Central (Fall). BS_{sp}: Baffin Island South (Spring). BS_s: Baffin Island South (Summer). BS_f: Baffin Island South (Fall). BS_w: Baffin Island South (Winter). Q_{sp}: Qaanaaq (Spring). Q_s: Qaanaaq (Summer). U_s: Upernavik (Summer). U_f: Ummannaaq (Fall). D_w: Disko Bay (Winter).These catches should be considered preliminary estimates as they are currently being updated and validated, but they are presented for illustrative purposes for the model runs. From 1970–1976 Canadian catches were not reported to season (Stewart 2009); in these cases the catches were assigned to seasons based on the average percent of the hunt in each season from 1977–2014.

Year	**G_{sp}**	**G_s**	**G_f**	**C_{sp}**	**C_s**	**C_f**	**A_{sp}**	**A_s**	**A_f**	**O_{sp}**	**O_s**	**O_f**	**B_{sp}**	**B_s**	**B_f**	**BS_{sp}**	**BS_s**	**BS_f**	**BS_w**	**Q_{sp}**	**Q_s**	**U_s**	**U_f**	**D_w**
1970	10	39	0	1*	24*	23*	65*	34*	0*	58*	64*	1*	2	11	7	3	1	1	0	0	184	70	86	129
1971	5	20	0	1*	26*	24*	69*	33*	0*	58*	62*	1*	5*	27*	20*	17*	3*	1*	0*	0	176	45	60	134
1972	1	5	0	1*	28*	21*	60	41	0	13	18	0	1	4	3	10	4	4	0	0	169	24	35	78
1973	4	16	0	2	49	4	89	61	0	84	113	3	1	7	4	0	0	0	0	0	162	53	83	120
1974	0*	7*	0*	1*	28*	19*	31	21	0	42	57	1	9*	37*	26*	24*	3*	0*	0*	0	155	35	61	83
1975	0*	8*	0*	0*	6*	0*	99	68	0	32	44	1	2	11	7	24*	3*	0*	0*	0	147	62	14	66
1976	2	9	0	1	13	1	68	47	0	53	71	2	2	12	7	6	2	2	0	0	140	25	35	74
1977	0	0	0	0	33	0	16	38	0	73	64	0	0	54	44	4	0	0	0	0	133	71	147	40
1978	0	0	0	2	26	5	72	12	0	102	91	0	4	18	17	2	0	0	0	0	116	64	238	342
1979	0	15	0	0	3	156	29	13	0	60	60	0	15	21	2	22	14	0	0	0	126	25	172	134
1980	0	0	0	1	31	0	120	8	0	65	58	0	11	54	42	24	0	0	0	0	137	70	190	163
1981	0	0	0	1	38	29	110	18	0	56	49	0	11	56	44	54	3	0	0	0	168	95	182	348
1982	0	36	0	3	57	0	59	53	3	0	128	0	9	43	37	60	3	0	0	0	172	68	211	99
1983	0	4	0	0	73	0	102	25	1	41	92	0	25	47	13	3	1	0	0	0	142	83	213	88
1984	0	2	0	0	0	0	115	4	0	48	10	0	9	56	44	41	1	0	0	0	288	92	273	87
1985	1	10	0	3	19	3	128	0	0	71	54	0	5	63	1	22	1	0	0	0	121	39	51	88
1986	0	2	0	1	11	3	110	18	0	68	60	0	2	8	6	38	2	0	0	0	173	93	126	203
1987	0	2	0	1	12	2	28	4	0	35	31	0	8	41	35	0	0	0	0	0	163	167	434	203
1988	0	9	0	1	17	2	95	15	0	36	32	0	10	48	32	2	0	0	0	0	153	98	294	203
1989	0	6	0	1	24	4	109	18	0	52	46	0	11	53	41	49	2	0	0	0	142	43	374	203
1990	3	21	0	0	28	0	74	12	0	33	55	0	4	26	68	3	2	1	0	0	132	146	1325	203
1991	1	24	0	0	36	0	143	3	0	68	60	0	5	81	22	10	0	0	0	0	122	104	290	203
1992	1	0	0	0	33	0	131	0	0	97	30	0	5	20	69	5	0	0	0	0	111	43	374	203
1993	0	12	0	0	44	0	49	58	1	59	42	0	12	26	72	24	0	6	0	4	109	117	391	134

Year	**G_{sp}**	**G_s**	**G_f**	**C_{sp}**	**C_s**	**C_f**	**A_{sp}**	**A_s**	**A_f**	**O_{sp}**	**O_s**	**O_f**	**B_{sp}**	**B_s**	**B_f**	**BS_{sp}**	**BS_s**	**BS_f**	**BS_w**	**Q_{sp}**	**Q_s**	**U_s**	**U_f**	**D_w**
1994	3	13	0	0	43	0	116	10	0	52	64	0	10	79	6	42	0	0	0	2	95	173	386	203
1995	1	10	0	1	33	0	34	25	0	58	35	0	7	59	31	3	0	5	0	0	92	130	207	163
1996	1	1	0	0	19	0	127	0	0	44	84	0	1	20	21	10	14	0	0	0	39	89	527	224
1997	0	1	0	0	34	0	52	32	0	12	84	0	5	47	31	0	3	0	0	4	57	113	495	272
1998	2	11	0	1	67	0	20	97	0	22	113	0	0	48	38	2	2	1	0	3	71	147	447	295
1999	0	20	0	4	18	1	14	100	0	18	151	0	3	13	88	24	0	18	0	18	91	150	329	335
2000	0	22	0	5	45	1	68	60	0	50	164	0	9	134	92	9	44	0	0	21	89	177	138	255
2001	4	27	0	0	96	0	51	116	1	29	54	0	13	69	82	20	0	5	0	32	103	198	124	182
2002	3	0	0	0	58	0	23	77	0	50	30	0	0	99	63	8	1	29	0	24	61	204	234	163
2003	0	10	0	4	33	0	63	102	0	34	49	3	12	166	1	36	0	1	0	37	69	182	226	157
2004	0	12	0	0	72	0	83	74	0	28	53	3	32	136	19	12	1	19	0	55	117	78	87	99
2005	1	0	0	0	81	0	79	87	1	29	50	0	14	55	93	0	0	6	0	55	83	89	209	51
2006	0	27	0	1	172	0	161	5	0	28	82	3	5	148	14	0	0	1	0	20	58	92	94	73
2007	4	22	0	0	65	0	86	73	0	9	72	3	10	130	27	4	1	0	0	0	141	123	87	86
2008	0	29	0	0	59	3	61	108	0	173	682	37	3	58	64	0	27	0	0	7	140	120	113	61
2009	5	1	0	4	79	0	22	143	0	27	26	4	9	100	23	10	21	21	0	6	97	177	118	116
2010	10	17	0	3	73	0	49	115	0	22	47	10	18	136	24	14	1	20	0	10	114	52	55	59
2011	14	13	0	9	77	0	36	131	0	50	93	0	8	63	92	0	1	5	0	2	56	91	100	52
2012	3	18	0	1	82	10	4	156	0	124	0	0	9	102	31	0	4	9	0	3	134	96	55	72
2013	3	6	0	4	57	0	43	161	0	67	110	8	16	101	51	2	18	4	0	0	87	82	101	66
2014	3	6	0	4	57	0	43	161	0	67	110	8	16	101	51	2	18	4	0	0	107	130	90	81

*represents years where catches were not reported and so an average catch based on values from the next 10 years was used.

Table 5. Parameter estimates for different runs of the models (M). Estimates are given by the median ($X_{0.5}$) and the 90% credibility interval ($X_{0.5}$-$X_{0.95}$) of the posterior distributions. Abundance (N_0, N_t and N^*) is given in thousands.

M		N_0	N^*	r	**msyr**	p	p_0	b	a_m	γ	**msyl**	c_h	N_t	d_t	r_t	β_a
Smith Sound	$X_{0.5}$	-	16	0.04	0.031	0.98	0.75	0.29	10	3	0.67	0.058	16	1	0.00051	-
	$X_{0.05}$	-	5.4	0.019	0.014	0.97	0.52	0.22	8.2	2.1	0.62	0.0064	5.3	0.98	0.00015	-
	$X_{0.95}$	-	44	0.064	0.05	0.99	0.98	0.38	12	3.9	0.71	0.32	44	1	0.0017	-
Jones Sound	$X_{0.5}$	-	12	0.041	0.031	0.98	0.74	0.29	10	3	0.67	0.3	12	0.99	0.0016	-
	$X_{0.05}$	-	7.3	0.019	0.014	0.97	0.53	0.22	8.2	2.1	0.62	0.18	7.2	0.98	0.00089	-
	$X_{0.95}$	-	21	0.063	0.049	0.99	0.97	0.38	12	3.9	0.7	0.63	21	1	0.0029	-
Inglefield Bredning	$X_{0.5}$	8	10	0.033	0.025	0.98	0.69	0.28	10	3	0.66	0.089	8.2	0.85	0.013	0.32
	$X_{0.05}$	5.5	7.5	0.01	0.0079	0.97	0.51	0.2	8.2	2.1	0.61	0.018	5.5	0.35	0.0081	0.23
	$X_{0.95}$	11	22	0.065	0.051	0.99	0.97	0.38	12	3.9	0.71	0.36	11	0.97	0.02	0.46
Melville Bay	$X_{0.5}$	3.5	7.1	0.043	0.033	0.98	0.77	0.3	9.9	3	0.67	0.15	3.2	0.46	0.035	-
	$X_{0.05}$	1.8	4.2	0.021	0.016	0.97	0.53	0.22	8.2	2.1	0.62	0.041	1.9	0.12	0.019	-
	$X_{0.95}$	6.2	24	0.065	0.051	0.99	0.98	0.38	12	3.9	0.71	0.5	5.3	0.82	0.054	-
Somerset Island	$X_{0.5}$	22	50	0.041	0.032	0.98	0.76	0.3	9.9	3	0.67	0.45	45	0.93	0.0096	-
	$X_{0.05}$	16	36	0.024	0.019	0.97	0.53	0.22	8.2	2.1	0.62	0.14	34	0.61	0.005	-
	$X_{0.95}$	31	81	0.064	0.051	0.99	0.98	0.38	12	3.9	0.71	0.83	60	0.98	0.023	-
Admiralty Inlet	$X_{0.5}$	-	21	0.04	0.031	0.98	0.74	0.29	10	3	0.67	0.34	19	0.94	0.0077	-
	$X_{0.05}$	-	17	0.018	0.014	0.97	0.52	0.22	8.2	2.1	0.62	0.087	15	0.88	0.0051	-
	$X_{0.95}$	-	26	0.063	0.049	0.99	0.97	0.37	12	3.9	0.71	0.72	24	0.97	0.011	-
Eclipse Sound	$X_{0.5}$	-	14	0.041	0.032	0.98	0.75	0.29	10	3	0.67	0.41	12	0.88	0.015	-
	$X_{0.05}$	-	11	0.018	0.014	0.97	0.53	0.22	8.2	2.1	0.62	0.14	8.8	0.7	0.0089	-
	$X_{0.95}$	-	19	0.064	0.05	0.99	0.97	0.38	12	3.9	0.71	0.66	17	0.96	0.022	-
East Baffin Island	$X_{0.5}$	-	13	0.041	0.032	0.98	0.76	0.3	10	3	0.67	0.51	12	0.93	0.0099	-
	$X_{0.05}$	-	9.3	0.019	0.015	0.97	0.52	0.22	8.2	2.1	0.62	0.2	8.3	0.84	0.0061	-
	$X_{0.95}$	-	19	0.064	0.05	0.99	0.98	0.38	12	3.9	0.71	0.83	18	0.97	0.015	-

Table 6. Catch objective trade-off per stock. The total annual removals per stock for different probabilities (P) of meeting management objectives. The simulated period is from 2015 to 2020 and assumes a 50% fraction of females in the catches.

P	**Smith Sound**	**Jones Sound**	**Inglefield Bredning**	**Melville Bay**	**Somerset Island**	**Admiralty Inlet**	**Eclipse Sound**	**East Baffin Island**
0.50	279	227	156	123	988	376	263	251
0.55	254	214	146	117	952	358	251	239
0.60	230	201	136	111	916	339	239	228
0.50	209	187	126	105	880	319	227	215
0.70	188	173	116	99	841	299	214	201
0.75	167	158	107	92	802	278	202	187
0.80	146	143	95	84	761	255	189	173
0.85	123	128	83	73	714	229	174	158
0.90	100	110	68	59	665	200	157	138
0.95	73	87	46	42	585	161	129	113

Table 7. Catch option examples of maximum yearly removal per hunting region. C represents the average catch during 2009-2013, and an alternative option for future catches (2015–2020).

Hunting localities	Season	C (2009-2013)	C (2015-2020)
Etah	Spring	4	5
Qaanaq	Summer	98	98
Grise Fiord	Spring	7	9
Grise Fiord	Summer	11	15
Grise Fiord	Fall	0	0
Upernavik	Summer	100	70
Ummannaaq	Fall	86	154
Disko Bay	Winter	73	97
Central Canadian Arctic	Spring	4	6
Central Canadian Arctic	Summer	74	118
Central Canadian Arctic	Fall	2	3
Arctic Bay	Spring	31	41
Arctic Bay	Summer	141	188
Arctic Bay	Fall	0	0
Pond Inlet	Spring	58	77
Pond Inlet	Summer	55	73
Pond Inlet	Fall	4	5
Baffin Island Central	Spring	12	11
Baffin Island Central	Summer	100	91
Baffin Island Central	Fall	44	40
Baffin Island South	Spring	5	5
Baffin Island South	Summer	9	8
Baffin Island South	Fall	12	11
Baffin Island South	Winter	0	0

Table 8. Examples of future annual removals (C#) per stock with associated probabilities (P#) of fulfilling a management objective of maintaining the maximum sustainable yield level at 60% of the carrying capacity. The different removals follow from the catch options in Table 7 and the 90% confidence intervals of the estimates are given in parentheses.

	C (2009-2013)	**P(0)**	**C (2015-2020)**	**P(1)**
Smith Sound	4 (4-4)	1.00 (1.00-1.00)	5 (5-5)	1.00 (1.00-1.00)
Jones Sound	18 (18-18)	1.00 (1.00-1.00)	24 (24-24)	1.00 (1.00-1.00)
Inglefield Bredning	98 (98-98)	0.79 (0.79-0.79)	98 (98-98)	0.79 (0.79-0.79)
Melville Bay	110 (102-132)	0.51 (0.34-0.57)	84 (73-114)	0.70 (0.48-0.77)
Somerset Island	224 (201-248)	1.00 (1.00-1.00)	350 (321-378)	1.00 (1.00-1.00)
Admiralty Inlet	214 (180-260)	0.88 (0.79-0.93)	280 (237-339)	0.75 (0.60-0.84)
Eclipse Sound	114 (84-141)	0.97(0.93-0.99)	147 (109-183)	0.92 (0.82-0.97)
East Baffin Island	143 (131-156)	0.89 (0.85-0.91)	130 (119-142)	0.92 (0.89-0.94)

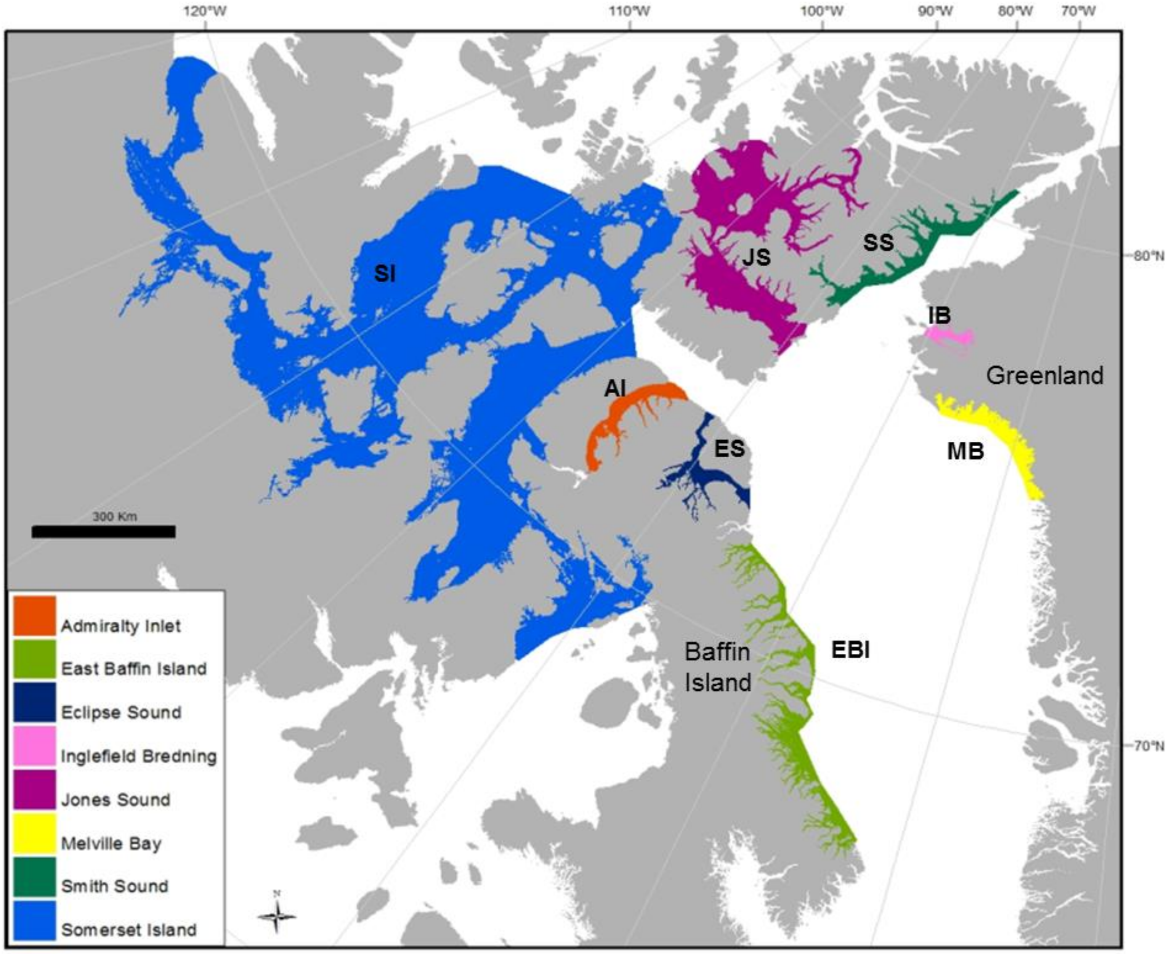

Figure 1. Map indicating the stocks of narwhals from the Baffin Bay population in Greenland and Canada.

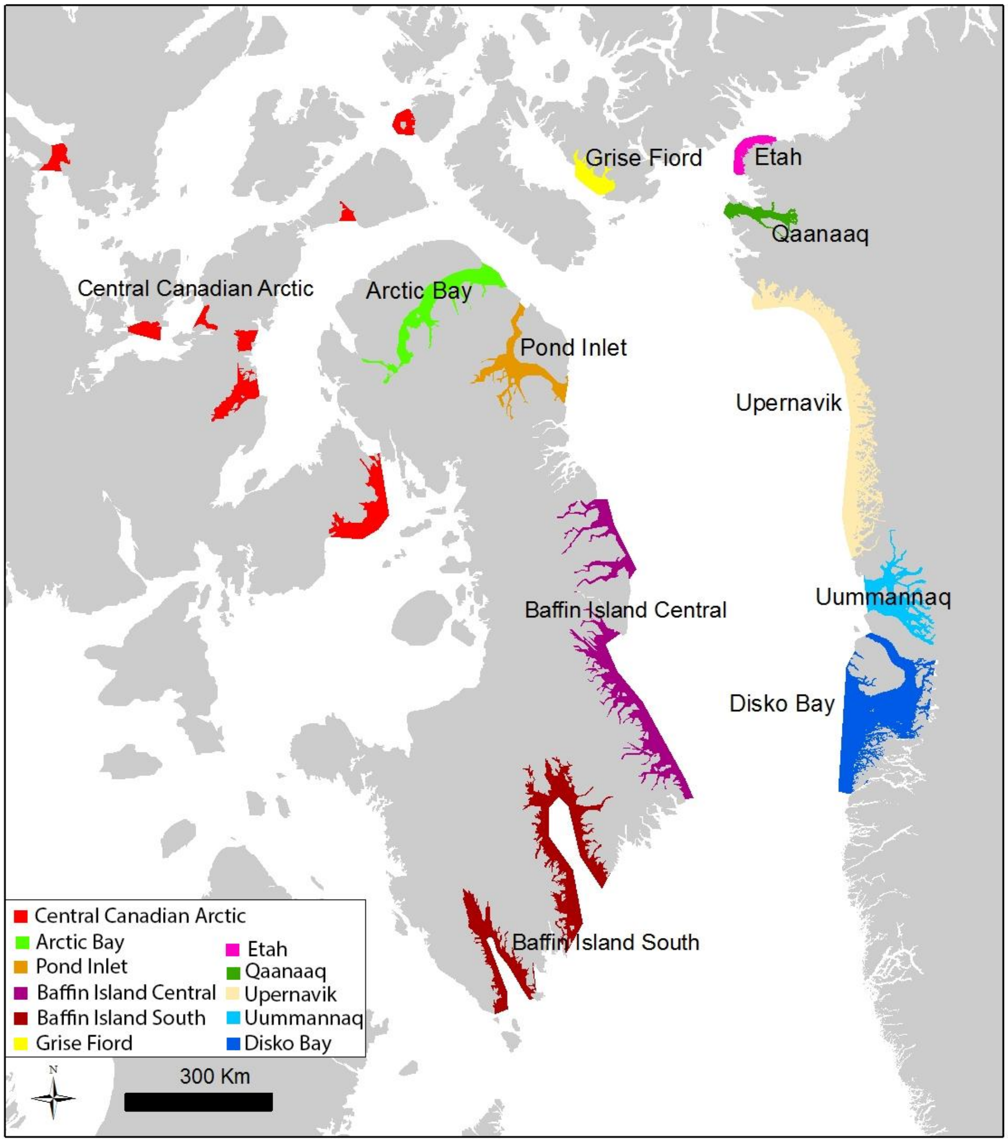

Figure 2. Map of the hunting locations for Baffin Bay narwhals in Canada and Greenland.

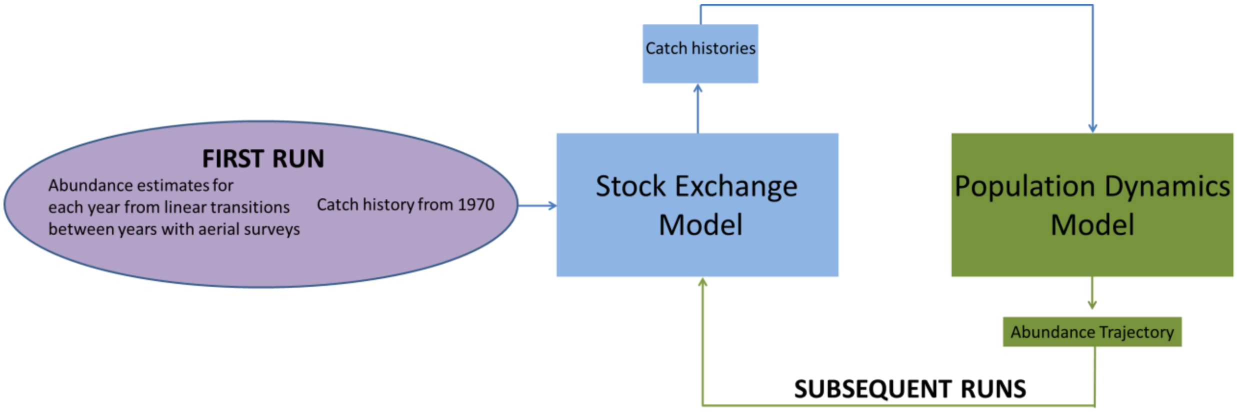

Figure 3.Schematic describing how the iterative runs of the stock exchange and population dynamics model were conducted.

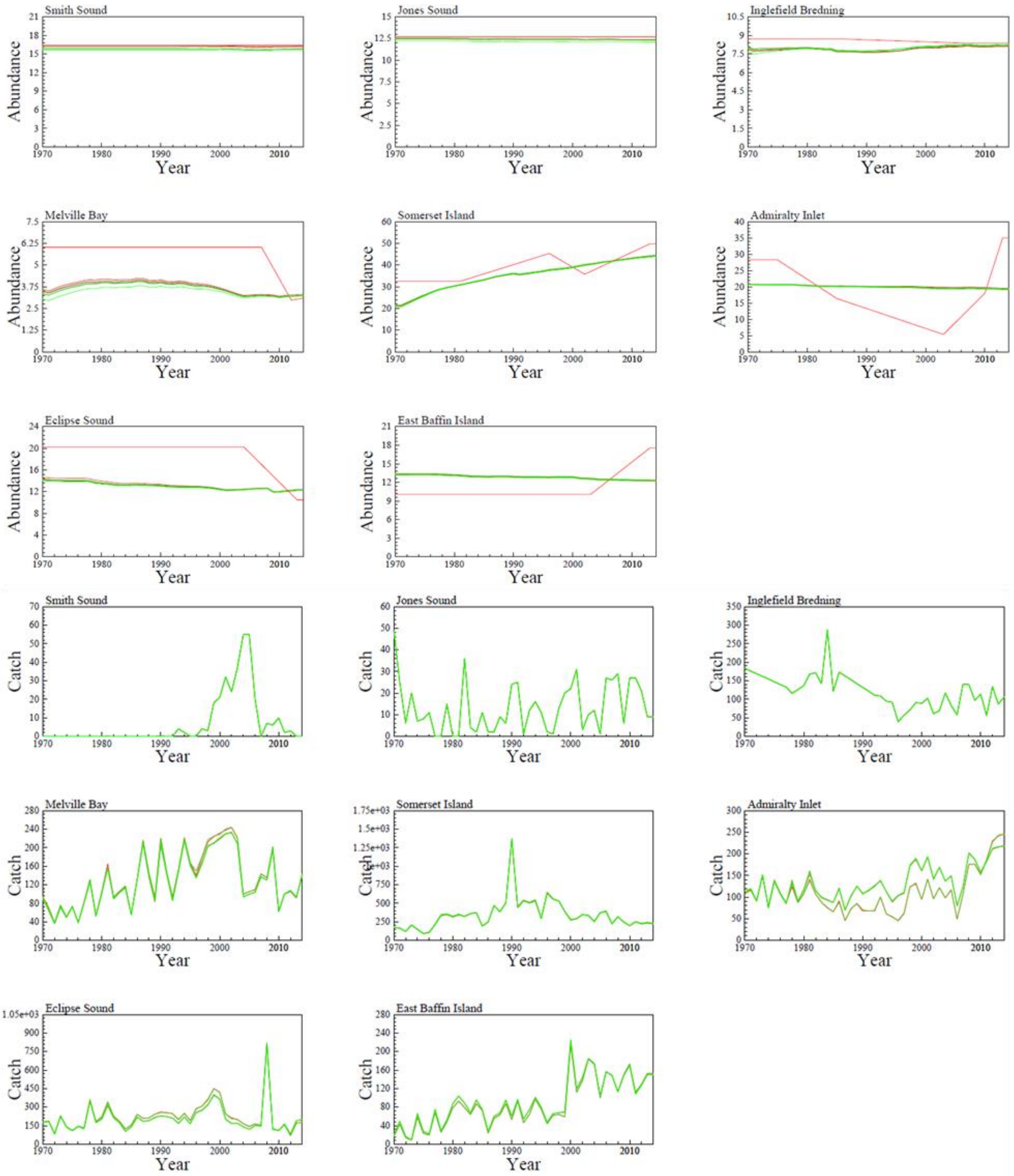

Figure 4. The convergence of the abundance trajectories and catch histories as a function of the number of iterations of the complete model, with iteration number increasing with colour transitions from clear red to clear green. Abundance is given in thousands.

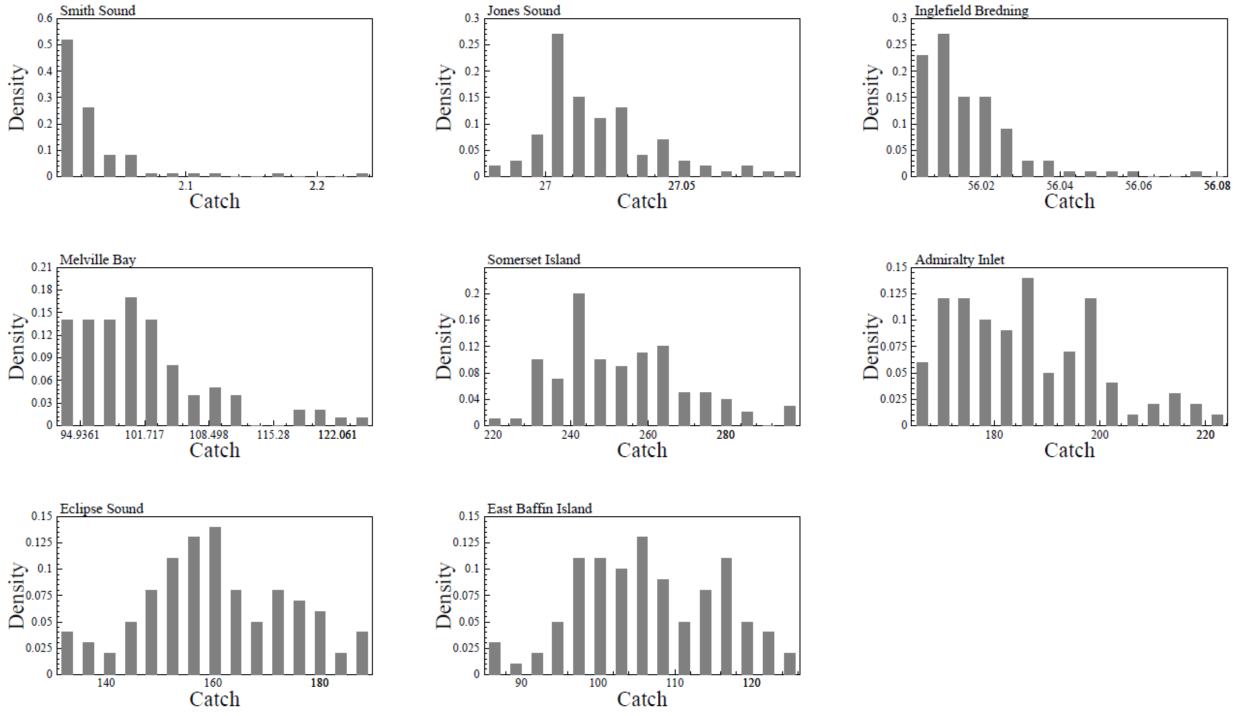

Figure 5. Estimated catch distributions per summer stock for 2011.

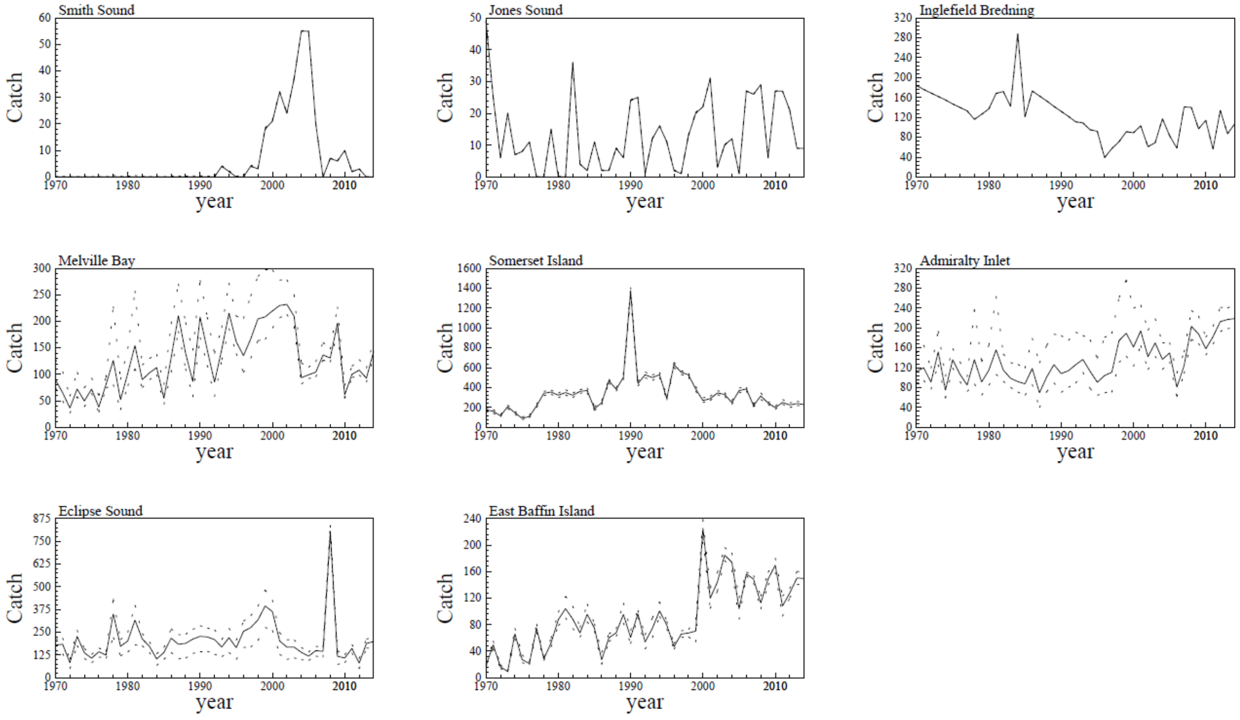

Figure 6. Estimated yearly catches for each stock with 90% confidence intervals shown as dotted lines.

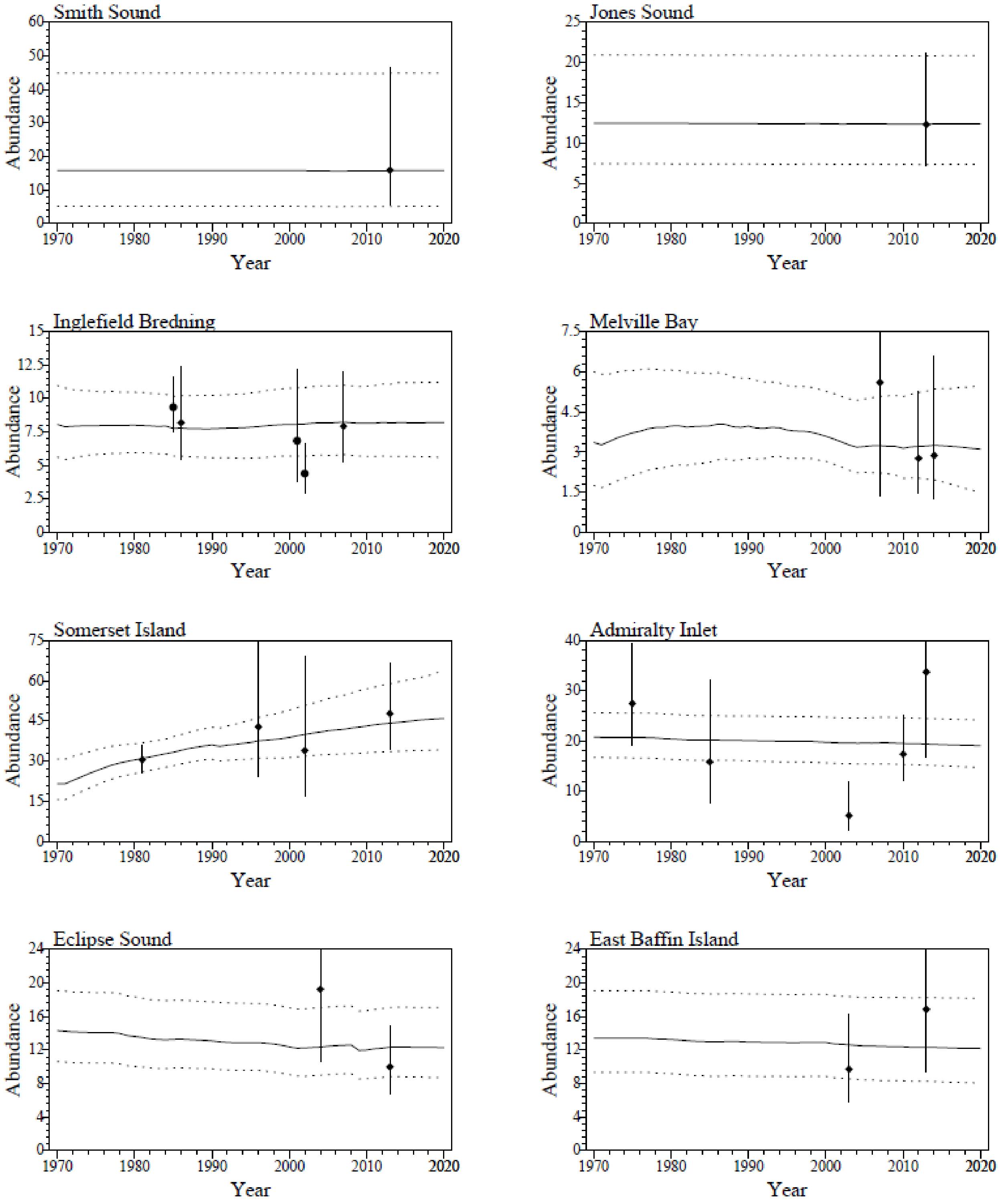

Figure 7. Estimated trajectories for the different narwhal stocks based on the population model. Points with bars are the abundance estimates with 90% confidence intervals, solid curves the median, and the dotted curves the 90% confidence intervals of the estimated models. Abundance is given in thousands.

APPENDIX

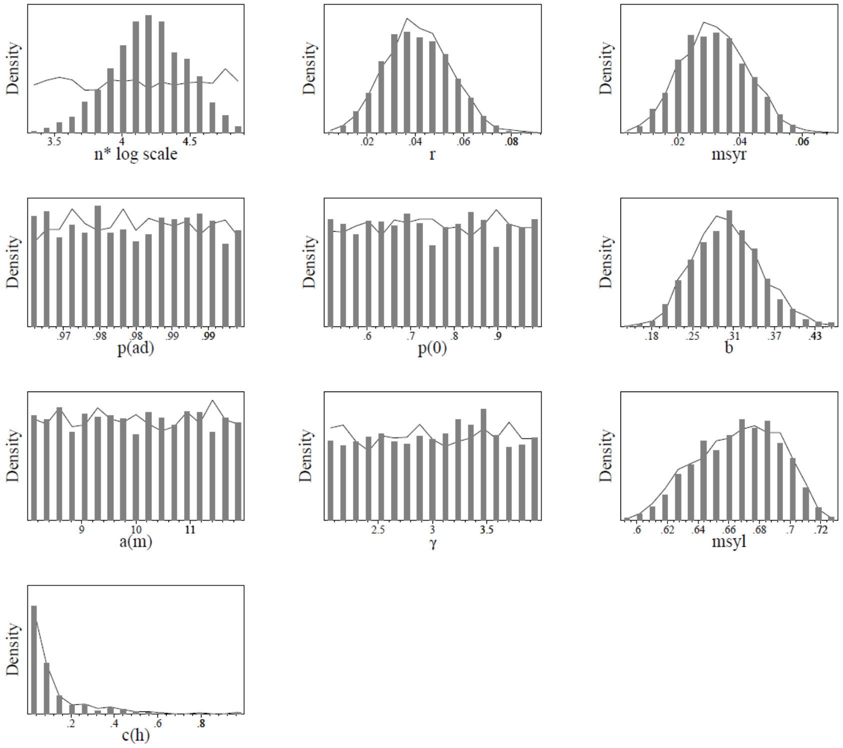

Figure A1. Realized prior (curve) and posterior (bars) distributions for Smith Sound.

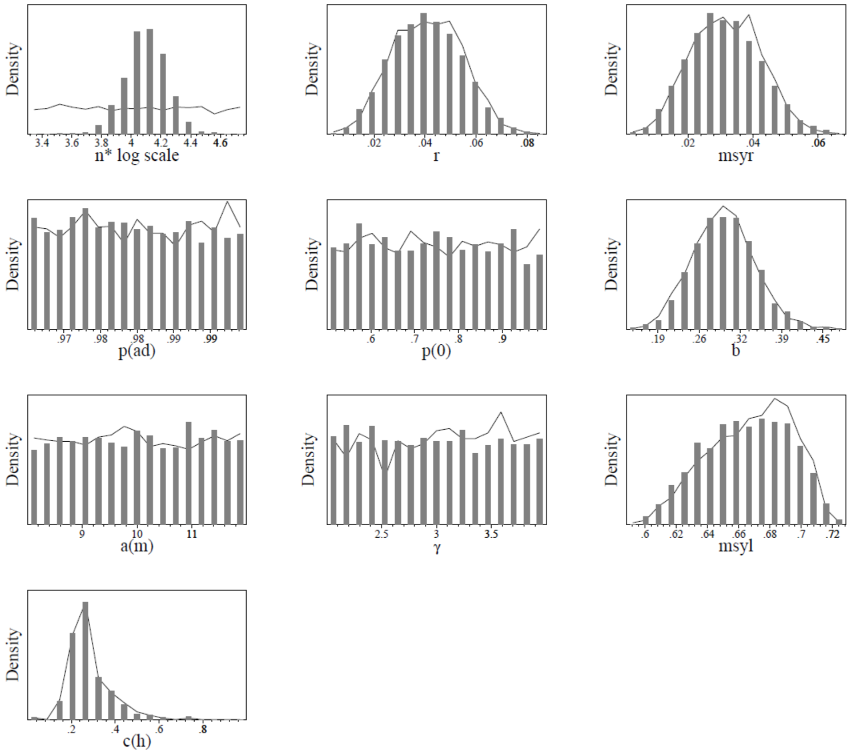

Figure A2. Realized prior (curve) and posterior (bars) distributions for Jones Sound.

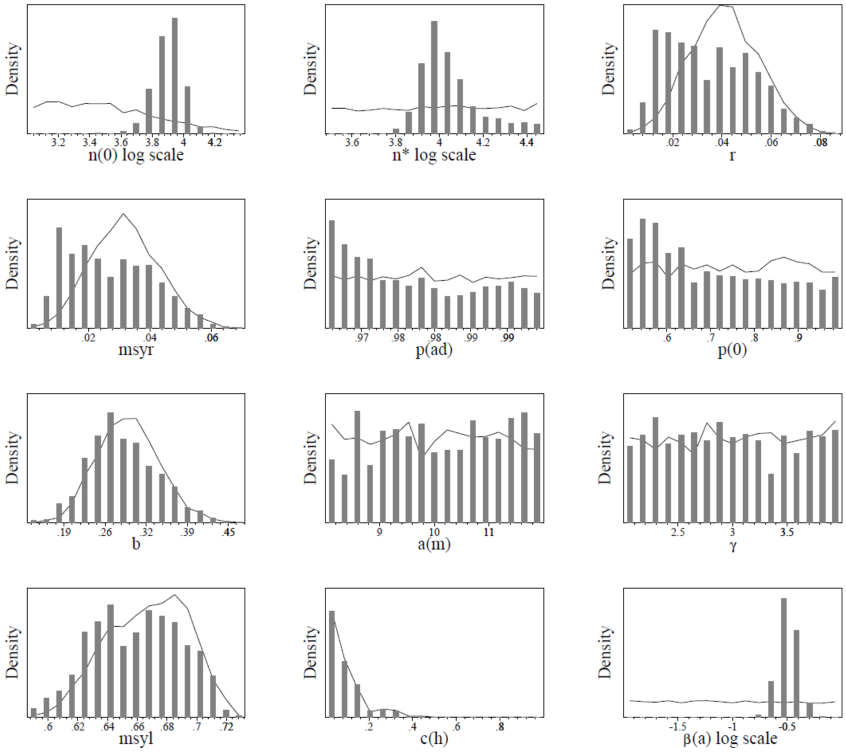

Figure A3. Realized prior (curve) and posterior (bars) distributions for Inglefield Bredning.

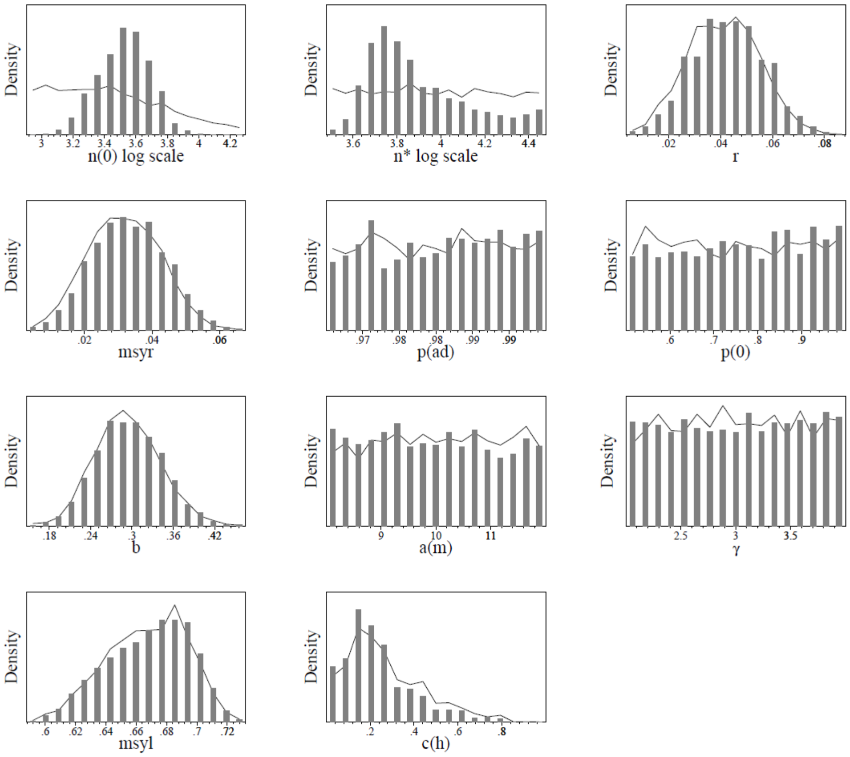

Figure A4. Realized prior (curve) and posterior (bars) distributions for Melville Bay.

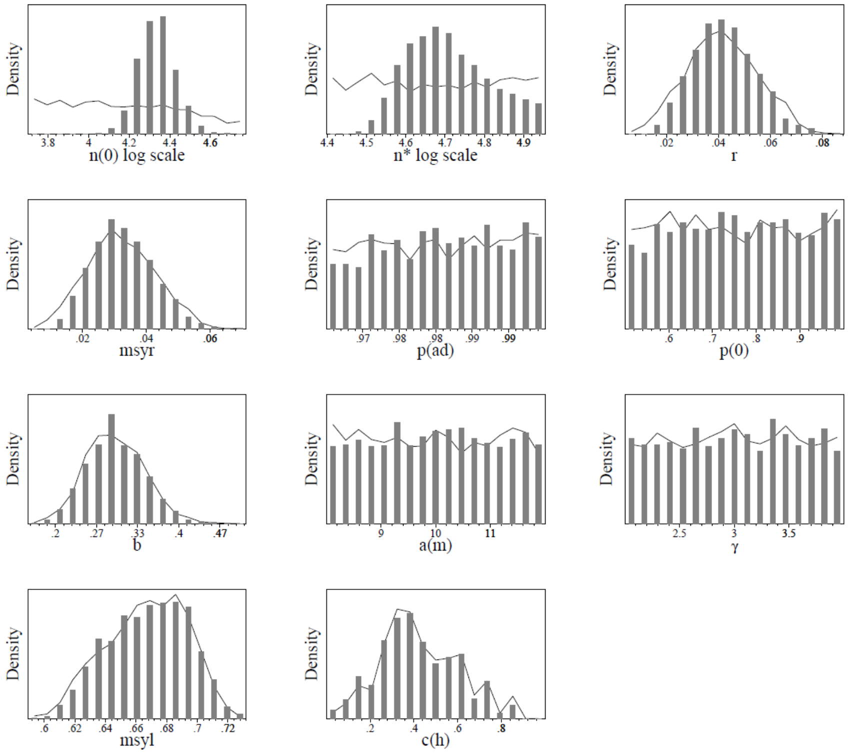

Figure A5. Realized prior (curve) and posterior (bars) distributions for Somerset Island.

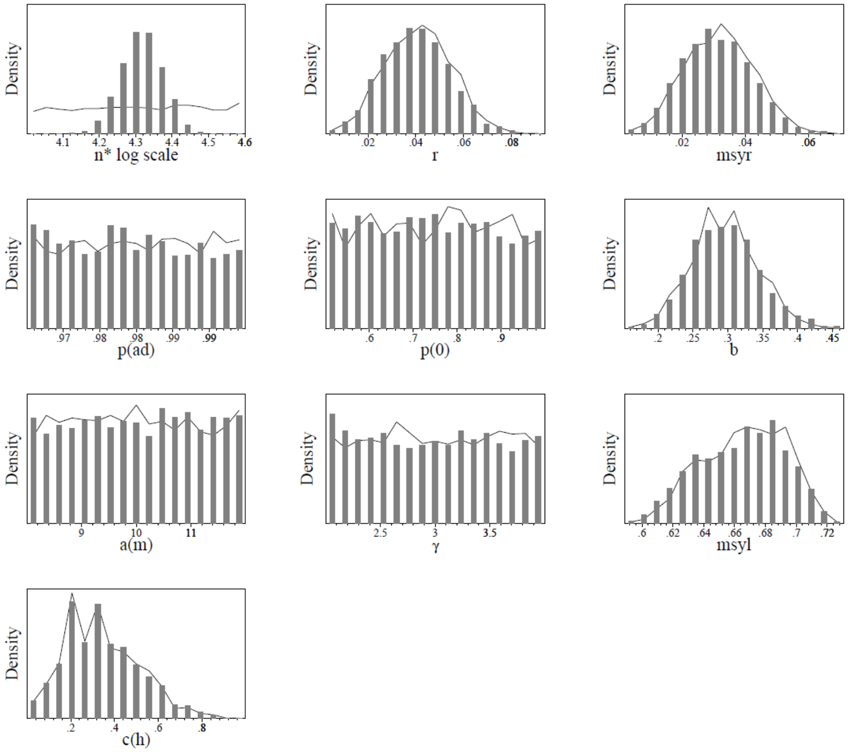

Figure A6. Realized prior (curve) and posterior (bars) distributions for Admiralty Inlet.

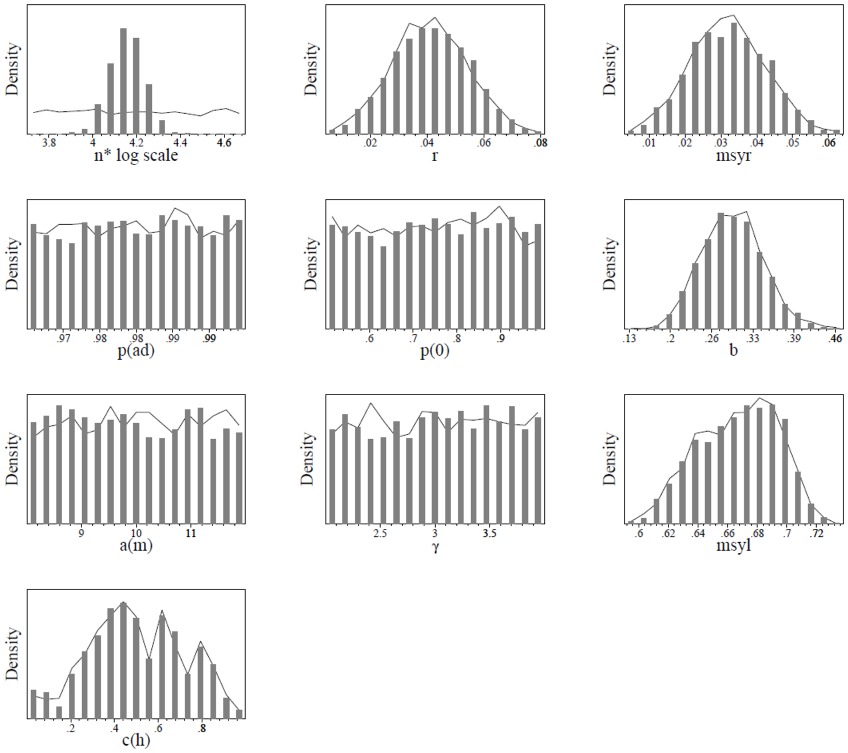

Figure A7. Realized prior (curve) and posterior (bars) distributions for Eclipse Sound.

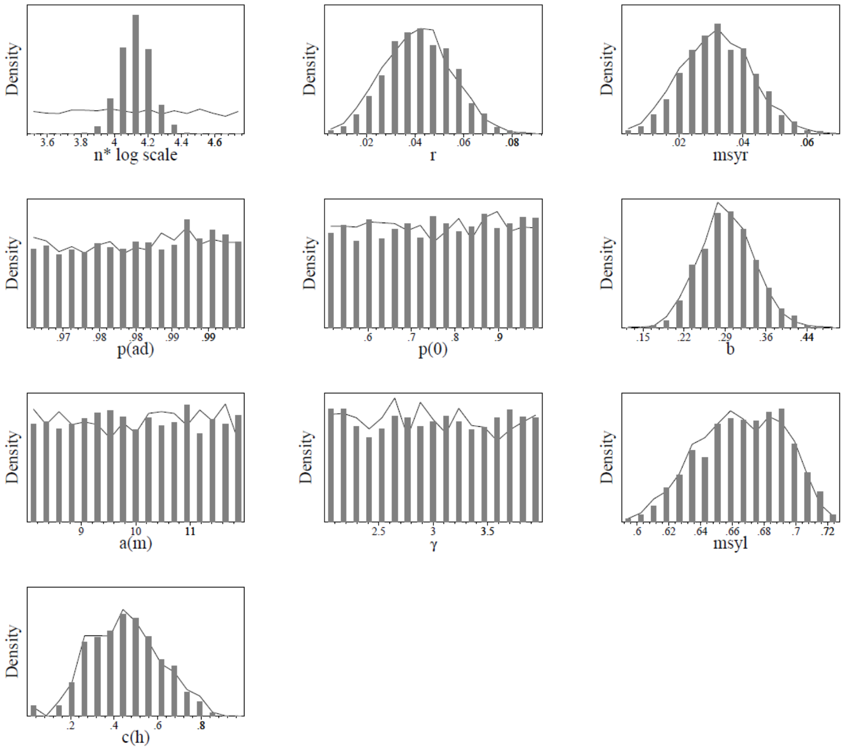

Figure A8. Realized prior (curve) and posterior (bars) distributions for East Baffin Island.